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17 **A systemic overreaction to years versus decades of warming in a**
18 **subarctic grassland ecosystem**

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49 **Summary**

50 Temperature governs most biotic processes, yet we know little about how warming affects whole
51 ecosystems. Here we examined the responses of 128 components of a subarctic grassland to 5-8
52 or >50 years of soil warming. Warming of >50 years drove the ecosystem to a new steady state
53 possessing a distinct biotic composition and reduced species richness, biomass and soil organic
54 matter. However, the warmed state was preceded by an overreaction to warming, which was
55 related to organisms' physiologies and was evident after 5-8 years. Ignoring this overreaction
56 yielded errors of more than 100% for 83 variables when predicting their responses to a realistic
57 warming scenario of 1 °C over 50 years, although some, including soil carbon content, remained
58 stable after 5-8 years. This study challenges long-term ecosystem predictions made from short-
59 term observations, and provides a framework for characterising ecosystem responses to sustained
60 climate change.

61 **Main Text**

62 Ecosystems are mosaics of plants, animals and microorganisms that, when undisturbed, interact in
63 a dynamic equilibrium (steady state) with each other and the physical environment connecting
64 them^{1,2}. Climate warming has been repeatedly shown to affect many biota and their interactions³⁻⁵,
65 often with consequences for ecosystem functioning^{6,7}. Yet most observations of warming effects on
66 ecosystems come from subsets of taxa^{8,9}, interactions¹⁰ or processes¹¹⁻¹³, and we know little about
67 the overall trajectory of ecosystems experiencing climate change. Indeed, notable exceptions to
68 this rule have largely focussed on carbon cycle processes¹²⁻¹⁴, and attempts to step beyond single
69 metrics of ecosystems have relied on composite proxies (for example, community biomass^{2,15,16}) or
70 *a priori* decisions about desired baseline conditions¹⁷, both of which ignore positive or negative
71 covariance^{12,18-20} among interacting components and risk distorting the view of an ecosystem's
72 steady state. No coherent framework exists to describe the interplay between the biotic and abiotic
73 components of a warming ecosystem, leaving us unable to accurately forecast the future of
74 ecosystems following decades to centuries of climate change.

75

76 An ecosystem's relationship with temperature can take one of four forms, which can be
77 conceptualised by resistance-resilience theory²⁰. First, an ecosystem may be entirely resistant to
78 temperature change. Second, an ecosystem may react rapidly and permanently to warming (low
79 resistance, low resilience). Third, an ecosystem may initially resist warming, but be driven to an
80 altered state by sustained or intense warming (high resistance, low resilience). Fourth, an
81 ecosystem may react strongly to the onset of warming, but recover under prolonged warming (low
82 resistance, high resilience). Both the duration and magnitude of warming will influence the nature
83 of this relationship, in that warming of high intensity may result in a faster transition between an
84 ecosystem's ambient and warmed states. However, to date no observations have allowed direct
85 comparison of how the numerous different components of an ecosystem react to temperature
86 change, if at all, or in what sequence. This is compounded by the short lifetime of ecological
87 experiments, most of which are less than 10 years old^{12,13,21} and typically fall short of known lags
88 and demographic processes in ecological systems^{18,19}. There is thus a pressing need to assess

89 warming effects on multiple components of an ecosystem collectively, and to examine their
90 persistence over timescales relevant to Earth's systems.

91

92 We used 128 measured variables representing a wide range of biotic (plants and soil organisms)
93 and abiotic properties, pools and processes of a subarctic grassland to make a comprehensive,
94 decadal-scale assessment of warming effects on an ecosystem. We exploited the longest known *in*
95 *situ* warming experiment²², which captures at least 50 years of soil warming (hereafter >50 years,
96 long-term) using geothermal gradients (0 to 18 °C above ambient temperature throughout the soil
97 profile), coupled with similar geothermal gradients capturing 5-8 years of warming in the same
98 landscape (hereafter 5-8 years, short-term). The large, stable, high-resolution temperature
99 gradients and long warming duration offered by geothermal systems make them uniquely placed to
100 give detailed mechanistic insight into the responses of ecosystems to sustained warming. In 2008,
101 new geothermal gradients emerged in the same grassland as the long-term warmed gradients with
102 similar ambient control plots, allowing us to compare the responses of the same ecosystem to 5-8
103 years versus >50 years of warming. Our approach was threefold. We first characterised how the
104 ecosystem had reacted to >50 years of warming. We then determined whether the ecosystem
105 showed the same response after 5-8 years of warming. Finally, we used these responses and
106 associations between individual variables to construct a framework describing how warming
107 affected the whole ecosystem.

108

109 **Ecosystem response to >50 years of warming**

110 We represented the ecosystem as the first axis (principal component; PC1) of an empirical
111 orthogonal function (EOF) containing all observations and combinations of warming intensity and
112 duration (see Methods). PC1 explained 33.7% of total variance, which was more than double the
113 variance collectively explained by PC2 and PC3 (8.8% and 6.2%, respectively; see Supplementary
114 Information). The variables with the highest loadings on PC1 described pools and processes
115 throughout the plant-soil system, including the soil carbon stock, large water-stable soil
116 aggregates, soil bacterial and fungal biomass, soil microbial community composition and plant
117 stoichiometry, phenology and species richness (Supplementary Table S1). PC1 was thus a good

118 representation of the ecosystem, but could not have been embodied by a single variable or several
119 variables from the same subsystem (for example, aboveground biomass^{2,15}). We found that PC1
120 was affected strongly by warming (LR = 68.87, df = 1,7, N = 59, $P < 0.0001$), but the nature of its
121 response depended on warming duration (LR = 9.89, df = 1,9, N = 59, $P = 0.0071$). After >50
122 years, warming had a linear effect on the ecosystem (Fig. 1a). This held true for warming up to 18
123 °C, encompassing and even widely surpassing the most severe climate scenarios for the next 300
124 years²³. As such, the ecosystem did not resist sustained warming, but instead changed linearly
125 with warming intensity, and no tipping points²⁴ in ecosystem structure or function were apparent
126 with warming up to 18 °C.

