1 2 2	Meta-analysis of high-latitude nitrogen-addition and warming studies implies ecological mechanisms overlooked by land models
3 4	Nicholas I Bouskill (nibouskill@lbl.gov). William I Riley (wiriley@lbl.gov).
5	Jinyun Tang (jinyuntang@lbl.gov)
6 7	Farth Sciences Division Lawrence Parkelov National Laboratory Parkelov CA
8	94720.
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10	
11	Reviewer comments, point by point responses and a marked up version of the
12	manuscript.
13	
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15	
17	Comment from Bond-Lamberty
18	comment nom bond lamberty
19	We thank Dr. Bond-Lamberty for this comment and have made the appropriate
20	change in the title.
21	
22	
23	Review from Steve Allison
24	
25	We thank Dr. Allison for his positive and constructive comments. We believe the
26	manuscript has been significantly improved by his comments on this draft of the
27	manuscript and a previously submitted draft.
20	That said. I think there are two key messages from the nitrogen analysis that
30	could be more explicit or delivered more concisely in the paper discussion.
31	One issue is that most addition rates are too high to represent what will
32	happen with global change in northern ecosystems. So we are lacking in
33	relevant data and manipulations. That said, the second message is that the
34	models cannot replicate the (unrealistic) experimental manipulations. A good
35	model should be able to replicate any observations if it has the right
36	underlying mechanisms. The question here is whether we care about the
37	mechanisms underlying microbial response to extremely high N addition in
38 20	the tundra and boreal. Maybe we don't, but the analysis is still disconcerting
39 40	because it means the models may fair in lower fatitude systems with higher N
41	mputs.
42	We believe Dr. Allison is right and in rewriting aspects of the discussion we have
43	included a more explicit statement representing both of these points.
44	, , , , , , , , , , , , , , , , , , ,
45	

12383:24- Report the error on the soil moisture change

47 48 49 50	This has been added to the results section.
51 52 53 54 55	12383:16- I don't think it's a good idea to abbreviate litter decomposition, or microbial biomass for that matter. The whole manuscript seems to have gone a bit overboard with the acronyms-don't use them unless they are necessary and well-established in the community. Otherwise it makes it hard for readers outside our discipline.
56 57 58 59 60	We have revised the manuscript to minimize the use of abbreviations. Only GPP and SOM are left as abbreviated response factors.
61 62 63	12384: What was the surface soil moisture response to warming in the models?
64 65 66 67 68	Soil moisture increased, but not statistically significantly, in both models (CLM-CN: $38\% \pm 42\%$; CLM-Century: $7\% \pm 33\%$). We have added a statement in the results to reflect this point.
69 70	12386:21- "of" emergent responses.
70 71 72 73	We have changed this now.
74 75	12387:14- "result in"
76 77 78	We have made this correction
79 80 81	12387:19-24- the writing on the priming mechanism is somewhat unclear here. There are also too many "howevers"
82 83 84	We have re-written this section to address this comment.
85 86 87 88 89	12389:9- I suggest avoiding the word "acclimation" or "adaptation" in this context because they have specific meanings that may not be intended here. Karhu et al. in a very recent Nature paper coined the term "community-level response" to describe these processes. I would use that.
90 91 92	We take Dr. Allison's point on the use of different terms and have re-written this section to remove any terms that might be confusing, including instead the term 'community-level response'.

93	
94	
95	12390:10- "published"
96	
97	We have made this correction
98	
99	
100	
101	Comments from Reviewer 2.
102	
103	The main strength of the paper is that it presents both a new meta-analysis of
104	high latitude warming/N additions experiments and a model-data comparison.
105	It uses the results to demonstrate key patterns that fundamentally differ
106	between the models and the field studies. The largest weaknesses of the paper
107	are the long and challenging to follow discussion and the lack of key
108	information for the simulation protocol that could influence the results.
109	L L
110	The discussion and conclusion section read like the authors are laying every
111	issue with the CLM on the table. The manuscript could greatly benefit from a
112	better-organized discussion that clearly distinguishes the important points
113	from the secondary points. Furthermore, section 4.3 seems to be about issues
114	associated with the model-data comparison, but most of the paragraphs in the
115	section don't address issues with benchmarking. For example, the paragraph
116	on nitrogen fixation only addresses issues with nitrogen fixation not
117	benchmarking. I recommend focusing this section.
118	
119	We thank the reviewer for their constructive comments on our manuscript, they have
120	been very helpful for re-focusing the manuscript. We agree with the reviewer that the
121	manuscript discussion was too long have revised it in the current draft of the
122	manuscript, reducing the length by 2 pages and introducing more sub-headings to help
123	with flow. Furthermore, we have restructured aspects in accordance with the
124	reviewer's comments below.
125	
126	
127	Individual scientific/issues
128	
129	Page 12377, Line 14: I would emphasize the role of nutrients in climate-
130	decomposition increased growth rates feedbacks. As it reads, decomposition
131	directly increases growth rather than increases in N mineralization increasing
132	growth.
133	
134	We have re-written this section for clarity.
135	
136	Page 12377, line 26 – Page 12378, line 10: The argument for why a meta-
137	analysis approach is different from the site-level comparison used in Thomas
138	et al. 2013 is not clear. Both approaches use perturbation simulations in ESMs

139 140	and extract gridcell level output that correspond to grid-cells with experiences. Both approaches use short-term perturbations. Both approaches		
141	focus on means across many sites. Is the unique contribution the use of meta-		
142	analysis statistics? It seems that the Thomas et al. study is broadly similar to		
143	this study and the key distinction being drawn here is between model-data		
144	comparisons that use many sites and focus on broad patterns but don't try to		
145	simulate each site perfectly and model-data comparisons that focus on a few		
146	sites but focus on matching the conditions of the study perfectly and examine		
147	detailed dynamics. (e.g., the FACE comparison by Zaehle et al. 2014). Overall, a		
148	better argument for why the meta-analysis approach is unique and		
149	particularly useful is needed.		
150			
151	It was not our original intent to directly compare our approach with that laid out in		
152	Thomas et al., 2013. However, we realize that it is easy to interpret this paragraph in		
153	this way. We believe the approach described by Thomas et al., 2013 and		
154	the approach laid out in the current manuscript are largely complementary. The point		
155	we were trying to make is that such an approach doesn't capture the spatial		
156	heterogeneity of responses the way a data synthesis of studies spanning thousands of		
157	kilometers might. We have re-phrased this paragraph to avoid confusion.		
158			
159	Page 12379, Line 7: How was GPP estimated? Was GPP a modeled outcome		
160	from the partitioning of NEE into GEP and RE? If so, this should be stated.		
161			
162	This line actually refers to the measured GPP from the field experiments. However, the		
163	modeled GPP was simulated directly from CLM as net leaf photosynthesis using the		
164	Farquhar model (Farquhar et al. 1980) for C3 plants and the Collatz model (Collatz et		
165	al., 1992) for C4 plants.		
166			
167	Page 12379, Line: It might be useful to list the summaries statistics (range and		
168	mean) for the warming in the observations. It would help the reader		
169	understand why -1C warming was targeted in the CLM simulations		
170			
171	This information is given in the results, however, we have added a sentence directing		
172	the reader to these data.		
173			
174	Page 12379, Line 20: The focus of the manuscript is on nitrogen-carbon		
175	interactions but studies with P and K were used. How many studies were		
176	multi-element additions? How would this influence the results?		
177			
178	In the present data set approximately 0 to 40% (depending on the response measured)		
179	of the studies used an NPK fertilizer instead of NH4NO3, and these studies were		
180	generally in Europe. Table S1 in the supplemental material breaks the responses down		
181	by N-species added and there is an affect on microbial biomass from using		
185	NPK compared with NH4NU3. However, other response ratios (e.g., below		

183 ground respiration) came from studies that only used NH4NO3 as the nitrogen source

- 184 and in general we included only data using $NH4NO_3$ fertilization, so we don't believe 185 the use of NPK has influenced the overall conclusions to a great degree. 186 187 Page 12382, first paragraph in section 2.3: Model protocol description is 188 severely lacking. For example, what resolution was the model run? What 189 climate forcing was used? Was 1500 years suitable for the carbon stocks to 190 come to equilibrium? 191 192 We have included additional information on the model protocol, specifically; 193 194 'All simulations were run at a spatial resolution of $1.9^{\circ} \times 2.5^{\circ}$, using the Qian et al., 195 {Oian:2006wd} dataset for atmospheric forcing. The models were spun up for 1500 196 years to preindustrial equilibrium following an improved spinup approach (Koven et 197 al., 2013) that allows the models to reach equilibrium after 1000 years. Simulations 198 were then run from 1850 to 1979 under contemporary climate forcing before the onset 199 of perturbation conditions over the following 21 years (from 1980 to 2000). Model 200 vegetation was specified according to the MODIS vegetation continuous fields (Oleson 201 et al., 2013).' 202 203 Page 12382, line 7: How does changing the atmospheric forcing violate the 204 energy budget? Can't the temperature in the input file be increased by 1C? 205 Understanding this better may help other models simulate warming 206 experiments. 207 208 *CLM4.5* calculates the surface energy budget explicitly, such that the soil thermal 209 dynamics are driven by residual energy flux from the net radiation, latent heat flux, 210 and sensible heat flux. We first attempted to increase the input temperature by 1C, but 211 the simulation failed to produce soil warming comparable to the available 212 observations. A second approach we tried was to directly warm the soil by 1 C, but this 213 approach creates unrealistic responses associated with the imposed energy imbalance. 214 We subsequently found modifying aerodynamic resistance produced a more realistic 215 warming compared to other approaches, such as changing wind speed. 216 217 Page 12382, Line 13-16: Well done with accounting for the intra-annual 218 experimental treatments. 219 220 We thank the reviewer for this comment. 221 222 Page 12382, Lines 17-27: More detail about the model simulations is 223 necessary. Did the plant functional type used in the simulation match the plant 224 type in the experiment? 225 226 As documented in the technique note for CLM4.5 (Oleson et al., 2013; section 21.3.3), 227 the plant functional types are specified based on MODIS vegetation continuous fields
- 228 product (Hansen et al., 2003). Therefore, although it is unlikely the model simulation
- 229 could match the site data perfectly everywhere, the agreement is expected to be
- 5

- 230 largely reasonable at the model's spatial resolution.
- 231
- 232 We have added a sentence to the materials and methods to reflect this.
- 233

234 Did the duration of the simulation match the duration of the experiment? For

example, if the N fertilization experiment was only 3 years was only the first 3

236 years of the 21-year N fertilization simulation used? If the entire 21-year 237 simulation was used then that would explain why the N fertilization response

simulation was used then that would explain why the N fertil
 in CLM was much higher than the observations.