127

128 **Ecosystem response to 5-8 years of warming**

129 We used the response to >50 years of warming as a benchmark model for contrasting short-term
130 and long-term warming effects on the ecosystem. Ambient temperature plots were similar between
131 short-term and long-term warmed grasslands (see Methods), and most (92 of 128) variables
132 shared the same relationship with temperature after short-term and long-term warming (see below;
133 Supplementary Table S1). As such, we considered the 5-8 year warmed ecosystem to represent
134 an intermediate state that will converge on the long-term response after >50 years. Despite this,
135 we found that short-term warming had a different (LR = 9.89, df = 1,9, N = 59, $P = 0.0071$), non-
136 linear (Fig. 1b), effect on the ecosystem, whereby 5-8 years of warming up to 14 °C had stronger
137 effects on PC1 from the same EOF than >50 years of warming (Fig. 1c). This stronger short-term
138 response was not a symptom of greater variability in the ecosystem's initial relationship with
139 warming, since coefficients of variation were consistent between short-term and long-term warmed
140 transects when calculated either for PC scores or for variables individually (Supplementary Figs 4
141 & 5). These results demonstrate that the ecosystem did not resist warming on either timescale,
142 and also that it overreacted to warming in the short-term. This overreaction was evident after 5-8
143 years of warming, but was lost entirely after >50 years. Thus, while the ecosystem remained
144 different from control plots following >50 years of warming, it recovered partially from its initial
145 reaction over 8 to 50 years. While temporary warming effects on components of ecosystems are
146 not uncommon^{1,25}, we show here that overreactions to warming are systemic because they were

147 detected in the most important axis of variation from a large set of ecosystem state and process
148 parameters. Moreover, warming effects were sustained well beyond the lifetime of such an
149 overreaction, not lost over periods of months or years (for example, ref. 25).

150

151 **Grouped variables and their responses to warming**

152 We grouped variables by their relationships with temperature to explore their individual roles in the
153 overreaction from the ecosystem. Variables ranged from being unresponsive to warming (32% of
154 variables, 16 plant-related, 8 microbe-related, 15 soil properties, 2 ecosystem fluxes; Extended
155 Data Fig. 1) to showing one of three response types (temporally consistent, overreacting, under-
156 reacting; Fig. 2), which we summarised using the first PCs of EOFs performed separately on each
157 group. Considering positive (Fig. 2a-c) and negative (Fig. 2d-f) relationships together, 15% of
158 variables (11 plant-related, 4 soil biota-related, 4 soil properties) responded more strongly to
159 warming of 5-8 years than >50 years (Fig. 2b,e). Although these variables were only a subset of
160 those measured, they were responsible for eliciting the same warming response from the EOF of
161 the full ecosystem. These variables included ephemeral increases in microbial activity¹, plant
162 phenology²⁶ and plant carbon to nitrogen ratios, temporary shifts in some aspects of soil fungal
163 community composition²⁷ and attenuating losses of root, soil fungal and soil bacterial biomass (Fig.
164 3b,e). Thus, while the ecosystem as a unit overreacted to warming, its response was governed by
165 a subset of components therein. Overreacting variables almost exclusively (15 of 19 variables)
166 described biotic pools and processes, yet none are measures classically used to represent
167 ecosystem stability or functioning^{2,15,16} and most are absent from even the most comprehensive
168 assessments of warming effects on ecosystems^{12-14,28}. It is clear from this finding that an
169 ecosystem's biota play a fundamental role in dictating the temporal variability of its response to
170 warming, but this role is often overlooked by *a priori* decisions about which components of
171 ecosystems to track over time.

172

173 We found that 39% of variables (17 plant-related, 9 soil biota-related, 24 soil properties, 1
174 ecosystem flux) displayed the same response type after 5-8 years and >50 years of warming (Fig.
175 2a,d). This group included rapid and temporally consistent shifts in soil abiotic properties, the

176 composition of plant and soil microbial, and particularly bacterial, communities²⁷ and declines in
177 the soil carbon stock and other organic matter pools²⁹ (Fig. 3a,d). These variables did not reflect
178 the ecosystem's overreaction to warming, but instead were stable after 5-8 years. Among this
179 group were variables that described aspects of community composition and carbon cycling, raising
180 confidence in existing assessments of warming-induced changes to ecosystem community
181 structure⁸ and soil carbon^{12,13}. A final smaller group (13% of variables, 6 plant-related, 3 microbe-
182 related, 8 soil properties) resisted 5-8 years, but not >50 years, of warming (Fig. 2c,f), and
183 represented apparently buffered changes to some aspects of plant metabolism³⁰, stoichiometry
184 and growth, alongside lagged declines in the richness of plant and soil fungal communities²⁷ (Fig.
185 3c,f). Short-term observations clearly underplay the influence of sustained warming on such
186 variables. For example, we underestimated plant species losses by 6 to 11 species over 50 years
187 of warming if we only used short-term data (see below). This prediction does not consider the
188 arrival of novel plant species in the community, which may mask losses of extant species, but is
189 more than the total species loss expected in similar ecosystems over the same timeframe³.

190

191 **A framework for the ecosystem's response to warming**

192 Our findings collectively suggest that the ecosystem had reached a new steady state after >50
193 years of warming, and that this steady state was dependent on warming intensity. This is because
194 temporally consistent changes occurred to most components of the ecosystem (Fig. 2a,d) despite
195 ephemeral (Fig. 2b,e) and delayed (Fig. 2c,f) changes to others, and the short-term response of
196 the ecosystem matched its long-term response at high warming intensities (Fig. 1c). Both imply
197 that the long-term response of the ecosystem is a temporally stable state that will not be surpassed
198 by further warming, barring future evolution³¹ or the arrival of new species in the community¹⁰, and
199 moreover that warming above 14 °C will accelerate the convergence of the ecosystem to its
200 warmed state.

201

202 With this, and the PC scores from the full ecosystem and groups of variables therein, we propose a
203 sequence to the ecosystem's response to warming. First, warming accelerates soil biotic activity¹
204 (for example, decomposition of litter and soil organic matter) and some aspects of plant physiology

205 (for example, minimum NDVI), while also lengthening the growing season²⁶ (Fig. 3a,b,e).
206 Accelerated biotic activity is facilitated by an abundance of soil carbon and nutrients, including
207 previously stable pools of soil organic matter²⁹. Most pools decline rapidly within 5-8 years (Fig.
208 3d), which changes the soil structure. Nevertheless, energy and nutrient exchange among biota,
209 as well as declines in plant and soil microbial and nematode abundance (Fig. 3d,e)^{1,32}, create a
210 transitory phase where elevated biotic activity persists after soil organic matter is depleted (here,
211 still occurring after 5-8 years of warming). Such “ecological inertia” is temporary because it reflects
212 a deficit between ecosystem supply and biotic demand, which selects against species with
213 exploitative resource use strategies (for example, arbuscular mycorrhizal fungi; see ²⁷) and leads
214 to community restructuring over 8 to 50 years (Fig. 3c,f). Our data suggest that long-term
215 persistence under warming may be limited to species with the capacity to adjust their resource use
216 strategies, such as some aspects of metabolism and elemental ratios (Fig. 3b,c,e,f). Ultimately, as
217 the community changes, the ecological inertia is lost and biotic activity, while still accelerated,
218 partially attenuates per unit of soil or area (Fig. 3b,e). The outcome for the ecosystem is the
219 emergence of a new warmed state with a different soil and biotic composition that is again in
220 balance with the biomass and activity of the biota therein (Fig. 1a)¹.