239

240 To account for this problem, we grouped our observationally-inferred effect sizes by

241 experiment duration bins, where it was practical (lines 148 – 149, 156, Figure 3,

242 Figure S1). The majority of the experimental studies were short-term (1 – 7 years long)

243 with fewer longer term (20 year studies), and those studies dominate the effect sizes

244 we report. For that reason, we evaluate our effect sizes with the same temporal

245 window since experiment inception.246

Page 1283, Line 25: Why were the models different? Don't they have the same bio-geophysics modules?

249

250 The models do have the same bio-geophysical formulations. However, differences

251 result from differences in the belowground carbon and nitrogen representations and

the resulting impacts on leaf phenology and gross primary production. In general,

253 CLM-CN and CLM-CENTURY behave quite differently in their soil carbon and nutrient

254 cycles, leading to different nitrogen regulation impacts on plant productivity. The

255 different plant productivity subsequently leads to different leaf phenology and

256 *different surface energy budgets.*

257

258 **Page 12384, Line 4-5: The average warming in the ESMs was different from**

each other and lower than the field studies. Since the models are sensitive to

warming, how would the 0.3 C difference between the models influence the results? Similarly, the CLM-CN was 0.5 C lower than the observed change in

temperature. This is half of the goal temperature change (1 C). What are the

263 implications of the temperature changes not matching?

264

265 The formulations of CLM-CN and CLM-CENTURY are linear functions of the relative

soil organic matter pools, and the temperature response functions are monotonic Q_{10}

267 based functions. The modeled magnitude of warming was not significantly different

268 from the observed increased soil temperatures, therefore we do not expect the modeled

269 functional response to change qualitatively (which is the focus in this study). In

270 *addition, given the large soil carbon stocks in cold regions and that the model*

271 simulated results are opposite to empirical data, additional warming in the model

272 would produce even stronger contrasts between model simulations and the

273 measurements. We have added a sentence to the Discussion section addressing this

274 point.

275

276	Page 12386, Line 21: This sentence isn't clear. If we don't benchmark using
277	observations then what do we use?
278	
279	We wished to emphasize that observations that are emergent and relatively small
280	responses compared to the component processes that affect them, and where those
281	component processes have different environmental, antecedent, or mechanistic
282	controls, are not good tests of model fidelity. We have clarified this point in the revised
283	manuscript.
284	•
285	Page 12386, Line 23: While it is important point that NEE is potentially a small
286	difference of two large fluxes (GPP and RE), it is also important to note that
287	GPP and RE are modeled fluxes based on NEE.
288	
289	Our original point was not to evaluate the methods used to disaggregate measured
290	NEE into inferred GPP and RH, but rather to indicate that an emergent system
291	response that is relatively small compared to it's component drivers (e.g., NEE) is likely
292	not a good variable to calibrate or test a model.
293	0
294	Discussion in general: I recommend a better presentation of the take-home
295	messages. I also recommend synthesizing what you learned across the N
296	fertilization and warming experiments? Are there common lessons learned in
297	the two experiment types? Are the lessons learned that would not be found by
298	focusing just on N fertilization or warming experiments?
299	6, 6, r
300	Overall, I am wondering what the priorities are for CLM development
301	based on the results from the study.
302	······
303	Also, the discussion uses the term "benchmarking" but doesn't providing
304	insights into the key metrics from the study that are benchmarks for other
305	models to use.
306	
307	What metrics do the authors think that ESMs should focus on?
308	
309	We have added an additional section (section 4.3, lines 697 - 744) prior to the
310	conclusions that identifies several metrics (e.g., nitrogen mineralization, litter
311	decomposition) that we recommend for benchmarking. Furthermore, we have also
312	highlighted conclusions reached from the meta-analysis that could contribute to the
313	development of the CLM-biogeochemistry codes.
314	
315	
316	Section 4.1: It seems that key result from the model-data comparison is the
317	lack of an N mineralization response in the warming studies and large
318	responses in the CLM. Why are the differences so large? What mechanisms
319	need to be included in CLM to capture this? Why to the N mineralization
320	response in the meta-analysis differ from other metaanalysis (Rustad et al

2001) and studies (Melillo et al. 2011)?

I would consider leading the discussion with the N mineralization response to warming because it is a core process in the climate-carbon feedback and the most striking difference between the observations and the models. We agree with the reviewer in this case and have rearranged the discussion section to begin with the focus on nitrogen mineralization. In this new text we have addressed all of the reviewer questions posed here. Page 12392, line 5: Other studies have found limited nitrate leaching in the CLM-CN (see Thomas et al. 2013). We have reworded this section to note that nitrate losses are mainly from denitrification. Section 4.3: This section does not maintain focus on the topic of barriers to experiment based model benchmarking. We know that CLM is lacking processes to perfectly simulate the globe but why is that a barrier to benchmarking. It seems that the processes that are listed should be the focus of model development through benchmarking. Overall, it seems like an odd place to provide model caveats (lack of P cycle, poor representation of N fixation, etc). The section would be more informative for other modeling groups if it explores the positives and negatives of the meta-analysis approach for benchmarking. We have re-focused this section into four parts that address four concerns for the model versus data comparison. We also added several sentences describing criteria to be used to ensure that the imposed perturbation in the model reasonably represents the perturbation impacts in the field sites. We have also added a further section that briefly highlights the positives and negatives of this approach. Figure 2: The current size of the figure and line thickness make the figure difficult to read. We have improved the spacing within these figures. Figure 3: Use either GEP or GPP. One is used in the figure and the other in the caption. We have altered this caption to reflect the use of GPP.

368	Meta-analysis of high-latitude nitrogen-addition and warming studies impl <u>ies</u> ,
369	ecological mechanisms overlooked by land models
370	
371	Nicholas J Bouskill (<u>njbouskill@lbl.gov</u>), William J Riley (<u>wjriley@lbl.gov</u>),
372	Jinyun Tang (<u>jinyuntang@lbl.gov</u>)
373	
3/4	Earth Sciences Division, Lawrence Berkeley National Laboratory, Berkeley, LA,
3/5	94720.
3/0	Dunning title , Testing model performance via mote analysis
378	Kunning title. Testing model performance via meta-analysis
379	Keywords: Carbon cycling High-latitude soils, climate change, nitrogen cycling
380	warming model henchmarking
381	warming, moder benefiniar king.
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384	Correspondence:
385	Nicholas Bouskill,
386	Earth Sciences Division,
387	Lawrence Berkeley National Laboratory,
388	Berkeley, CA, 94702.
389	E-mail: <u>njbouskill@lbl.gov</u>
390	Tel: (+1) 510-486-7490
391	Fax: (+1) 510-486-7152
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415 Abstract

416	
417	Accurate representation of ecosystem processes in land models is crucial for \checkmark
418	reducing predictive uncertainty in energy and greenhouse gas feedbacks with the
419	<u>climate</u> . Here we describe an observational and modeling meta-analysis approach to
420	benchmark land models, and apply the method to the land model CLM4.5 with two
421	versions of belowground biogeochemistry. We focused our analysis on the above
422	and belowground responses to warming and nitrogen addition in high-latitude
423	ecosystems, and identified absent, or poorly parameterized mechanisms in CLM4.5.
424	While the two model versions predicted similar soil carbon stocks trajectories
425	following both warming and nitrogen addition, other predicted variables (e.g.,
426	belowground respiration) differed from the observations in both magnitude and
427	direction, indicating <u>CLM4.5 has inadequate underlying</u> mechanisms for
428	representing high-latitude ecosystems. <u>On the basis of</u> observational synthesis we
428 429	representing high-latitude ecosystems. <u>On the basis of</u> observational synthesis <u>we</u> attribute these differences to missing representations of microbial dynamics,
428 429 430	representing high-latitude ecosystems. <u>On the basis of observational synthesis we</u> attribute these differences to missing representations of microbial dynamics, characterization of above and belowground <u>coupling</u> , and nutrient competition. We
428 429 430 431	representing high-latitude ecosystems. <u>On the basis of observational synthesis we</u> attribute these differences to missing representations of microbial dynamics, characterization of above and belowground <u>coupling</u> , and nutrient competition. We use the observational meta-analyses to discuss potential approaches to improving
428 429 430 431 432	representing high-latitude ecosystems. <u>On the basis of observational synthesis we</u> attribute these differences to missing representations of microbial dynamics, characterization of above and belowground <u>coupling</u> , and nutrient competition. We use the observational meta-analyses to discuss potential approaches to improving the current models (e.g., the inclusion of dynamic vegetation or different microbial
428 429 430 431 432 433	representing high-latitude ecosystems. <u>On the basis of observational synthesis we</u> attribute these differences to missing representations of microbial dynamics, characterization of above and belowground <u>coupling</u> , and nutrient competition. We use the observational meta-analyses to discuss potential approaches to improving the current models (e.g., the inclusion of dynamic vegetation or different microbial functional guilds). <u>However</u> , we also <u>caution</u> the selection of data sets and
428 429 430 431 432 433 434	representing high-latitude ecosystems. <u>On the basis of observational synthesis we</u> attribute these differences to missing representations of microbial dynamics, characterization of above and belowground <u>coupling</u> , and nutrient competition. We use the observational meta-analyses to discuss potential approaches to improving the current models (e.g., the inclusion of dynamic vegetation or different microbial functional guilds). <u>However</u> , we also <u>caution</u> the selection of data sets and experiments <u>for</u> meta-analysis. For example, the concentrations of nitrogen applied
428 429 430 431 432 433 434 435	representing high-latitude ecosystems. <u>On the basis of observational synthesis we</u> attribute these differences to missing representations of microbial dynamics, characterization of above and belowground <u>coupling</u> , and nutrient competition. We use the observational meta-analyses to discuss potential approaches to improving the current models (e.g., the inclusion of dynamic vegetation or different microbial functional guilds). <u>However</u> , we also <u>caution</u> the selection of data sets and experiments <u>for</u> meta-analysis. For example, the concentrations of nitrogen applied in the synthesized field experiments (average = 72 kg ha ⁻¹ yr ⁻¹) are many times
428 429 430 431 432 433 434 435 436	representing high-latitude ecosystems. <u>On the basis of observational synthesis we</u> attribute these differences to missing representations of microbial dynamics, characterization of above and belowground <u>coupling</u> , and nutrient competition. We use the observational meta-analyses to discuss potential approaches to improving the current models (e.g., the inclusion of dynamic vegetation or different microbial functional guilds). <u>However</u> , we also <u>caution</u> the selection of data sets and experiments <u>for</u> meta-analysis. For example, the concentrations of nitrogen applied in the synthesized field experiments (average = 72 kg ha ⁻¹ yr ⁻¹) are many times higher than projected soil nitrogen concentrations (from nitrogen deposition and
428 429 430 431 432 433 434 435 436 437	representing high-latitude ecosystems. <u>On the basis of observational synthesis we</u> attribute these differences to missing representations of microbial dynamics, characterization of above and belowground <u>coupling</u> , and nutrient competition. We use the observational meta-analyses to discuss potential approaches to improving the current models (e.g., the inclusion of dynamic vegetation or different microbial functional guilds) <u>. However</u> , we also <u>caution</u> the selection of data sets and experiments <u>for</u> meta-analysis. For example, the concentrations of nitrogen applied in the synthesized field experiments (average = 72 kg ha ⁻¹ yr ⁻¹) are many times higher than projected soil nitrogen concentrations (from nitrogen deposition and release during mineralization), which preclude <u>s</u> a rigorous evaluation of the model
428 429 430 431 432 433 434 435 436 437 438	representing high-latitude ecosystems. <u>On the basis of observational synthesis we</u> attribute these differences to missing representations of microbial dynamics, characterization of above and belowground <u>coupling</u> , and nutrient competition. We use the observational meta-analyses to discuss potential approaches to improving the current models (e.g., the inclusion of dynamic vegetation or different microbial functional guilds). <u>However</u> , we also <u>caution</u> the selection of data sets and experiments <u>for</u> meta-analysis. For example, the concentrations of nitrogen applied in the synthesized field experiments (average = 72 kg ha ⁻¹ yr ⁻¹) are many times higher than projected soil nitrogen concentrations (from nitrogen deposition and release during mineralization), which preclude <u>s</u> a rigorous evaluation of the model responses to <u>likely</u> nitrogen perturbation <u>s</u> . Overall, we demonstrate that elucidating

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Nicholas Bouskill 11/6/14 8:28 PM Deleted: the underlying Nicholas Bouskill 11/6/14 8:28 PM Deleted: are inadequate Nicholas Bouskill 11/6/14 8:29 PM Deleted: The Nicholas Bouskill 11/6/14 8:30 PM Deleted: functional processes

Nicholas Bouskill 11/6/14 8:31 PM Deleted: , h Nicholas Bouskill 11/6/14 8:31 PM Deleted: raise a cautionary note on Nicholas Bouskill 11/6/14 8:31 PM Deleted: to be included in a

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452 ecological mechanisms via meta-analysis can identify deficiencies in ecosystem

453 models and empirical experiments.

454

455 **1** Introduction456

457 Northern Hemisphere high latitude soils are among the largest global stores 458 of soil organic matter (SOM) (Grosse et al., 2011). Recent studies have estimated 459 SOM storage within permafrost regions to be ~ 1700 Pg to 3 m depth (Schuur et al., 460 2012), representing nearly 50% of global terrestrial organic carbon, or nearly twice 461 that currently in the atmosphere (King et al., 2007). Permafrost SOM is stabilized by 462 cold temperatures, and is therefore vulnerable to the warming that high-latitude 463 regions will experience over the next century (Schuur and Abbott, 2011). However, 464 the response of high-latitude ecosystems to global climate change is complex. Under 465 warming, the active layers of permafrost soils thicken, and may serve as a reservoir 466 of chemically labile organic carbon. Carbon released from these soils (mostly as CO2 467 or CH₄) may accelerate the rate of warming and form a positive feedback to climate 468 change (Koven et al., 2011). Alternatively, elevated rates of organic matter 469 decomposition release limiting nutrients (e.g., nitrogen) that could stimulate plant 470 productivity, sequestering CO_2 from the atmosphere, serving as a negative feedback 471 on climate change (Shaver et al., 1992). 472 Predictions of how future climate change will alter high-latitude soil carbon 473 are derived mainly from (a) conclusions of in situ field manipulation studies and (b) 474 output of land models either coupled or uncoupled with an atmospheric model. The 475 coupled Earth System Models (ESMs) couple land and atmospheric processes by

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477	simulating land biogeochemical and biophysical states and fluxes (including soil
478	carbon dynamics and effluxes) and feedbacks to atmospheric carbon concentrations
479	across decadal, centennial, and millennial time scales (Kaplan et al., 2002; Koven et
480	al., 2011) . Current ESMs have high uncertainty in their predicted magnitude of
481	carbon-climate feedbacks (Arora et al., 2013; Friedlingstein et al., 2006) because of
482	insufficiencies in model structure and parameterization (Bonan et al., 2011; Jung et
483	al., 2007; Zaehle et al., 2005).
484	Benchmarking the performance of land models has been challenging (Luo et
485	al., 2012) . One approach has been to compare model output against the output of
486	distinct manipulation studies (Thomas et al., 2013b) that acutely perturb

487 ecosystems on short time scales (months to years). However, the broad spatial

488 heterogeneity of high-latitude soils may not be well represented by the

489 concentration of high-latitude field studies within a few sites. Herein, we benchmark

490 the models by compiling data from a range of studies measuring the same variables

491 across spatial gradients. This approach can determine an overall ecosystem

492 response to perturbation, eliminating the weight placed on any one study. Data

493 compilation can also identify important mechanisms that determine the fate of soil

494 carbon but are currently not represented in the land models.

495 In the present study, we examined the fate of high-latitude soil carbon based

496 on conclusions drawn from (1) meta-analyses of high-latitude field studies ($\geq 60^{\circ}$ N)

497 focusing on ecosystem responses to <u>warming</u> and nitrogen <u>additions</u> and (2) meta-

498 analyses of simulations mimicking the experiments using the land component

499 (CLM4.5) of the Community Earth System Model (CESM). We address four

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Deleted: field experiments with short experimental timeframes (months to years) and high rates of perturbation may not be representative of the long-term (decadal to centennial), and chronic nature of anthropogenic climate change. Furthermore,

Nicholas Bouskill 11/6/14 8:36 PM Deleted: temperature Nicholas Bouskill 11/6/14 8:37 PM Deleted: perturbations

512	questions: (1) Do the models and synthesized data predict a similar response of	
513	carbon and nutrient cycling to ecosystem <u>warming and nitrogen addition</u> ? (2) In	Nicholas Bouskill 11/6/14 8:37 PM
514	what areas do the models and experiments diverge? (3) What are the mechanisms,	Deleted: perturbation
515	including those absent in the models, the field experiments demonstrate to be	
516	important for evaluating the fate of soil C? (4) What types of observationally derived	
517	model benchmarks are appropriate for the various ecosystem processes relevant to	
518	high-latitude soil C dynamics?	
519		
520	2 Materials and Methods	
521		
522	2.1 Literature search	
523	We compiled published observations for replicated field studies from high-	Nicholas Bouskill 11/6/14 8-38 DM
524	latitude ecosystems (\geq 60° N) (Fig. 1) examining responses of belowground	Formatted: Indent: First line: 0.5"
525	biogeochemistry to warming and nitrogen addition. The data were mainly extracted	
526	from published figures or tables, or directly from the authors in cases where	
527	unpublished results were referenced in a published study. Manipulation studies	
528	were located by searching the ISI Web of Knowledge, using the following principal	Nicholas Bouskill 10/26/14 7:13 PM
529	terms: "Arctic", "Permafrost", "High-latitude", paired with: "Manipulation",	Deleted: (MB) Nicholas Bouskill 10/26/14 7:13 PM
530	"Nitrogen", "Warming". Where available, we collected data from control and	Deleted: (FB) Nicholas Bouskill 10/26/14 7:13 PM
531	perturbed soils on microbial (i.e., bacterial + fungal) biomass, fungal biomass,	Deleted: (AGB) Nicholas Bouskill 10/26/14 7:13 PM
532	aboveground biomass, belowground respiration, heterotrophic respiration, gross	Deleted: (R _B), Nicholas Bouskill 10/26/14 7:13 PM
533	primary productivity (GPP), litter decomposition, soil organic matter content (SOM),	Deleted: (R _H) Nicholas Bouskill 10/26/14 7:13 PM
		Deleted: (GPP)

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542	net nitrogen-mineralization, and soil and microbial nitrogen and phosphorus	Nicholog Deuglill 40/06/44 7:42 DM
543	concentrations.	Deleted: (N _{min}),
544	To characterize the response of high-latitude soils to warming we collected	Nicholas Bouskill 10/26/14 7:13 PM Deleted: (P)
545	data from studies that passively warmed soil using open top chambers (OTC) or	
546	greenhouses (OTG) and snow manipulation studies. We also collected data from	
547	studies that used incubations to increase temperature. We collected more than 2800	
548	entries from 53 field studies across 17 different high-latitude ecosystems. We	
549	present, the data as a response ratio across all of the studies. We also sought to	Nicholas Bouskill 11/6/14 8-38 DM
550	understand the influence of duration on certain responses, and where appropriate,	Deleted: ed
551	data was further partitioned by experimental duration: short-term (< 2 yrs), long-	
552	term (> 5yrs) and intermediate (2 – 4 yrs).	
553	For nitrogen addition, we collected studies that applied nitrogen as either	
554	ammonium nitrate (NH_4NO_3) or nitrogen phosphorus potassium fertilizer (NPK).	
555	We analyzed over 2,300 entries (i.e., individual measurements of each metric)	Nicholas Rouskill 10/26/14 0:51 DM
556	across 37 nitrogen addition field studies from 14 geographically distinct sites (Table	Deleted: (MB, R _H , etc.))
557	S1). We examined the influence of geography on the response of our data sets by	
558	partitioning the data between that collected from European and North American	
559	manipulation studies. The data <mark>were</mark> also temporally disaggregated in a similar	Nicholas Bouskill 11/6/14 8:39 PM
560	manner as described above for the warming experiments.	Deleted: was
561	Data were extracted from figures using the Data Thief software (Tummers,	
562	2006). Comparison data were standardized to units of "g m-3" prior to calculating a	
563	response ratio. Bulk density measurements for the different soils were extracted	
564	from the published studies or through personal communication with the authors. In	

570 the cases where authors could not be contacted, bulk density was estimated using a

571 previously published approach (Calhoun et al., 2001).