221

222 **General implications**

223 We have shown here that the outcome of warming for this ecosystem is characterised by both an
224 initial reaction and its convergence to a less extreme long-term response. This is important
225 because it suggests that ecosystem responses to warming may only become predictable after
226 several decades, making inferences from short-term experiments challenging^{12,13}. We confirmed
227 this reasoning by testing whether the temporal dynamics we observed had a bearing over
228 predictions of long-term ecosystem change under realistic rates of climate warming. Specifically,
229 we calculated the potential magnitude of error generated when using short-term observations to
230 predict the long-term responses of all measured variables to 1 °C of warming, which corresponds
231 to the magnitude of warming expected over 50 years under the IPCC's most conservative climate
232 change scenario (RCP 2.6). We found that short-term observations yielded predictions that were,
233 on average, 124.6% larger than those arising from long-term observations (Fig. 4), translating to

234 errors of greater than 50% for 113 out of 128 variables and errors of greater than 100% for 83 out
235 of 128 variables. This exercise not only confirmed that large errors can be made when using short-
236 term (here, 5-8 year) responses to make long-term predictions, but also revealed that even small
237 responses to minor warming can have implications for an ecosystem when considered over
238 timescales relevant to climate change. Crucially, without making such calculations we may have
239 wrongly concluded that expected warming in this region will have a negligible effect on the
240 ecosystem, given our observations that warming effects on PC scores became most evident with
241 warming above 3 °C (Figs 1 & 2). We posit that the apparent discrepancy between conclusions
242 drawn from prediction errors (Fig. 4) and PC scores (Figs 1 & 2) arose due to heterogeneity in the
243 ecosystem's biota under ambient temperature conditions³³, leading to uncertainty regarding the
244 ecosystem's pre-warmed state. Indeed, we suggest that the large warming range exploited by this
245 experiment helped to characterise the responses of variables to low intensity warming in the face
246 of such heterogeneity, and to constrain resulting predictions over 50 years of expected climate
247 change. Taken together, these findings provide evidence that warming effects on ecosystems are
248 relevant at low warming intensities, irrespective of uncertainty around them or their associated
249 statistical significance, and advocate consideration of timescales and temperature ranges that go
250 beyond those captured by the majority of existing warming experiments.

251

252 In summary, this study demonstrates a clear need to target indicators of both the temporal
253 dynamics and future warmed state of an ecosystem to fully understand its response to temperature
254 change. Variables related to soil microbial activity and plant phenology, which here overreacted to
255 5-8 years of warming^{1,26}, may be useful metrics for tracking an ecosystem's trajectory following the
256 onset of warming. At the same time, plant and soil community composition and the soil carbon
257 stock, which here were stable after 5-8 years of warming, may be appropriate indicators of the
258 likely state of an ecosystem experiencing sustained warming. Our results originate from a subarctic
259 grassland exposed to two discrete timescales of warming, so we call for future work to interrogate
260 these variables as potential proxies against the existing suite of warming experiments worldwide¹²⁻
261 ^{14,28,33}. We also call for further studies to use such existing platforms to validate the sequence of
262 the warming response we report here, perhaps in the context of a hierarchical response

263 framework³⁴, with particular attention to how species richness in both plant and soil communities
264 changes between 10 and 50 years. In conclusion, the framework presented here is the first
265 timeline for simultaneously mapping many properties, pools and processes onto an ecosystem's
266 overall trajectory under temperature change. It also delivers a list of variables that separately
267 describe the temporal dynamics and warmed state of an ecosystem experiencing long-term
268 warming. We urge consideration of this framework in future assessments of climate warming
269 impacts on ecosystem structure and functioning, including decadal- to centennial-scale feedbacks
270 to Earth's systems.

271 **Methods**

272 **Site description.** We made use of the geothermal warming sites of the ForHot experiment²² near
273 Hveragerdi in Iceland (64°00'01" N, 21°11'09" W, 83-168 m a.s.l.). The experiment is situated on
274 unmanaged grasslands in two valleys dominated by *Agrostis capillaris*, *Ranunculus acris* and
275 *Equisetum pratense* over a Brown Andosol of approximately pH 5.7. One valley has been warmed
276 consistently for at least 50 years, but likely since records began in 1708²² (>50 years; long-term),
277 whereas the other has been warmed since an earthquake on 29 May 2008 (5-8 years; short-term).
278 The valleys each contain five replicated soil warming gradients (50-100 m length) ranging from
279 ambient temperature (mean annual soil temperature: 5 °C) to + 20 °C, all of which are associated
280 with different geothermal sources (see Supplementary Fig. S9). Warming in all gradients is
281 seasonally consistent and has been stable since measurements began in 2013²². To avoid
282 confounding effects of geothermal activity on soil hydrology, half of the gradients were established
283 uphill from a heat source and the other half downhill from a heat source. No substances associated
284 with geothermal activity have been found in any plot since the experiment began^{1,22,27,29}. While
285 short-term and long-term transects were situated in adjacent valleys that shared the same geology,
286 climate and land use history, we caution that it is not possible to eliminate the potential for pre-
287 existing differences between valleys to have influenced comparisons between them. Nevertheless,
288 we found no evidence that such differences occurred, for four reasons. First, considering all 128
289 variables together, ambient temperature plots were as similar within the short-term and long-term
290 warmed transects as between them (Euclidean Distances: LR = 1.18, df = 1,3, N = 45, $P =$
291 0.2765). Second, 122 out of 128 variables (95%) did not significantly differ between ambient
292 temperature plots (Bonferroni-adjusted $P > 0.05$ in all cases, N = 10), with only soil small and large
293 macro-aggregate contents, soil sulphur and aluminium concentrations and plant potassium and
294 manganese concentrations differing in baseline conditions between short-term and long-term
295 warmed transects. Third, PC1 scores from the full empirical orthogonal function (EOF) containing
296 all variables and plots (see below) did not differ between the short-term and long-term warmed
297 transects independently of warming intensity and prior to normalising baselines (LR = 0.51, df =
298 1,3, N = 59, $P = 0.4742$). Finally, PC1 scores from the EOF of the full ecosystem not only shared
299 the same pre-warmed state, but also converged on the same state with warming above 14 °C (Fig.

300 1). It is extremely unlikely that any pre-existing differences between valleys would be detectable
301 under minor to moderate warming but be undetectable under ambient conditions or extreme
302 warming. Given this, we considered ambient temperature plots to be equivalent across all
303 transects irrespective of warming duration. While no experimental system is without limitations, our
304 approach overcomes some major criticisms of warming experiments to date^{12,13,21,35}, specifically by
305 considering two timescales of warming throughout the soil profile over a large warming range and
306 in a regression-style design.