572

573 2.2 Meta analysis

574Data were analyzed using the MetaWin 2.2 software package (Rosenberg et575al., 2000), using the standard deviation (SD) reported from each individual576observation. In the majority of cases, SD was calculated from the reported standard577error and number of replicates. A response metric was calculated as the natural log578of treatment group relative to a control:

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

579 Where \overline{X}^T and \overline{X}^A are the mean values for the treatment and ambient response 580 variable, respectively. The sampling variance (V_{lnR}) was calculated as:

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

Where s^T and s^A represent the normalized standard deviations around the mean 581 values and N^T and N^A are the number of replicate studies from treatment and 582 583 ambient experiments, respectively. The effect size for different response metrics 584 was subsequently calculated using a weighted average value, where the weight for 585 the ith study is the reciprocal of its sampling variance. 586 A mixed model was used to calculate the cumulative differences in the 587 response variables in treatment versus control plots. These cumulative differences 588 were calculated for the overall dataset, and also after constraining the datasets to 589 similar conditions and forcings (e.g., geographic location, magnitude of N added).

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590	When an effect size was drawn from a low number of contributing studies (< 15),	
591	the data was resampled (using 2500 iterations) by bootstrapping to give a	
592	conservative estimate of the confidence interval (CI). Data was also gathered on	
593	climate conditions (mean annual air temperature (MAT) and precipitation (MAP),	
594	and growing season mean air temperature (GSMT)) and experimental conditions	
595	(experimental duration and magnitude of warming or nitrogen added) for each site	
596	sampled. We used a regression analysis to examine whether variability in response	
597	variables (e.g., belowground respiration and microbial biomass) was due to spatial	Nicholas Bouskill 10/26/14 7·11 PM
598	differences in climate or due to experimental manipulation (e.g., warming or	Deleted: (R _B)
599	nitrogen added).	Deleted: (MB)
600		
601	2.3 CLM-BGC spin-up and experimental manipulation scenarios.	
602	We simulated the ecosystem perturbation experiments using the community \checkmark	Nicholas Bouskill 11/6/14 8:39 PM
603	land model (CLM4.5) with two different representations of belowground	Formatted: Indent: First line: 0.5"
604	biogeochemistry; a vertically resolved belowground module with similar	
605	biogeochemistry to the Century model (termed CLM-Century, (Koven et al., 2013),	
606	and the Carbon-Nitrogen biogeochemistry module (termed CLM-CN, (Thornton et al.,	
607	2007). CLM-Century and CLM-CN share the same formulation of aboveground	
608	biogeochemical processes and land biogeophysics, but differ in their representation	
609	of belowground carbon turnover and nitrogen cycling. For example, CLM-CN	
610	represents the belowground decomposition cascade as four discrete pools with	
611	faster turnover times than the three-pool approach used by CLM-Century (Koven et	
612	al., 2013). Furthermore, the nitrogen cycle of CLM-CN is much more open (i.e.,	

615	higher cycling rates and losses) than that of CLM-Century. Finally, CLM-CN does_not
616	resolve the vertical biogeochemical gradients characteristic of CLM-Century. <u>All</u>
617	simulations were run at a spatial resolution of 1.9° × 2.5°, using the Qian et al.,
618	{Qian:2006wd} dataset for atmospheric forcing. The models were spun up for 1500
619	years to preindustrial equilibrium <u>following an improved spinup approach (Koven</u>
620	et al., 2013) that allows the models to reach equilibrium after 1000 years.
621	Simulations were then run from 1850 to 1979 under contemporary climate forcing
622	before the onset of perturbation conditions over the following 21 years (from 1980
623	to 2000). Model vegetation was specified according to the MODIS vegetation
624	continuous fields (Oleson et al., 2013). Model simulations were parameterized to
625	replicate the field experiments: the soil was warmed by scaling the aerodynamic
626	resistance by a factor of 10, a value obtained by trial and error to achieve a desired
627	warming of ~1 °C <u>(in accordance with the average temperature increase noted for</u>
628	the experimental manipulations, see results section below), while keeping sufficient
629	spatial variability of the warming. CLM forces the soil heat transport process
630	through the residual flux from incoming radiation, latent heat, and sensible heat.
631	Increasing aerodynamic resistance reduces the sensible and latent heat fluxes and
632	warms the soil during the growing season. We tried warming the soil by increasing
633	the surface air temperature (which is a diagnostic variable in CLM), but this
634	approach violated CLM's surface energy budget and was therefore avoided.
635	Furthermore, increasing aerodynamic resistance is more analogous to the approach
636	of installing open-top chambers to warm the soil.

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640	Nitrogen was added in the form of NH_4NO_3 at concentrations that replicated
641	the very high concentrations of the nitrogen addition experiments (20, 40, 60, 80
642	and 100 kg-N ha ⁻¹ yr ⁻¹). However, for comparison, we also simulated the model
643	response to a range of nitrogen concentrations that reflect more realistic nitrogen
644	deposition scenarios up to 2050 (0.2, 1.0, 2.0, 3.0 kg-N ha ⁻¹ yr ⁻¹ , (Galloway et al.,
645	2004). To mimic the approach of most field studies, we began the perturbation
646	(warming or nitrogen addition) when a given model grid was snow free for 7 days
647	(< 1 mm standing stock) and ended after more than 7 days with standing snow (> 1 $$
648	mm standing stock).
649	Model output was collected for each site considered in the meta-analysis (Fig.
650	1) using a 3×3 grid that surrounded the experimental manipulation site at the
651	center. The mean and standard deviation (SD) of predictions from the 9 grid cells
652	were then used to calculate the response ratios from that site. For coastal sites,
653	some modeled grid cells were not on land due to model spatial resolution, and data
654	statistics were therefore scaled with the actual number of data points accordingly.
655	For all sites we took the mean and SD of the grid cells and analyzed the data using
656	the meta-analysis approach applied to the observations and described above. Our
657	model analysis was limited to the output from the surface soil (10 cm for CLM-
658	Century and bulk prediction for CLM-CN, which represents approximately the top
659	20 cm of soil) where the majority of the collected studies focused their
660	measurements.

3 Results.

663 3.1 Response of belowground C-cycling to warming

664	On average, experimental warming increased soil temperatures by 1.4°C (±
665	0.7°C). Belowground respiration increased significantly under warming by 9% (±
666	5%) compared to the controls. This increase in belowground respiration was largely
667	driven by the response of European soils, where increase was 33% (± 11%) above
668	control soils. Conversely, <u>belowground respiration</u> from North American soils
669	showed a more modest, and non-significant, increase ($2.5\% \pm 6.5\%$; Fig. 2a, S1b). It
670	is unlikely that this <u>spatial</u> difference is due to greater experimental warming of
671	European soils: passive warming increased soil temperatures by 1.4 \pm 0.6 °C in
672	Europe and 1.3 \pm 0.5 °C in North American experiments. A transient effect of
673	belowground respiration, in high-latitude soils was also noted in the data set. Short
674	term experiments (< 2 years), showed a large significant increase ($34.4\% \pm 16\%$) in
675	belowground respiration, which was not evident in studies lasting 2 – 4 years.
676	However, studies lasting \geq 5 years also had significant increases in <u>belowground</u>
677	respiration, GPP increased significantly (11.8%) in warmed soils (Fig. 2a) and
678	showed a positive relationship with <u>belowground respiration</u> (Fig. 3).
679	Despite elevated GPP, litter decomposition declined significant by 9% (± 5%), $/$
680	while SOM did not change significantly from control values (Fig. 2a). Both microbial
681	and fungal biomass increased non-significantly under warming: <u>microbial biomass</u>
682	increased 3.8% (± 12%) while <u>fungal biomass</u> increased by 11.5% (± 19%).
683	Under warming, soil nitrogen mineralization and soil nitrogen
684	concentrations both declined non-significantly (<u>nitrogen mineralization</u> : 7.6% ±
685	15%, soil <u>nitrogen</u> ; 5.1% ± 9%) below the control soils. Soil <u>phosphorus</u> increased

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705 non-significantly above the control soils (1	12.5% ± 9%, Fig. S1b). Finally, the use of
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the OTC and OTG to passively warm high-latitude soils significantly lowered soil

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

708	Modeled warming experiments increased soil temperature by 1.21 °C \pm
709	0.47 °C in CLM-CN and 0.91 °C \pm 0.35 °C in CLM-Century. In response the two
710	models <u>wach predicted a</u> stronger relative and absolute increase <u>in belowground</u>
711	respiration, compared with the observational data. The models predicted higher
712	litter decomposition in response to warming, which is in contrast with the
713	decreasing trend found in the observational data. Both models also predicted
714	increased nitrogen mineralization following warming, contrary to the observational
715	data. The relative changes in SOM under warming were consistent between the
716	model predictions and observations. <u>Soil moisture increased non-significantly in</u>
717	both models (CLM-CN: 38% ± 42%; CLM-Century: 7% ± 33%), in contrast to the
718	observations, but with a wide variability. In general, CLM-CN tended to predict a
719	much stronger temperature response than CLM-Century (Fig. 2a).
720	
721	3.2 Response of belowground carbon cycling to nitrogen addition
722	The field experiments added an average of 72 kg-N ha ⁻¹ yr ⁻¹ (± 38 kg-N ha ⁻¹
723	yr ⁻¹) of nitrogen to soils, with a range of 1 – 100 kg-N ha ⁻¹ yr ⁻¹ . This additional N
724	reduced belowground respiration and resulted in a larger sink for SOM, indicating a
725	negative feedback to atmospheric CO ₂ concentrations (Fig. 2b). <u>Belowground</u>
726	respiration, in soils receiving additional nitrogen, (in the form NH4NO3) declined
727	11.8% (± 7%), significantly below control soils (Fig. 2b). This pattern was consistent

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737	for the two geographical regions examined and was not dependent on the duration	
738	of the experiment. Belowground respiration, in European soils declined, non-	
739	significantly, by 7% (± 9.5%) below control soils (Fig. S1a). Belowground	Nicholas Bouskill 10/26/14 7:18 PM Deleted: R _B
740	respiration, in North American soils also declined significantly by 12.7% (± 9%).	Nisheles Bauskill 10/26/14 7-10 DM
741	Belowground respiration, showed a negative relationship with increasing soil	Deleted: R _B Nicholas Bouskill 10/26/14 7:19 PM
742	nitrogen concentration (Fig. 4a). Linear regressions failed to uncover a significant	Deleted: R _B
743	relationship between the response of <u>belowground respiration</u> , and climate (MAT,	Nicholas Bouskill 10/26/14 7·19 PM
744	MAP) or experimental factors (experimental duration and magnitude of nitrogen	Deleted: R _B
745	added). Heterotrophic respiration, showed no significant change under nitrogen	
746	addition; however, the data are highly variable (\pm 12%). Nitrogen addition resulted	Deleted: R _H
747	in a significant decline in <mark>litter decomposition (</mark> % mass loss/ yr .1) of 4.8% (± 3%),	
748	while SOM increased significantly 19.5 % (\pm 10 %) in perturbed soils.	Nicholas Bouskill 10/26/14 7:19 PM Deleted: LD Nicholas Bouskill 11/6/14 8:44 PM
749	GPP increased significantly under nitrogen addition (44.3% \pm 7.5%)	Formatted: Superscript
750	compared with the control soils (Fig. 2b). On average, aboveground biomass	
751	(vascular + non-vascular plants) non-significantly increased upon nitrogen addition	
752	(15% ± 22%). Vascular plant biomass increased significantly (33 % ± 8 %) over that	
753	of the control soils (Fig. S1b).	
754	Overall, a non-significant increase in <u>microbial biomass</u> was observed for	Nicholas Bouskill 10/26/14 7:20 PM
755	experimental soils (Fig. 2b), yet, declined with increasing concentrations of nitrogen	Deleted: MB
756	added to the soil (Fig. 4b). When factoring in geographical location, microbial	
757	biomass in European soils increased significantly above the controls (17.5% \pm 9%),	
758	but decreased non-significantly relative to control soils in North American soils (Fig.	
759	S1a). While different forms of nitrogen were applied in the experiments (e.g.,	

767	$\rm NH_4NO_3$ or NPK), the most significant factors, explaining 37 % of the variance in
768	microbial biomass, were site-specific pH and mean annual temperature. Finally,
769	fungal biomass increased significantly by 23% (± 20.5%) compared to the control
770	soils.
771	For nitrogen perturbed CLM-CN and CLM-Century simulations we analyzed
772	the relative response of variables complementary to the observational meta-
773	analysis. Under nitrogen addition, the modeled response variables matched
774	observations for only two parameters: GPP and SOM, and only at the lowest
775	nitrogen addition concentrations (i.e., ≤ 1 kg-N ha ⁻¹ yr ⁻¹ , Fig. S3). Neither model
776	accurately replicated the trend in the observed response of <u>belowground</u>
777	respiration, litter decomposition, and nitrogen mineralization (Fig. 2b), while both
778	models overestimated the response of <u>heterotrophic respiration</u> .
779	
780	4 Discussion
781	Accurate representation of the processes governing soil carbon cycling in high-
782	latitude soils is crucial for reducing model uncertainty in energy and greenhouse gas
783	feedbacks with climate. By comparing meta-analyses based on model output and
784	observations, we show that <u>two belowground biogeochemical representations in</u>
785	<u>CLM4.5</u> are unable to adequately represent many of the observed high-latitude
786	ecosystem responses to <u>two important climate change variables: temperature and</u>
787	nitrogen availability. We focus our discussion on the potential reasons for the
788	discrepancies in responses by highlighting: (1) the most important mechanisms
789	currently missing from, or poorly represented in, the models; and (2) instances

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798	where deficiencies in the experimental approaches prohibits the data from being
799	used for benchmarking the model. We also recommend further approaches to
800	improve the mechanistic basis of the belowground biogeochemistry representation
801	in ESMs.

803 4.1 Response of belowground carbon cycling to warming

804	The observational meta-analysis suggests that elevated belowground
805	respiration is balanced by elevated GPP (and associated increases in soil organic
806	matter). We therefore conclude that the coupling of aboveground and belowground
807	processes resulted in these soils being carbon neutral under modest (+ 1.3 $^{\circ}$ C)
808	warming. The models also predicted no significant changes to belowground SOM
809	content under warming due to concomitant increases in <u>belowground respiration</u> ,
810	and GPP. However, the magnitude of the modeled fluxes is many times larger than
811	the observed fluxes. Therefore, the net impact of the manipulation <u>on SOM</u> was
812	predicted by the models, but with incorrect mechanisms.
813	As a broader point, we believe this result illustrates a common problem
814	among tests of land model performance, i.e., inferences of model fidelity based on
815	comparisons solely with observations <u>of emergent responses that has low signal to</u>
816	noise ratio. For example, it is insufficient to use of net ecosystem exchange (NEE) as
817	a sole model benchmark (Schwalm et al., 2010) <u>, because it</u> ignores that: (1) NEE is
818	typically a small difference between ecosystem respiration and assimilation and (2)
819	models separately represent these gross fluxes as being differently controlled by
820	climate and antecedent system states. We contend that representing this type of

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850	emergent ecosystem <mark>net</mark> flux <u>within the observational uncertainty</u> gives little
851	information as to whether the model is accurately representing the underlying
852	mechanisms appropriately.
853	
854	4.1.1 Nitrogen cycling under warming: Confronting the model outputs with
855	observations showed a consistent overestimation of key variables in the model
856	predictions (Fig. 2a). One potential reason for a larger modeled response is the
857	approaches CLM-CN and CLM-Century take to representing the nitrogen cycle. The
858	inclusion of nitrogen cycling in coupled carbon-nitrogen climate models is
859	consistent with the idea that nitrogen is a significant determinant of carbon cycling
860	in many ecosystems (Hungate, 2003; Vitousek and Howarth, 1991), and modeled
861	nitrogen input, retention, and loss have been shown to have a large impact on
862	ecosystem carbon sequestration (Thomas et al., 2013b; Zaehle and Dalmonech,
863	2011). Moreover, data based modifications to ESM nitrogen cycling mechanisms
864	may further improve the correspondence between observations and model output
865	<u>(Thomas et al., 2013a).</u>
866	CLM-CN predicts much higher rates of nitrogen loss from denitrification than
867	CLM-Century, and is therefore more responsive to changing nitrogen availability
868	from inputs, mineralization, and losses. Under warming CLM-CN predicted a
869	significant loss of soil nitrogen not predicted in CLM-Century, which has a more
870	closed nitrogen cycle, possibly more representative of the nitrogen cycle in high-
871	latitude soils (Barsdate and Alexander, 1975). Rates of nitrogen fixation, deposition
872	and redox cycling (i.e., nitrification and denitrification) are low at high latitudes

874	(Cleveland et al., 1999; Giblin et al., 1991), and hydrological loss of nitrogen at the
875	beginning of the growing season is relatively large (Harms and Jones, 2012; Jones et
876	al., 2005). Mineralization is, therefore, the main source of nitrogen for plant and
877	microbial growth (Shaver et al., 1992).
878	Mineralization rates are controlled by the depolymerization of proteinaceous
879	(Jones et al., 2009; Schulten and Schnitzer, 1997), leading to the release of amino
880	acids (Schimel and Bennett, 2004) that are rapidly utilized by plants and microbes
881	(Kielland, 1994; Weintraub and Schimel, 2005). Ammonia is then released during
882	turnover of the dead microbial biomass. Depolymerization is the critical step in this
883	process and, like organic matter decomposition, is dependent on microbial
884	physiology and subject to the biotic and abiotic controls described above. Modeled
885	nitrogen mineralization, however, increases under warming with a concomitant
886	increase in soil nitrogen in the CLM-Century framework. CLM-CN, with its high rates
887	of mineral nitrogen losses shows a very large decline in soil nitrogen, possibly
888	rendering the above- and belowground communities nitrogen limited throughout.
889	In our data analyses, nitrogen mineralization declined as microbial nitrogen (i.e.,
890	immobilization) increased. The end result in both cases (i.e., the models and
891	observations) is the potential limitation of plant growth over long time scales. Our
892	data synthesis suggests that the release of nitrogen from increased decomposition is
893	used to meet microbial demands or immobilized. Microbial immobilization is
894	regulated by the stoichiometric imbalance between the substrate being
895	depolymerized and the physiological nutrient demand. While analogous to the CUE,
896	nitrogen use efficiency (NUE), which relates immobilization and mineralization to

898maintain cell stoichiometry. Some attempts have been made to incorporate NUE899controls into ecosystem models (Manzoni and Porporato, 2009), but further900experimental and modeling work is required to understand NUE's plasticity and901impacts on soil carbon dynamics.902.9034.1.2, Aboveground dynamics: The biogeochemical coupling between aboveground904and belowground components of the ecosystem is crucial for understanding high-905latitude carbon cycling under a changing climate. The meta-analysis of field906measurements showed a general stimulation of aboveground activity under907warming, while previous field studies have noted a shift in plant community908composition with warming, favoring the establishment of deciduous shrubs and graminoids against mosses and lichens (Schuur et al., 2007; Sistla et al., 2013;909Walker et al., 2006). This shift toward more woody plants changes the ecosystem911carbon balance and nutrient dynamics (Jackson et al., 2002; Welker et al., 2004), as912shrubs tend towards higher internal carbon allocation toward woody tissue, but	897
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	912
913 also may increase belowground carbon allocation (as both litter and exudates) Deleted: higher Nicholas Bouskill 11/6/14 8:52 PM	913
914 relative to mosses (Street et al., 2013). This <u>change in</u> belowground allocation may Nicholas Bouskill 10/27/14 8:30 AM	914
915 result in the observed relationship between GPP and <u>belowground respiration</u> (Fig. <u>Deleted: s</u> Nicholas Bouskill 10/26/14 7:39 PM	915
916 3), indicating a close coupling between these two processes. This positive Deleted: R _B Nicholas Bouskill 10/27/14 8:44 AM	916
917 relationship may develop due to higher rates of belowground labile root exudation, Nicholas Bouskill 10/27/14 9:32 AM	917
918 which may be respired directly by the plants themselves (Luo, 2007), or <u>prime</u> the Nicholas Bouskill 10/27/14 9:32 AM	918
919 microbial community <u>leading to the destabilization and decomposition of chemically</u> Deleted: of Nicholas Bouskill 10/27/14 9:32 AM Deleted: and elevation of overall	919