307

308 **Data collection & pre-processing.** We collected data representing the per plot relative
309 abundances of 11424 soil bacterial/archaeal operational taxonomic units (OTUs), 1447 soil fungal
310 OTUs, 16 soil microbial phospholipid fatty acid markers, 43 plant species and 52 metabolites from
311 two plant species, as well as another 110 variables representing other properties, pools and
312 processes of the plant and soil system (Supplementary Table S1). All measurements were taken
313 between 2013 and 2016 and expressed according to standard protocols (see Supplementary
314 Table S3). Response variables with more than 50% missing values were removed (19 variables).
315 The four-year sampling period was small compared to the difference between 5-8 years and >50
316 years of warming, which was a minimum of 42 years. Nevertheless, climatic variation unrelated to
317 the warming transects resulted in interannual variability in some multi-year measurements (see
318 Supplementary Information). We accounted for this by measuring plant phenology, biomass and
319 ecosystem CO₂ fluxes, which are variables known to be seasonally variable, on multiple dates over
320 the four-year period and expressing each as the plot-level mean of all dates. We also only
321 considered variables collected for all plots within the same year(s). Ecosystem CO₂ flux data were
322 further corrected for unrelated covariance in abiotic variables by expressing them as the residuals
323 of models including photosynthetically active radiation, soil moisture and excess soil temperature
324 variation as explanatory variables (see Supplementary Information). We collapsed multivariate
325 datasets, namely microbial community composition, plant community composition and
326 *Anthoxanthum odoratum* and *Ranunculus acris* metabolism, to three axes of an ordination and a
327 measure of richness each (see Supplementary Information). We standardised the final 128
328 variables by centring around the mean and dividing by two standard deviations, and expressed

329 every variable as the within-grassland difference between plot values and the mean value of
330 ambient temperature plots. This approach yielded three ecosystem states: (i) a non-warmed
331 ecosystem; (ii) the ecosystem following 5-8 years of warming; and (iii) the ecosystem following >50
332 years of warming. Thus, we could characterize the temporal dynamics of warming effects on the
333 ecosystem in a fully replicated design using plots possessing a numerically identical pre-warmed
334 state. Finally, mean summer temperature (MST: May to September, 2013 to 2016) at 10 cm depth
335 was derived from hourly records (HOBO TidbiT V2 Water Temperature Data Loggers; Onset
336 Computer Corporation, USA) in each plot. We expressed warming ($^{\circ}\text{C}$) as the within-transect
337 differences between a plot's MST and the mean MST for ambient plots, and removed one plot with
338 MST warming $>20^{\circ}\text{C}$.

339

340 **Representing the ecosystem.** We expressed the full ecosystem as the first axis (PC) of an EOF
341 containing a total of 128 variables. An EOF is functionally comparable to a Principal Component
342 Analysis but is not constrained by the same assumptions and accepts missing values³⁶. In doing
343 so, we were able to consider a large number of state and process parameters simultaneously, with
344 no *a priori* decisions about their weighting (with the exception of multivariate data, see *Data*
345 *collection & pre-processing*, above) and irrespective of possible covariance among them¹⁷. The
346 EOF yielded a similar ordination to a Principal Coordinates Analysis (PCoA; Extended Data Fig. 2),
347 which is a classical ordination approach that also accepts missing values. PC1 of the EOF
348 explained 33.7% of total variance, with PC2 and PC3 explaining 8.8% and 6.2%, respectively.
349 Given the large decline in explained variance between the first and next axes, we considered PC1
350 scores to be a good representation of the ecosystem, but note that informative warming effects
351 were also found on PC2 and PC3 (see Supplementary Information).

352

353 **Grouping variables by their warming response.** We explored the different types of response
354 exhibited by components of the ecosystem by grouping variables based on their relationships with
355 warming and summarising these groups using separate EOFs. Grouping was performed using a
356 three-step process. First, we used the *P*-values of warming effects and warming \times duration
357 interactions (Supplementary Table S1) with an α cut-off of 0.05 to categorise variables as

358 temporally dynamic ($W \times D: P < 0.05$), temporally consistent ($W \times D: P > 0.05$, $W: P < 0.05$) or
359 unresponsive ($W \times D: P > 0.05$, $W: P > 0.05$). Second, we used coefficients from the same models
360 to attribute a positive or negative direction to warming effects. Finally, we visually inspected
361 temporally dynamic variables to determine whether warming effects were larger or smaller in the
362 short-term versus the long-term, which we described as overreactions or under-reactions,
363 respectively. It is important to note that P -values were used to define a cut-off in the first step of
364 this process, but were not used as evidence of statistically significant warming effects on individual
365 variables. Rather, statistical significance was tested at the group level on PC1 scores from EOFs
366 performed separately on each group (see *Statistical analysis*, below), and was interpreted with
367 reference to the per °C changes of individual parameters reported in Fig. 3 (see *Plotting*
368 *relationships*, below). While grouping based on any criterion is subjective, we used P -values
369 because they are an established metric for examining the probability of biologically meaningful
370 relationships, are functionally equivalent to using likelihood ratios, effect sizes or coefficients and,
371 as opposed to these alternatives, already possess accepted thresholds. Here, we considered an α
372 threshold of 0.05 because histograms of P -value distributions for warming effects and warming \times
373 duration interactions showed that $\alpha = 0.05$ marked a threshold below which the frequency of P -
374 values increased (Supplementary Fig. 6b,d). Despite this, we performed a sensitivity analysis to
375 determine how changing the α cut-off between 0.05 and 0.01 in 0.01 steps would alter the
376 composition of groups (Supplementary Table S4). For variables categorised as temporally dynamic
377 at $\alpha = 0.05$, a change in the threshold to $\alpha = 0.01$ resulted in 9 out of 36 moving to a temporally
378 stable group and 4 out of 36 becoming non-responsive. For variables categorised as temporally
379 stable at $\alpha = 0.05$, a change in the threshold to $\alpha = 0.01$ resulted in 15 out of 76 becoming non-
380 responsive. Despite some reshuffling of variables between groups, PC1 scores from the EOFs
381 performed on separate groups remained numerically similar at all α cut-offs tested (Pearson
382 Product Moment correlation: $r > 0.8$ and $P < 0.0001$ in all cases; Supplementary Fig. S7), meaning
383 that the impact on the grouping process was negligible and general patterns of over- and under-
384 reactions held true irrespective of the cut-off chosen. We thus proceeded with the groupings
385 arising from the most inclusive α threshold of 0.05, but caution that the membership of a variable to

386 a particular group is not definitively proven and there is a risk of misclassification for a small
387 number of variables (Supplementary Table S4). This approach yielded a total of seven groups
388 representing positive and negative temporally consistent, overreacting and under-reacting
389 responses to warming, in addition to the unresponsive group.

390

391 **Statistical analysis.** We used generalized least squares (GLS) models to determine the effects of
392 warming intensity ($^{\circ}\text{C}$ above ambient MST), warming duration (transects warmed for 5-8 or >50
393 years) and their interaction on the PC1 scores from the EOF representing the full ecosystem, as
394 well as on the PC1 scores from the EOFs representing different groups of variables therein
395 (Supplementary Table S2). We also used GLS models with the same structure to generate *P*-
396 values for effects of warming intensity, warming duration and their interaction on variables
397 individually (Supplementary Table S1), but note that statistics performed on individual variables
398 were used only to assign variables to groups (see *Grouping variables by warming response*,
399 above) and no corrections were made for multiple testing. While the frequency of significant *P*-
400 values observed for warming and warming \times duration effects was higher than expected based on
401 chance alone (Supplementary Fig. S6a,c), we advise against interpreting effects on individual
402 parameters without considering further *P*-value corrections. GLS models were used so that, where
403 necessary, we could account for unequal variance in explanatory variables. We scrutinized GLS
404 model fits using residuals versus fitted values plots, histograms of residuals and boxplots of
405 residuals against individual explanatory variables. In all cases, models included warming as a
406 second-order polynomial, which was simplified to a linear term if it was non-significant ($P > 0.05$).
407 Test statistics were obtained using sequential single-term deletions followed by likelihood ratio
408 tests between models including and excluding explanatory terms.

409

410 **Plotting relationships.** We plotted PC1 scores from all EOFs against warming intensity grouped
411 by warming duration. We also derived a new variable to illustrate whether PC1 scores changed
412 more or less under short-term versus long-term warming. Given that exact temperatures differed
413 between all plots, this was achieved using fitted GLS models to predict values for a long-term
414 response using the temperatures from the short-term warmed plots. We then calculated the

415 difference between the short-term response and the expected long-term response, creating a
416 variable representing the reaction to short-term warming. Positive reaction values indicated a
417 larger response to 5-8 years than >50 years of warming, negative reaction values indicated a
418 smaller response to 5-8 years than >50 years of warming, and reaction values of zero indicated no
419 change in the response to warming between 5-8 and >50 years. Finally, we expressed the
420 changes of individual variables under warming using standardised (Fig. 3, graphs) and original-unit
421 (Fig. 3, values in columns) per °C changes over the full warming intensity range.

422

423 **Validating relationships with null models.** We performed a series of empirically-derived
424 simulation analyses based on null models to rule out the possibility that observed effects on PC
425 scores could have been caused by bias introduced through the data handling process. This was
426 necessary for three reasons. First, original data was centred around the within-grassland means of
427 ambient temperature plots. Using mean values alone ignored possible variance in the ambient
428 temperature treatment, which has the potential to yield error in centred values that could amplify or
429 dampen observed differences between warmed and ambient plots. Second, error in the centring
430 process could have been incorporated into the EOF and, in an unlikely worst-case scenario,
431 become the most important axis of variation (PC1) in ordinated data. While linear models formally
432 include a null hypothesis that no relationship between X and Y exists, in light of such potential error
433 it is not necessarily intuitive how PC scores would behave given no relationships with warming
434 intensity or duration. Finally, it is not obvious how error and uncertainty surrounding real
435 relationships with warming and PC scores would together proliferate through calculations of the
436 ecosystem's reaction to short-term warming, which we derived from observed and predicted PC
437 scores. We thus used a simulation analysis to create null models based on 4000 randomised
438 permutations that accounted for these potential sources of error. This was achieved by first
439 calculating the within-grassland upper and lower 95% confidence intervals for ambient treatment
440 mean values and creating four datasets that were centred around each of the four possible
441 combinations of these intervals. Second, for each dataset separately we performed an EOF and
442 created 1000 randomised permutations of the resulting PC scores. This yielded a total of 4000 sets
443 of randomised PC scores that incorporated error arising from the centring process and for which

444 we expected no relationships with warming intensity or duration. Third, we performed GLS models
445 including warming intensity, warming duration and their interaction to predict values for all sets of
446 randomised PC scores in 1 °C steps over a 0 to 20 °C warming range and in each grassland
447 separately. We interpreted these predicted values as a set of 4000 null datasets for the effects of
448 warming intensity and duration on PC scores. We then used randomised PC scores and
449 corresponding predicted values from the same models to calculate the differences between short-
450 term and long-term warmed grassland PC scores across a warming range of 0 to 20 °C (see
451 *Plotting relationships*, above). We interpreted these differences as a set of 4000 null datasets for
452 the reaction of the ecosystem to short-term warming. Finally, we expressed both sets of null
453 models as the 95% confidence intervals of all permutations therein, calculated separately for every
454 1 °C warming step and, in the case of warming effects on PC scores, also separately for
455 grasslands. In doing so, we used the largest possible confidence interval range for each warming
456 step and grassland combination. We visualised 95% confidence intervals of null models as ribbons
457 underlying corresponding figure panels for PC scores of the full ecosystem (Fig. 1) and an
458 additional figure for PC scores of grouped variables (Supplementary Fig. S8). Overall, this process
459 yielded null models that were in all cases unrelated to warming intensity or duration, eliminating the
460 possibility that warming effects on PC scores were an artefact of the data handling process.

461

462 **Prediction errors.** We estimated the potential magnitude of error generated when using short-
463 term observations to predict the responses of all variables to 1 °C of warming. We selected 1 °C
464 because it reflected the magnitude of warming expected under the most conservative IPCC climate
465 change scenario over a 50-year period (RCP 2.6), which is the minimum possible warming
466 duration captured by the long-term warmed transects. We used predicted values from GLS models
467 (see *Statistical Analysis*, above) to estimate the change in each variable between 0 and 1 °C of
468 warming separately for the short-term and long-term warmed transects. We then used these
469 values to derive a prediction error (%) associated with the short-term responses, which we defined
470 as the absolute percent difference between the changes in short-term versus long-term transects:

471

$$\text{Prediction error (\%)} = \frac{|(ST_w - ST_a) - (LT_w - LT_a)|}{|(LT_w - LT_a)|} \times 100$$

472

473 where ST_w and LT_w represent the predicted values for a variable at 1 °C warming in the short-term
474 and long-term warmed transects, respectively, and ST_a and LT_a are the predicted values for the
475 same variable at 0 °C in the short-term and long-term warmed transects, respectively. In doing so,
476 we approximated the magnitude of error generated when making long-term predictions using data
477 from short-term observations, which we plotted using a histogram and boxplot on a \log_{10} scale
478 (Fig. 4).

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548 **Supplementary Information** is linked to the online version of the paper at

549 www.nature.com/nature.

550

551 **Data Availability**

552 Raw sequences (FASTQ format) are accessible through the NCBI Sequence Read Archive (SRA)

553 under accession numbers SRP099121 and SRP075563 for bacteria (16S) and fungi (ITS1),

554 respectively. Other data supporting the findings of this study are available in Figshare with the data

555 DOI doi:10.6084/m9.figshare.9958931.

556

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573

574

575

576 **Author contributions**

577 IAJ, BDS and NIWL established and maintained the field experiment. TWNW, IAJ, AR, BDS and
578 EV conceived the study. TWNW, IAJ, BDS, AR, JP, NIWL, MBahn, MBartrons, CDJ, LF, AG-G,
579 GEG, SM-J, ESO, IO, CP, JP, DR, JS, PS, JLS, SV, HW, KI-M and EV provided data (see
580 Supplementary Table S3 for specific contributions) and/or contributed interpretation. TWNW
581 performed the data analysis and wrote the manuscript in close collaboration with EV, and support
582 from IAJ, JTW, BDS, AR, JP and NIWL.