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935	complex SOM (Fontaine et al., 2004). Our data <u>analysis</u> cannot directly distinguish	Nic De
936	between the two pathways, <u>although an</u> observed <u>drop</u> in litter decomposition rates	Nic De
937	<u>could indicate that</u> the mineralization of plant exudates spurs the degradation of	Nic De
938	older <u>SOM</u> (Hartley et al., 2012), resulting in elevated belowground respiration rates,	Nic De
939	Further field studies and more data (e.g., radiocarbon measurements) are required	Nic De
940	to verify this conclusion.	Nic De
941	Current models crudely represent above- and belowground biogeochemical 🖪	res pri Nic
942	coupling and do not represent some of the crucial roles plants play in soil carbon	De Nic
943	dynamics (Ostle et al., 2009; Schmidt et al., 2011). Of particular relevance to high-	De Nic
944	latitude ecosystems is the lack of any representation of cryptogams or bryophytes in	De Nic
945	<u>CLM4.5</u> . These plants contribute substantially to aboveground biomass and	De Nic
946	biogeochemical processes in tundra soils (Cornelissen et al., 2007; Elbert et al.,	Fo Nic
947	2012) and are clearly important for accurate simulations of tundra carbon dynamics.	De obs
948	Few ESM land models (including CLM4.5) include dynamic vegetation, and when it	mo
949	is included, representation tends to be coarse (Ostle et al., 2009). Ongoing work will	nit sev bio
950	attempt to address some of these deficiencies, by including representations of	and hig
951	aboveground ecosystem demography (Huntingford et al., 2008; Moorcroft et al.,	Nic De
952	2001), and soil carbon dynamics (Riley et al., 2014), Integration of these approaches	De pre
953	into the CLM framework may improve the robustness of long-term tundra soil	une
954	simulations and reduce uncertainty associated with the aboveground model	cha (Co mo
955	response.	wh pri Nic

holas Bouskill 10/27/14 9:32 AM leted: decomposition rates holas Bouskill 10/27/14 9:34 AM eleted: however, t eleted: he holas Bouskill 10/27/14 9:33 AM leted: decline holas Bouskill 10/27/14 9:34 AM leted: indicate holas Bouskill 10/27/14 9:34 AM leted: that the elevated belowground spiration rates principally reflect the ming mechanism, as holas Bouskill 10/27/14 9:35 AM leted: soil organic matter holas Bouskill 10/27/14 9:40 AM leted: ; however, holas Bouskill 10/27/14 9:40 AM eleted: m holas Bouskill 10/27/14 9:41 AM eleted: ore data holas Bouskill 10/28/14 9:50 PM rmatted: Indent: First line: 0" holas Bouskill 10/28/14 9:50 PM eleted: A comparison of the servational and modeled response to rming shows an overestimation by the dels for a number of variables, and the posite response sign for others (e.g., rogen mineralization). Below, we identify

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

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1010	<u>4.1.3 Belowground Ecology:</u> The observational data indicated elevated belowground	
1011	respiration under warming. The response of microbial heterotrophs to warming can	
1012	partially be explained by kinetic theory, whereby biochemical reaction rates	
1013	increase with increasing temperature (Davidson and Janssens, 2006). Hydrolytic	
1014	and oxidative extracellular enzymes, secreted to depolymerize complex organic	
1015	matter (Allison et al., 2010), are sensitive to temperature (German et al., 2012).	
1016	Structural modifications in cold ecosystems maximize their specific activity under in	
1017	situ temperatures relative to temperate ecosystems (Hochachka and Somero, 2002),	
1018	which may result in significantly enhanced activity under warming (Koch et al.,	
1019	2007). This theory fits with the short-term (<2yr) data from the current meta-	
1020	analysis showing increasing belowground respiration despite no increase in	
1021	microbial biomass.	
1022	However, we also identified a drop in <u>belowground respiration in studies</u>	
1023	lasting longer than 2 years and shorter than 5 years (Fig. S1b), Belowground	
1024	respiration, has consistently been reported to decline under prolonged warming	
1025	(Rustad et al., 2001) and attributed to substrate limitation (Hartley et al., 2008) or a	
1026	<u>community-level response</u> of microbial populations to warmer temperatures	
1027	offsetting the kinetic response of individual microbes (Bradford, 2013; Bradford et	
1028	al., 2008). Given the increased GPP found in our meta-analysis, belowground	
1029	communities are unlikely to be substrate limited. Therefore, we hypothesize that the	
1030	community <u>-level response</u> is likely responsible for the drop in <u>belowground</u>	
1031	respiration, under <u>2 – 5 years of</u> warming.	

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	turnover are complex, but can alter the

functional potential of soils, which in turn may alter the rate of organic matter breakdown and nutrient cycling.

1058	The subsequent increase in <u>belowground respiration</u> , over prolonged
1059	warming (> 5 years) could represent either the decomposition of leaf litter driven
1060	by changes in microbial community composition, or thawing subsurface organic
1061	matter (Dorrepaal et al., 2009). This <mark>Jatter hypothesis is relevant</mark> to the long-term
1062	fate of high-latitude carbon. In the current analysis, NEE appears balanced, with no
1063	change in SOM. However, temporal patterns of vegetation response to warming
1064	show a transient response to warming, with nutrient limitation reducing plant
1065	productivity on longer time scales (Arft et al., 1999; Chapin and Shaver, 1996). It is
1066	possible, given the large nitrogen immobilization under warming, that <u>belowground</u>
1067	respiration, may continue longer than productivity, unbalancing NEE and leading to
1068	net carbon loss.
1069	Temperature is a key factor influencing biogeochemical mechanisms in the
1070	model. CLM models belowground respiration, using a static Q_{10} and fixed carbon use
1071	efficiencies (CUE) for different SOM pools size. This approach may result in the large
1072	modeded increase in belowground respiration, In reality, both Q ₁₀ and CUE vary on
1073	spatial and temporal scales, and respond non-linearly to changes in temperature
1074	(Janssens & Pilegaard, 03; Sinsabaugh et al., 2013). Recent microbe-explicit models
1075	(MEMs) that consider basic microbial physiology (e.g., Lawrence et al., 2009)
1076	introduce direct biological control over soil carbon cycling and different conclusions
1077	on soil carbon pool size and dynamics under warming (Allison et al., 2010; Wieder
1078	et al., 2013). For example, by scaling the CUE value with temperature, in accordance
1079	with publish <u>ed</u> observations (Luo et al., 2001; Melillo, 2002), the MEMs show a
1080	decline in soil carbon turnover under warming (Li et al., 2014; Wieder et al., 2013).

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1097extracellular enzymes, and mineral surfaces (Tang & Riley 2014), demonstrates to1098both decomposition temperature sensitivity and CUE are hysteretic and cannot1099easily be represented by a simple function of soil temperature. However, it is also1100important to note that microbial CUE is not solely temperature-dependent, and1101other factors, some of which are already present in CLM-CN and CLM-Century1102(including nutrient limitation, and soil moisture limitations), may uncouple grow1103and respiration and change CUE (Manzoni et al., 2008; Sinsabaugh et al., 2013). To1104predictions of the microbe-explicit models (MEM) provide further impetus for1105greater representation of the structure and function of belowground biomass.1106Other aspects of belowground ecology in high-latitude tundra that are not	hat h
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1106 Other aspects of belowground ecology in high-latitude tundra that are not	
1107 included in the models can have a significant impact on the stability of soil carbon	L
1108 (also see discussion below on barriers to benchmarking). For example, while the	е
1109 is little evidence that fungal: bacterial ratios are altered by warming, either in our	
1110 observational meta-analysis or in previous work (Strickland and Rousk, 2010), th	е
1111 community composition may change without altering fungal: bacterial ratios	
1112 (Strickland and Rousk, 2010). <u>Certain traits that separate the main decomposing</u>	
1113 <u>functional guilds , such as biomass stoichiometry, nutrient use efficiency, substra</u>	:e
1114 utilization and response to environmental variables (e.g., temperature or soil	
1115 moisture) <u>(Six et al., 2006)</u> can bring about changes in the <u>decomposition rates</u> .	
These factors are arguably more important than climate when modeling	
1117 decomposition at local and regional scales (Bradford et al., 2014).	
1118	-

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1136	4.1.4 Litter Decomposition: Disagreement between the observations and model	
1137	predictions, was also <u>noted</u> for litter decomposition. Under warming, <u>litter</u>	
1138	decomposition declined in the observations, possibly contributing to SOM	
1139	accumulation, but <u>increased</u> in the models. In previous studies, the response of <u>litter</u>	
1140	decomposition, to warming was largely dependent on the method used to increased	
1141	soil temperature (Aerts, 2006). OTCs tend to warm the soil and reduce soil moisture,	
1142	limiting litter decomposition by saprotrophic fungi. Soil moisture in the models	
1143	showed a non-significant increase with warming as the permafrost began to thaw	
1144	(Fig. 2a). The difference between the observational meta-analysis and the models	
1145	represents a potentially confounding factor in using this data to benchmark the	
1146	model. A <u>previous</u> meta-analysis <u>focused solely on</u> litter decomposition in Arctic and	
1147	Alpine tundra found that warming induced a small increase in decomposition	
1148	provided sufficient soil moisture (Aerts, 2006). This response was not apparent in	
1149	our data syntheses, but suggests the model results, while overestimating <u>litter</u>	
1150	decomposition, were at least in the appropriate direction. Soil moisture is an	
1151	important controller on decomposition (Aerts, 2006; Hicks Pries et al., 2013).	
1152	However, changes to surface hydrology during permafrost thaw are dependent on	
1153	thermokarst formation and topological features of the landscape (Jorgenson and	
1154	Osterkamp, 2005) and may result in increased or decreased soil moisture. We	
1155	identify these issues as important for further experimental and modeling work in	
1156	order to better represent future changes in surface hydrology and the consequences	
1157	for <u>litter decomposition</u> ,	
1158		