583

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587

588 **Competing Interests Statement**

589 The authors declare no competing interests.

590 **Figure legends**

591

592 **Figure 1 | Whole-ecosystem responses to soil warming.** Responses of grasslands (N = 59) exposed to (a) long-term
593 (>50 years, yellow) or (b) short-term (5-8 years, red) soil warming. Data are PC1 scores (33.7% explained variance) from
594 a single empirical orthogonal function (EOF) containing 128 variables (see Methods). Statistics and fit lines reflect
595 significance of warming (W), duration (D) and their interaction (W × D), as determined by GLS models (see
596 Supplementary Table 2 for test outputs). (c) The reaction (Δ response) of the ecosystem to short-term warming,
597 calculated as the difference between responses to short-term and long-term warming. Fit line is a loess smoothing
598 function. In all panels, grey ribbons represent 95% confidence intervals of a null model testing for artefacts arising
599 through data handling (see Methods).

600

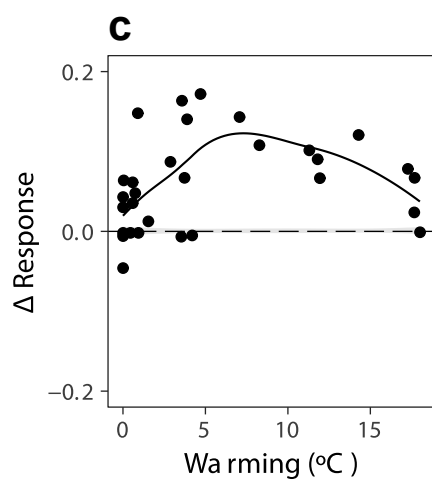
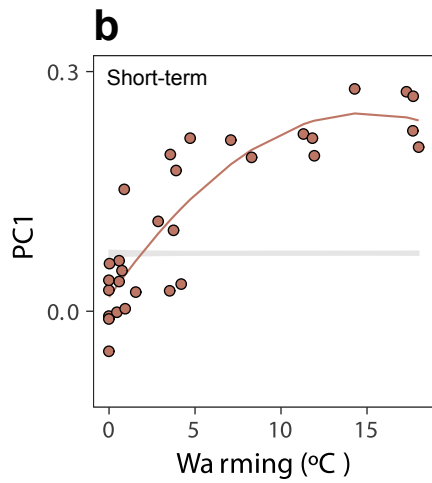
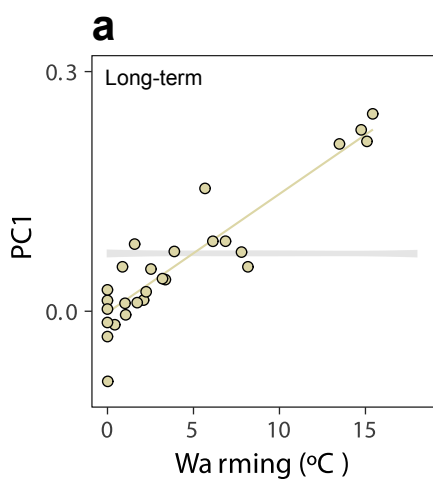
601 **Figure 2 | Response shapes under soil warming.** (a-c) Positive and (d-f) negative responses of grouped variables
602 exposed to long-term (>50 years, yellow/dashed; LT) or short-term (5-8 years, red/solid; ST) warming (N = 59 in all
603 cases). Data are PC1 scores from EOFs performed separately on groups displaying (a,d) stable (ST = LT), (b,e)
604 overreacting (ST > LT) and (c,f) under-reacting (ST < LT) responses to warming (see Fig. 3 for individual responses).
605 Statistics and fit lines reflect significance of warming (W), duration (D) and their interaction (W × D), as determined by
606 GLS models (see Supplementary Table 2 for test outputs). Yellow/dashed and red/solid lines illustrate LT and ST
607 responses, respectively, and black lines illustrating the response where no significant W × D interaction occurred. Inlays
608 show reactions (Δ responses) to ST warming, calculated as for Fig. 1c.

609

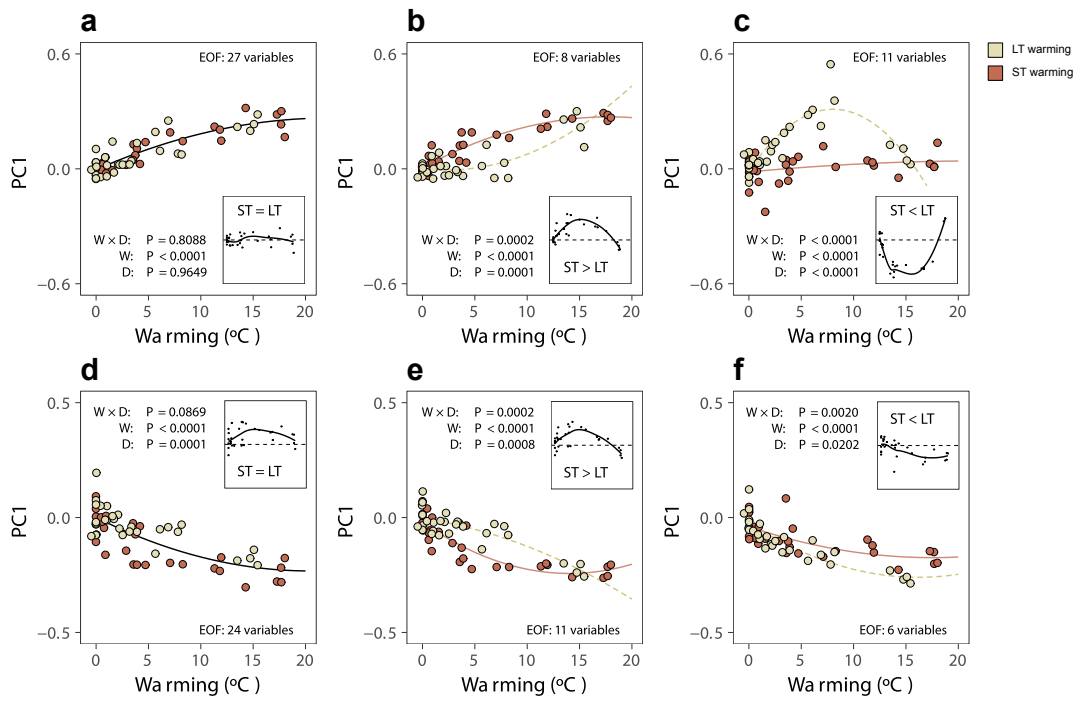
610 **Figure 3 | Variable groups and their responses to warming.** Positive (left) and negative (right) responses of
611 ecosystem properties, pools and processes to short-term (ST; 5-8 years) and long-term (LT; >50 years) warming (N = 20
612 in all cases). Variables were manually grouped by relationships with temperature (see Supplementary Table S1): (a,d)
613 permanent/stable (ST=LT; orange), (b,e) overreactions (ST>LT; red), (c,f) underreactions/buffered (ST<LT; blue).
614 Graphs show standardised per °C changes with warming up to 20 °C, with points right and left of zero (dotted-line)
615 indicating increases (red) and decreases (blue), respectively, and diamonds indicating means. Columns show a
616 variable's within-group importance (that is, relative loading; %) and change per °C in original units (where "=" means no
617 difference between ST and LT warming). See Supplementary Table S1 for full variable names.

618

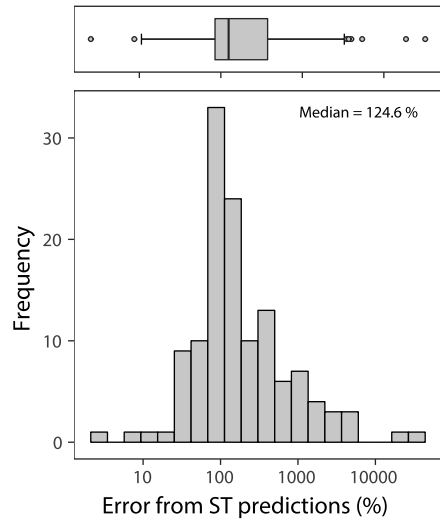
619 **Figure 4 | Prediction errors from short-term observations.** The distribution of error (%) generated when making long-
620 term predictions from short-term observations (N = 128). Error was calculated as the absolute discrepancy between long-
621 term and short-term responses of all 128 variables to 1 °C of warming, reflecting the change expected over 50 years
622 under the most conservative IPCC climate scenario (RCP 2.6). The x-axis is on a \log_{10} scale, with a value of 100
623 indicating a magnitude of error of 100%.

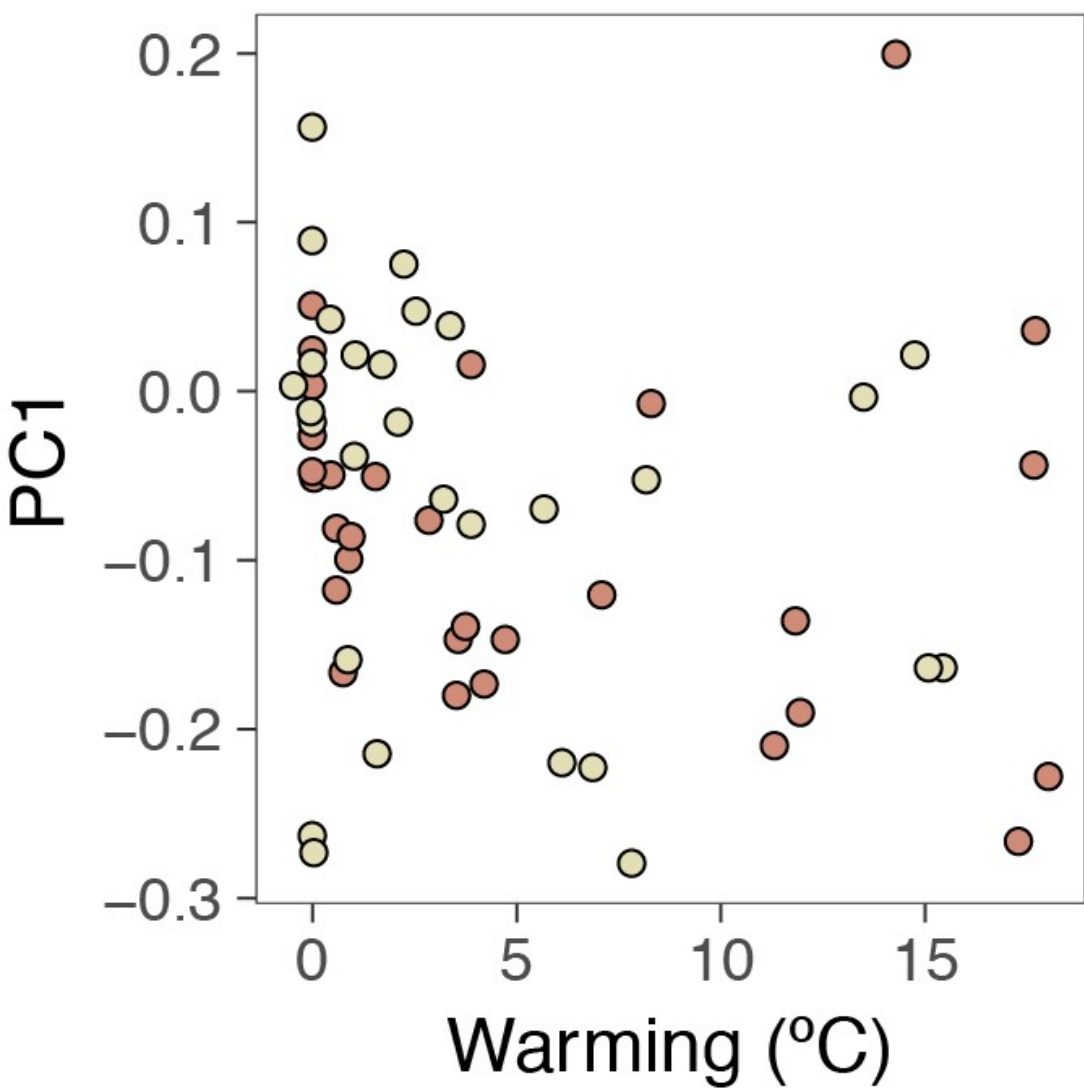


W x D: $P = 0.0071$
W: $P < 0.0001$
D: $P = 0.0010$
PC1 var: 33.7 %



	Response to warming			Loading	Change per °C				Response to warming			Loading	Change per °C						
	ST		LT		(%)	ST			LT	units	ST		LT	(%)	ST		LT	units	
POSITIVE RESPONSE TO WARMING																			
	a																		
Microbe composition (#1)				7.0	0.01	=													
Bacterial composition (#1)				6.7	0.01	=													
Moss C				6.4	0.21	= %													
Length of season (NDVI)				6.3	1.44	= days													
Decomposition (red tea)				5.7	0.54	= % y ⁻¹													
Plant Zn				5.6	0.61	= g kg ⁻¹													
Soil silt/clay (%)				5.4	0.18	= %													
Soil pH (in H ₂ O)				5.3	0.06	=													
Soil sand (grain size)				5.0	1.84	= %													
Soil small MI (%)				5.0	0.69	= %													
Plant Cu				4.7	0.17	= g kg ⁻¹													
Monocot C				4.3	0.09	= %													
Litter N				4.1	0.01	= %													
Plant K				4.1	0.19	= g kg ⁻¹													
Soil bulk density				3.4	0.02	= g cm ⁻³													
Net CO ₂ exchange				3.3	0.06	= μmol CO ₂ m ⁻² s ⁻¹													
Soil Fe (PRS)				2.6	0.66	= μg cm ⁻² y ⁻¹													
Soil Cu (PRS)				2.5	0.11	= μg cm ⁻² y ⁻¹													
Soil silt/clay (dm ⁻¹)				2.5	0.39	= %													
Soil pH (in KCl)				2.4	0.02	=													
A. odoratum metabolism (#1)				2.3	0.38	=													
Soil Ca (PRS)				2.2	51.6	= μg cm ⁻² y ⁻¹													
Plant composition (#2)				1.0	0.01	=													
Fern biomass				0.8	3.23	= g m ⁻²													
R. acris metabolism (#2)				0.7	0.15	=													
Bacterial composition (#2)				0.5	1 e-3	=													
Plant composition (#1)				0.4	3 e-3	=													
b																			
Dicot CN				20.0	1.61	-0.31													
Decomposition (green tea)				13.8	0.96	0.05	% y ⁻¹												
Fungal composition (#1)				13.7	0.05	1 e-3													
Plant Na				13.4	0.02	0.01	g kg ⁻¹												
Monocot C:N				12.1	1.32	0.41													
Soil small Ma (%)				10.9	3.02	0.02	%												
Plant min. NDVI				10.5	0.01	3 e-3	NDVI												
Litter C				5.6	0.06	-0.54	%												
c																			
Plant S				14.7	0.03	0.08	g kg ⁻¹												
R. acris metabolite richness				14.5	-2 e7	8 e7	#												