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1171	4.2 Response of belowground carbon cycling to nitrogen addition
1172	Our meta-analysis of field observations found that the addition of inorganic nitrogen
1173	to traditionally nitrogen limited ecosystems enhances the carbon sink, consistent
1174	with previous studies (Luo et al., 2012; McGuire et al., 2012). Interactions between
1175	the carbon and nitrogen cycles resulting in soil carbon accumulation in different
1176	ecosystems have been reported previously (Magnani et al., 2007; Thomas et al.,
1177	2013b), and have been attributed to an increased carbon allocation to woody tissue
1178	(Ciais et al., 2008; Tummers, 2006) and reduction in the SOM decomposition rate
1179	(Olsson et al., 2005). Overall, our data-synthesis is largely consistent with the
1180	overarching conclusions of previous meta-analyses (Janssens et al., 2010; Knorr et
1181	al., 2005).
1101	
1182	A question remains, however, about the value of the responses synthesized
1182 1183	A question remains, however, about the value of the responses synthesized from studies that add fertilizer ($NH_{d}NO_{3}$ or NPK) as a source of nitrogen far in
1182 1183 1184	A question remains, however, about the value of the responses synthesized from studies <u>that add fertilizer (NH_dNO₃ or NPK) as a source of nitrogen far in excess of anticipated global change scenarios for high-latitude ecosystems</u> . The
1182 1183 1184 1185	A question remains, however, about the value of the responses synthesized from studies <u>that add fertilizer (NH_dNO₃ or NPK) as a source of nitrogen far in</u> <u>excess of anticipated global change scenarios for high-latitude ecosystems</u> . The average concentration of nitrogen added to the soils in the tundra studies (~ 72 kg
1182 1183 1184 1185 1186	A question remains, however, about the value of the responses synthesized from studies <u>that add fertilizer (NH₄NO₃ or NPK) as a source of nitrogen far in</u> <u>excess of anticipated global change scenarios for high-latitude ecosystems</u> . The average concentration of nitrogen added to the soils in the tundra studies (~ 72 kg ha ⁻¹ yr ⁻¹) is extremely high when compared with (1) estimates of nitrogen fixation
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1182 1183 1184 1185 1186 1187 1188	A question remains, however, about the value of the responses synthesized from studies <u>that add fertilizer (NH_dNO₃ or NPK) as a source of nitrogen far in</u> <u>excess of anticipated global change scenarios for high-latitude ecosystems</u> . The average concentration of nitrogen added to the soils in the tundra studies (~ 72 kg ha ⁻¹ yr ⁻¹) is extremely high when compared with (1) estimates of nitrogen fixation (< 10 kg ha ⁻¹ yr ⁻¹ , (Cleveland et al., 1999); (2) nitrogen deposition (both current rates of deposition 0.2 – 0.24 kg ha ⁻¹ yr ⁻¹ , (Jones et al., 2005) and projections of
1182 1183 1184 1185 1186 1187 1188 1188 1189	A question remains, however, about the value of the responses synthesized from studies <u>that add fertilizer (NH_dNO₃ or NPK) as a source of nitrogen far in</u> <u>excess of anticipated global change scenarios for high-latitude ecosystems</u> . The average concentration of nitrogen added to the soils in the tundra studies (~ 72 kg ha ⁻¹ yr ⁻¹) is extremely high when compared with (1) estimates of nitrogen fixation (< 10 kg ha ⁻¹ yr ⁻¹ , (Cleveland et al., 1999); (2) nitrogen deposition (both current rates of deposition 0.2 – 0.24 kg ha ⁻¹ yr ⁻¹ , (Jones et al., 2005) and projections of future deposition (Galloway et al., 2004)); and (3) potential nitrogen availability
1182 1183 1184 1185 1186 1187 1188 1189 1189	A question remains, however, about the value of the responses synthesized from studies <u>that add fertilizer (NH_dNO₃ or NPK) as a source of nitrogen far in</u> <u>excess of anticipated global change scenarios for high-latitude ecosystems</u> . The average concentration of nitrogen added to the soils in the tundra studies (~ 72 kg ha ⁻¹ yr ⁻¹) is extremely high when compared with (1) estimates of nitrogen fixation (< 10 kg ha ⁻¹ yr ⁻¹ , (Cleveland et al., 1999); (2) nitrogen deposition (both current rates of deposition 0.2 – 0.24 kg ha ⁻¹ yr ⁻¹ , (Jones et al., 2005) and projections of future deposition (Galloway et al., 2004)); and (3) potential nitrogen availability from organic matter mineralization under a warming climate (Harden et al., 2012).
1182 1183 1183 1184 1185 1186 1187 1188 1189 1190 1191	A question remains, however, about the value of the responses synthesized from studies <u>that add fertilizer (NH_dNO₃ or NPK) as a source of nitrogen far in</u> <u>excess of anticipated global change scenarios for high-latitude ecosystems</u> . The average concentration of nitrogen added to the soils in the tundra studies (~ 72 kg ha ⁻¹ yr ⁻¹) is extremely high when compared with (1) estimates of nitrogen fixation (< 10 kg ha ⁻¹ yr ⁻¹ , (Cleveland et al., 1999); (2) nitrogen deposition (both current rates of deposition 0.2 – 0.24 kg ha ⁻¹ yr ⁻¹ , (Jones et al., 2005) and projections of future deposition (Galloway et al., 2004)); and (3) potential nitrogen availability from organic matter mineralization under a warming climate (Harden et al., 2012). Consequentially, we question whether such data lends itself to understanding the

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Deleted: Confronting the model outputs with observations showed a consistent overestimation of key variables in the models (Fig. 2a). One potential reason for a larger modeled response is the approaches CLM-CN and CLM-Century take to representing the nitrogen cycle. The inclusion of nitrogen cycling in coupled carbon-nitrogen climate models is consistent with the idea that nitrogen is a significant determinant of carbon cycling in many ecosystems (Hungate, 2003; Vitousek and Howarth, 1991), and modeled nitrogen input, retention, and loss have been shown to have a large impact on ecosystem carbon sequestration (Thomas et al., 2013b; Zaehle and Dalmonech, 2011). Moreover, data based modifications to ESM nitrogen cycling mechanisms may further improve the correspondence between observations and

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1218	availability, and the benefit of benchmarking the ecosystem models against such a		
1219	dataset. On the other hand, if the models include the relevant underlying		
1220	mechanisms, then they should reproduce the field studies regardless of the amount		
1221	of nitrogen added. We give further examples below of where the high nitrogen		
1222	concentrations may confound the interpretation of the experiments with respect to		
1223	the model predictions.		
1224			
1225	<u>4.2.1 SOM dynamics</u> : SOM accumulation under nitrogen addition experiments is a		Nicholas Bouskill 10/28/14 10:05 PM
1226	common feature of both the field experiments and the model simulations. However,		Deleted: Nicholas Bouskill 10/28/14 10:05 PM
1227	the underlying mechanisms leading to SOM accumulation are very different, adding		Formatted: Font:Italic
1228	uncertainty to the model predicted soil carbon fate over longer timescales. In both		
1229	versions of CLM, the alleviation of nitrogen limitation stimulates a number of		
1230	ecosystem processes including aboveground primary productivity, litter		
1231	decomposition, and organic matter decomposition, The accumulation of SOM		Nicholas Bouskill 10/26/14 9:46 PM
1232	indicates the stimulation of GPP and <u>litter decomposition</u> (as a source into the SOM		Deleted: (R _B) Nicholas Bouskill 10/26/14 9:47 PM
1233	pools) must outweigh losses from increased <u>belowground respiration</u> .	\searrow	Deleted: LD Nicholas Bouskill 11/6/14 9:07 PM
1234	The observations, on the other hand, show a significant decline in		Deleted: the carbon cascade simulate decomposition of litter
1235	belowground respiration and litter decomposition, under nitrogen addition.		Nicholas Bouskill 10/26/14 9:47 PM Deleted: R _B
1236	Belowground respiration depends on the decomposition and substrate utilization		Nicholas Bouskill 10/26/14 9:47 PM Deleted: R _B
1237	capabilities of the microbial (i.e., bacterial and fungal) community to mineralize root		Nicholas Bouskill 10/26/14 9:47 PM Deleted: LD
1238	exudates and litter. A drop in belowground respiration, may, therefore, be		Nicholas Bouskill 10/26/14 9:47 PM Deleted: R _B
1239	attributable to several mechanisms not included in either version of CLM. A recent		Nicholas Bouskill 10/26/14 9:47 PM Deleted: R _B
1240	meta-analysis examined the response of Boreal forest ecosystems to added nitrogen		

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las Bouskill 10/26/14 9:46 PM ted: (R_B) las Bouskill 10/26/14 9:47 PM ted: LD las Bouskill 11/6/14 9:07 PM ted: the carbon cascade simulates the nposition of litter las Bouskill 10/26/14 9:47 PM ted: R_B las Bouskill 10/26/14 9:47 PM ted: R_B las Bouskill 10/26/14 9:47 PM ted: LD las Bouskill 10/26/14 9:47 PM ted: R_B las Bouskill 10/26/14 9:47 PM ted: R_B

1251 (Ja	nssens et al.,	2010), and	concluded	that the internal	reallocation of carbon i	n
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- 1252 plants and trees reduced the rate of exudation to belowground ecosystems,
- 1253 resulting in microbial biomass becoming carbon limited with a concomitant decline
- 1254 in biomass and belowground respiration (Janssens et al., 2010). Our empirical data
- 1255 shows increased GPP and vascular plant biomass, possibly indicating a reallocation
- 1256 of newly fixed carbon in vascular plants (Ciais et al., 2008) and a drop in

1257 belowground exudation.

1258

<u>4.2.2 Belowground Ecology:</u> Overall, the current observational meta-analysis found a • 1259 1260 non-significant increase in microbial biomass (i.e., bacterial and fungal) but a 1261 significant increase in fungal biomass under nitrogen addition. This response 1262 appears contrary to previous studies that have recorded a drop in microbial 1263 biomass under nitrogen addition (Treseder, 2008), but in line with fertilization 1264 studies in tundra ecosystems (Clemmensen et al., 2006). We also note that microbial 1265 biomass (and belowground respiration) are inversely related to the amount of 1266 nitrogen added to the soils (Fig. 4a, b). At low nitrogen concentrations microbial 1267 community activity can be stimulated (Allison et al., 2009) and decomposition elevated, as indicated by the models (Fig. 2b) and some of the observations (Fig. 4b). 1268 1269 Elevated nitrogen concentrations, however, have a negative impact on microbial 1270 biomass (Treseder, 2008) and decomposition (Janssens et al., 2010). This response 1271 can occur through the inhibition of lignin-degrading enzymes produced by 1272 saprotrophic fungi (Sinsabaugh et al., 2002; but see Hobbie, 2008), or the increased 1273 chemical recalcitrance of soil carbon undergoing condensation reactions with

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1283	<u>inorganic nitrogen</u> (Dijkstra et al., 2004), increasing the physical protection of	
1284	organic matter from decomposition. Therefore, under the high nitrogen inputs used	
1285	in the present field studies, the coupling between above- and belowground	
1286	ecosystems can decrease <u>belowground respiration</u> and <u>litter decomposition</u>	
1287	resulting in an accumulation of SOM.	
1288	Whereas the warming meta-analysis yielded results that could be used to	
1289	constrain model mechanisms, the same cannot be concluded for the nitrogen-	
1290	addition studies due to the uncertainty of how high-latitude soils will respond to	
1291	lower concentrations of nitrogen. However, we suggest two potential model changes	
1292	that could rectify the different conclusions derived from the observations and	
1293	models, (1) <u>A dynamic vegetation approach sensitive to changes in nitrogen</u>	
1294	inventory could represent compositional changes across the tundra with important	
1295	ramifications for root biomass, litter quality, and plant exudates that play a	
1296	significant role in soil carbon dynamics (Aerts et al., 2005). (2) Representation of	
1297	discrete belowground biomass functional groups (e.g., heterotrophic and fungal	
1298	decomposers) alongside their dependencies on soil nitrogen <u>may</u> help to constrain	
1299	the belowground response to nitrogen addition. <u>Finally, while the model</u>	
1300	mechanisms should ideally be able to reproduce the observed response to high	
1301	nitrogen loading, we believe that future manipulation studies in high-latitude soils	
1302	that use realistic nitrogen additions would be more relevant for understanding the	
1303	tundra soil response. For example, recent studies have added nitrogen to tundra	
1304	soils at magnitudes one order of magnitude higher than measured concentrations	
1305	{Lavoie:2011da} or guided by soil mineralization rates {Sistla:2012dq}. The	