Soil NH ₄ -N (PRS)				12.8	-0.02	0.63	μg cm ⁻² y ⁻¹												
Moss N				12.5	0.01	-0.01	%												
Fungal composition (#2)				12.1	-1 e-3	0.02													
R. acris metabolism (#1)				9.9	-0.06	0.77													
A. odoratum growth				7.2	-0.07	0.19	RNA-DNA												
Soil P (PRS)				6.9	0.09	0.10	μg cm ⁻² y ⁻¹												
Fungal composition (#3)				5.3	-0.01	0.01													
Soil amino acids				2.8	-0.13	0.18	μg N g ⁻¹												
Soil DOC				1.2	-2.21	3.06	μg C g ⁻¹												
NEGATIVE RESPONSE TO WARMING																			
	d																		
Topsoil C stock				7.5	-1.79	=	ton ha ⁻¹												
Soil large WS-Ma N				6.9	-0.03	=	%												
Soil small Ma C				6.2	-0.41	=	%												
Soil small Ma N				5.9	-0.04	=	%												
Soil small MI N				5.7	-0.04	=	%												
Soil silt/clay N				5.6	-0.03	=	%												
Soil small Mi C				5.6	-0.42	=	%												
Soil silt/clay C				5.4	-0.26	=	%												
Nematode fungivore #				4.9	-0.03	=	# × 10 ³ m ⁻²												
Soil Zn (PRS)				4.9	-0.02	=	μg cm ⁻² y ⁻¹												
Dicot C				4.2	-0.07	=	%												
Nematode total #				4.1	-0.19	=	# × 10 ³ m ⁻²												
Litter biomass				4.0	-0.05	=	g kg ⁻¹												
Plant Ca				3.9	-7.42	=	g m ⁻²												
Soil silt (grain size)				3.7	-1.64	=	%												
Soil clay (grain size)				3.3	-0.20	=	%												
Nematode herbivore #				3.3	-0.09	=	# × 10 ³ m ⁻²												
Nematode bacterivore #				3.0	-0.05	=	# × 10 ³ m ⁻²												
Soil water content				2.8	-0.42	=	%												
Bacterial OTU richness				2.7	-18.4	=	# OTUs												
Soil POM (dm ⁻¹)				2.4	-0.14	=	%												
Soil sand (dm ⁻¹)				2.1	-0.25	=	%												
Plant Fe				1.2	-1.59	=	g kg ⁻¹												
Moss C:N				0.9	-0.05	=													
e																			
Start of season (NDVI)				12.0	-2.13	-0.77	day of year												
Fungal biomass				11.3	-3.81	-1.93	nmol g ⁻¹												
Soil large WS-Ma C				10.9	-0.62	-0.10	%												
Bacterial biomass				10.6	-15.4	-9.54	nmol g ⁻¹												
Dicot N				10.5	-0.13	0.01	%												
Topsoil N				9.1	-0.04	-0.03	%												
Topsoil root biomass				8.1	-67.5	-26.9	g m ⁻²												
Subsoil root biomass				7.8	-35.0	1.32	g m ⁻²												
Monocot N				7.8	-0.03	-0.02	%												
Soil large WS-Ma (%)				7.0	-4.44	-0.35	%												
Plant NDVI range				4.8	-0.01	2 e-3	NDVI												
f																			
Plant species richness				37.2	-0.45	-0.70	# species												
Topsoil C				28.9	-0.44	-0.34	%												
Soil K (PRS)				14.5	-0.60	-1.18	μg cm ⁻² y ⁻¹												
Soil Mg (PRS)				8.7	10.57	-5.74	μg cm ⁻² y ⁻¹												
Soil S (PRS)				6.3	4.69	-0.72	μg cm ⁻² y ⁻¹												
Fungal OTU richness				4.4	8.02	-5.21	# OTUs												

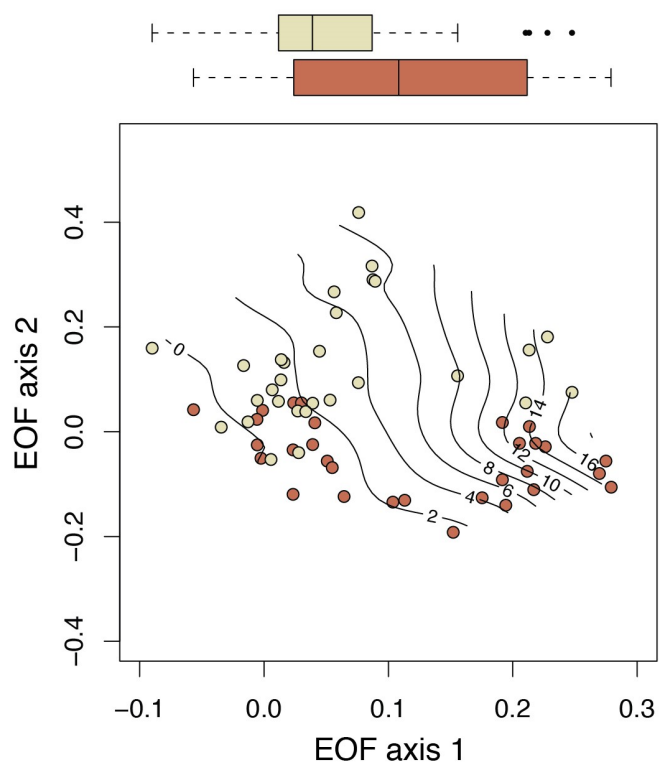




W x D: $P = 0.9097$

W: $P = 0.0858$

D: $P = 0.4580$

a**b**