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1365	ecosystem response is therefore more likely to reflect future responses under
1366	anticipated mineralization or deposition scenarios {Galloway:2004th}.
1367	
1368	4.3 Barriers and criteria for successful experiment-based model benchmarking
1369	While we were able to benchmark some aspects of the model predictions
1370	using the observational meta-analysis, we acknowledge several concerns that may
1371	have complicated the data-model comparison. First, no general protocol consistent
1372	with field experiments is available for setting up model perturbations. Although
1373	different land models have different structures and degrees of complexity, a
1374	standard approach to establishing perturbations would be beneficial. In our model,
1375	atmospheric warming resulted in unrealistic uniform soil warming across the study
1376	domain and therefore underestimated the spatial heterogeneity found in passive
1377	warming experiments (Bokhorst et al., 2012). On the other hand, solely reducing the
1378	wind speed failed to alter the soil thermal regime, indicating a possible problem in
1379	the formulation of CLM's surface boundary layer resistance. However, our approach
1380	of warming via enhanced aerodynamics resistance is not transferable to models
1381	using atmospheric temperature, rather than a surface energy balance scheme, to
1382	force soil thermal dynamics.
1383	Therefore, criteria need to be established to ensure, regardless of the method
1384	used, that the experimental manipulation is reproduced in the model with sufficient
1385	fidelity that the predicted and observed responses can be reasonably compared. We
1386	consider the criterion used here for the warming experiments (i.e., that the mean
1387	predicted manipulation soil temperatures are not significantly different from the

1388	observations) to be a minimally acceptable criterion. Ideally, the predicted response
1389	of soil temperature, soil moisture, and radiation under warming would emerge in a
1390	statistically similar manner to the observations. In the current study, this criterion
1391	was not met for soil moisture, where the observations found that soil moisture
1392	declined (by 8% ± 6%) under warming and the model predicted large increases
1393	CLM-CN: 38% ± 42%; CLM-Century: 7% ± 33%).This may be an important given the
1394	significant impacts moisture has on decomposition and nitrogen cycling.
1395	Second, the spatial discrepancy between the model predictions and
1396	observational data is large. This mismatch arises from several sources, including
1397	uncertainties: (1) in the climate and environmental forcing data used to drive the
1398	models; (2) in soil and plant characterization; (3) caused by spatial heterogeneity in
1399	the site and experimental manipulation (e.g., unequal heating within the open-top
1400	chambers, energy leaking at the boundary with surrounding soil); and (4) in
1401	accurate model characterization of the growing season.
1402	Third, while we acknowledge the complexity of interpreting single-factor
1403	manipulation experiments, the multifaceted nature of climate change calls for more
1404	multifactorial experiments and models that can reproduce any response. The few
1405	studies we could find measuring the response of similar variables to combined
1406	warming and nitrogen addition (e.g., Shaver et al., 1998) found an even larger
1407	warming response than for the single-factor experiments. However, there were too
1408	few studies measuring complementary variables to conduct a meta-analysis.
1409	Previous studies conducted in high-latitude soils have recorded a stronger response
1410	of decomposition following perturbation by a combination of drivers (e.g., elevated

1411	temperature and CO ₂) than if those factors were considered in isolation (Fenner et
1412	al., 2007). In contrast, Leuzinger et al. (Leuzinger et al., 2011) give several examples
1413	where the opposite occurs: a combination of multiple drivers lessens the ecological
1414	response relative to individual drivers. These contradictory results call for further
1415	consideration of the impact of multiple drivers in high-latitude ecosystems that
1416	might be used to benchmark model performance.
1417	Fourth, the field observational data lacks sufficient spatial coverage to
1418	characterize high-latitude spatial heterogeneity accurately. There are many studies
1419	that cluster in a few regions, represented in the model by only a few grid cells. While
1420	we obtained some insights into the deficiencies of the model from this
1421	benchmarking exercise, more work is required to develop confidence in our
1422	conclusions given the spatial heterogeneity of high-latitude ecosystems.
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1423 1424	4.4 Overall Recommendations
1423 1424 1425	4.4 Overall Recommendations We have demonstrated here that despite some experimental drawbacks, the
1423 1424 1425 1426	4.4 Overall Recommendations We have demonstrated here that despite some experimental drawbacks, the underlying biogeochemical mechanisms of CLM-CN and CLM-Century are
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1423 1424 1425 1426 1427 1428 1429 1430 1431	4.4 Overall Recommendations We have demonstrated here that despite some experimental drawbacks, the underlying biogeochemical mechanisms of CLM-CN and CLM-Century are insufficient to accurately reproduce the observations of a number of high-latitude perturbation experiments. However, we can identify several metrics from the meta- analyses, including nitrogen mineralization and litter decomposition, which may serve as useful indices of model performance. The sign and magnitude of these response ratios were incorrectly predicted by the models in under both warming
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1423 1424 1425 1426 1427 1428 1429 1430 1431 1432 1433	4.4 Overall Recommendations We have demonstrated here that despite some experimental drawbacks, the underlying biogeochemical mechanisms of CLM-CN and CLM-Century are insufficient to accurately reproduce the observations of a number of high-latitude perturbation experiments. However, we can identify several metrics from the meta-analyses, including nitrogen mineralization and litter decomposition, which may serve as useful indices of model performance. The sign and magnitude of these response ratios were incorrectly predicted by the models in under both warming and nitrogen addition. This error in the sign of the response also occurred for simulated belowground respiration under nitrogen addition, where the model was

1434	unable to capture the detrimental impact of very high nitrogen concentrations. In
1435	contrast, the SOM response under temperature and nitrogen perturbations appears
1436	to be a poor metric to benchmark the models, possibly owing to the large size and
1437	undefined composition of the soil organic matter stock.
1438	Future development of biogeochemistry representation in CLM should focus
1439	on improvements to the nitrogen cycle. Recent work has shown that specific
1440	modifications to different nitrogen cycle pathways (e.g., redox cycling, plant-
1441	microbial interactions) can improve the correspondence between model predictions
1442	and observational data (Thomas et al., 2013a). Development should also may focus
1443	on improved kinetics (e.g., equilibrium chemistry approximations, (Tang and Riley,
1444	2013) to regulate competition for nutrients between biotic and abiotic sinks (e.g.,
1445	plants, microbes, minerals) as an alternative to the current allocation schemes of
1446	CLM-CN (Thornton et al., 2007). In addition, the integration of dissolved organic
1447	nitrogen cycling as a nutrient source for microbes and plants appears to be an
1448	important source of nitrogen in high-latitude soils (Hobbie et al., 2009; Weintraub
1449	and Schimel, 2005). However, insufficient data were available to include DON as a
1450	response factor in the meta-analysis.
1451	The lack of explicit coupling between plant functional types (PFT) and
1452	belowground microbial ecosystems in the model fails to capture the importance of
1453	this interaction for carbon and nutrients cycling and SOM stability. The PFT concept
1454	could be further extended to characterize differential belowground carbon
1455	allocation (Street et al., 2013). In addition, symbiotic relationships between
1456	different plants and mycorrhizal fungi can increase nutrient acquisition (Hobbie et

1457	al., 2009), by facilitating nitrogen fixation (Nasto et al., 2014), and phosphorus
1458	acquisition (Smith et al., 2011), thereby increasing photosynthetic rates (Jia et al.,
1459	2004). Improving and expanding the definition of the PFT to include these
1460	associations may serve to improve coupling between nutrient cycling with
1461	belowground biogeochemistry.
1462	Finally, while the magnitudes of nitrogen added to tundra soils were very
1463	high, the threshold relationship (Fig. 4) that describes the alleviation of nitrogen
1464	limitation and stimulation of ecosystem processes at low concentrations from their
1465	inhibition at high nitrogen concentrations has support from previous studies (Knorr
1466	et al., 2005). However, mechanisms have not yet been integrated in the model to
1467	capture this range of responses. The model should be able to reproduce the impact
1468	of high nitrogen concentrations associated with agriculture soils, and more work is
1469	required to further characterize this threshold effect. It is unlikely, however, that the
1470	model-predicted linear relationship between nitrogen availability and ecosystem
1471	processes will, in general, be true.
1472	
1473	5 Summary and conclusions
1474	We have shown that certain mechanisms poorly represented in land models,
1475	as highlighted by ecological meta-analysis, can undermine conclusions regarding the
1476	stability of high-latitude soil carbon. We found that two versions of CLM
1477	biogeochemistry (1) poorly replicated coupling of the aboveground and
1478	belowground components of the carbon cycle; (2) poorly represented nitrogen

1479	cycling; (3) inaccurately grouped belowground processes, and (4) insufficiently	
1480	represented plant community dynamics.	
1481	The use of a meta-analysis to benchmark models has a distinct advantage of	
1482	aggregating the response of a number of different climate change experiments	
1483	across spatial and temporal scales to converge upon an average ecosystem or biome	
1484	response. This aggregation reduces the weight that any one study has on the	
1485	development of a model benchmark metric. This approach is particularly valuable in	
1486	ecosystems in which a large number of studies have been performed (e.g.,	
1487	temperate systems, (Lu et al., 2013). However, we also caution that the field	
1488	experiments used in a benchmarking meta-analysis must be carefully chosen. We	
1489	demonstrated the utility of benchmarking land models using studies and	
1490	measurements that attain a realistic ecosystem response to warming, and the	
1491	difficulties associated with comparing model performance against nitrogen addition	
1492	studies that do not replicate conditions under current, or anticipated future climate.	
1493	Υ	
1494	Author contribution	
1495 1496 1497 1498 1499	NJB and WJR designed the experiment. NJB develop the meta-analysis. JYT developed model perturbation approach and carried out the simulations. NJB analyzed the results and wrote the manuscript with input from WJR and JYT. Acknowledgements	
1500 1501	We acknowledge the constructive comments of two anonymous reviewers that improved this manuscript. This research was supported by the Director. Office of	

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 Ecosystems Experiments (NGEE Arctic) and the Regional and Global Climate

1505 Modeling (RGCM) Program.

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

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

- Figure 3: Relationship between GPP and heterotrophic respiration in warmed plots.
- Data points from the graph also represent the duration of warming. Each point
- represents the effect size expressed as a percentage and the calculated bootstrapped
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- variance (across the x and y axis). Figure 4: The effect of increasing N-addition on (a) Belowground respiration, and (b) microbial (i.e., bacterial + fungal) biomass.











