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Methods

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A hierarchical, multivariate meta-analysis approach to synthesizing global change experiments

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22 Summary

- Meta-analyses enable synthesis of results from globally distributed experiments to draw general
- 24 conclusions about the impacts of global change factors on ecosystem function. Traditional meta-
- analyses, however, are challenged by the complexity and diversity of experimental results. We

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- 26 illustrate how several key issues can be addressed via a multivariate, hierarchical Bayesian meta-27 analysis (MHBM) approach applied to information extracted from published studies.
- We applied an MHBM to log-response ratios for aboveground biomass (AB, n = 300),
- belowground biomass (BB, n = 205), and soil CO₂ exchange (SCE, n = 544), representing 100
- 30 studies. The MHBM accounted for study duration, climate effects, and covariation among the AB,
- 31 BB, and SCE responses to elevated CO_2 (eCO₂) and/or warming.
- The MHBM revealed significant among-study covariation in the AB and BB responses to
 experimental treatments. The MHBM imputed missing duration (4.2%) and climate (6%) data,
 and revealed that climate context governs how eCO₂ and warming impact ecosystem function.
 Predictions identified biomes that may be particularly sensitive to eCO₂ or warming, but that are
- 36 under-represented in global change experiments.
- The MHBM approach offers a flexible and powerful tool for synthesizing disparate experimental
 results reported across multiple studies, sites, and response variables.

39 Keywords

Bayesian meta-analysis, climate warming, global change experiments, elevated CO₂, hierarchical
 model, incomplete reporting, multivariate meta-analysis

42 Introduction

43 A plethora of manipulative field experiments have been conducted to evaluate the impacts of various 44 global change factors—e.g., warming, elevated CO₂ (eCO₂), drought, or nitrogen deposition—on ecosystem structure and functioning of intact or managed ecosystems (e.g., Wu et al., 2011; Dieleman 45 46 et al., 2012; Yue et al., 2017a; Gao et al., 2019; Komatsu et al., 2019; Song et al., 2019). Over the decades, global change experiments have been applied via a broad range of approaches and protocols, 47 have tested different ranges and combinations of global change factors, and have been performed in 48 49 diverse environmental contexts. Meta-analyses aim to provide quantitative syntheses of general 50 ecosystem responses across a larger number of independently conducted experiments (Arnqvist & Wooster, 1995; Gurevitch et al., 2018). However, the incoherence across studies (datasets)—in terms 51 52 of, for example, methods used, variables measured and reported, timing of measurements, intensity of 53 measurements (sample sizes) ---- represents a major challenge for meta-analyses (e.g., Spake & 54 Doncaster, 2017; Gurevitch et al., 2018).

Regardless, meta-analysis techniques are being increasingly applied to evaluate global or 55 56 broad-scale responses to experimental manipulations of environmental conditions (e.g., Arnqvist & 57 Wooster, 1995; Koricheva & Gurevitch, 2014). Many meta-analyses evaluate response ratios or 58 related metrics (Koricheva & Gurevitch, 2014) of multiple response variables (e.g., above- and 59 belowground biomass, soil carbon and nitrogen, CO₂ fluxes) (Wu et al., 2011; Dieleman et al., 2012; 60 Yue et al., 2017a; Song et al., 2019), but they typically treat these variables as independent. The 61 assumption of independent response variables ignores the potential for covarying or coordinated 62 responses (Nakagawa & Santos, 2012), and the fact that individual field experiments may produce 63 data on simultaneously measured variables. While standard multivariate modeling approaches can be 64 leveraged to account for correlations among response variables within a meta-analysis (Nakagawa & 65 Santos, 2012; Komatsu et al., 2019), such multivariate meta-analyses are rare (Nakagawa & Santos, 66 2012). For example, Pappalardo et al. (2020) reviewed 96 published meta-analyses focused on the 67 ecological impacts of global change or climate change factors; 34 of the 96 studies analyzed multiple 68 response variables, but only three employed a multivariate meta-analyses approach.

Moreover, while existing meta-analyses provide quantitative insight into overall responses
across multiple studies (e.g., Arnqvist & Wooster, 1995)—e.g., the overall effect of eCO₂ on soil

71 carbon (Hungate et al., 2009), plant biomass (Terrer et al., 2016), or plant C:N:P stoichiometry (Yue 72 et al., 2017a)—it is difficult to fully account for site-level variables that partly explain differences 73 among sites. Even if such meta-analyses do incorporate site-level covariates (e.g., Martin *et al.*, 2018; 74 Falaschi et al., 2019), potentially important covariates are unlikely to be available for each study 75 (Ogle et al., 2013). Such missing information—related to issues of incomplete reporting (Gurevitch & 76 Hedges, 1999; Ogle et al., 2013; Vicca et al., 2018)—often leads the researcher(s) to discard records 77 lacking this information (e.g., Gurevitch & Hedges, 1999; Lajeunesse & Forbes, 2003; Shantz et al., 78 2016) or to ignore potentially important covariates due to inconsistent reporting across studies (e.g., 79 Vicca et al., 2018).

80 While classical meta-analysis falls short on accounting for multiple response variables, site-81 level covariate data, and non-linear responses to global changes, hierarchical Bayesian modeling 82 approaches can accommodate these issues via multivariate model components, even when faced with 83 incomplete reporting (e.g., Nakagawa & Santos, 2012). Bayesian meta-analysis approaches are 84 relatively new in ecology, with recent examples including evaluations of the impacts of multiple 85 global change factors on plant community composition (Komatsu et al., 2019), the competitive 86 abilities of non-native versus native plant species (Golivets & Wallin, 2018), the effects of nutrient 87 loading on mutualism performance (Shantz et al., 2016), and functional traits of multiple species or 88 functional groups (e.g., Lebauer et al., 2013; Ogle et al., 2013; Ogle et al., 2014; Shiklomanov et al., 89 2020). Komatsu et al. (2019) and Shiklomanov et al. (2020) uniquely employed Bayesian multivariate 90 models to account for potential covariation among multiple responses. However, these studies 91 apparently ignored estimates of uncertainty associated with reported responses, and they did not 92 incorporate incompletely reported covariate data. While these studies represent significant advances 93 towards more flexible and powerful meta-analysis approaches, we are not aware of existing Bayesian 94 meta-analyses that simultaneously accommodate multivariate responses, multiple treatment factors (e.g., both eCO₂ and warming), and study- or site-level covariates that are incompletely reported. For 95 96 example, in the review conducted by Pappalardo et al. (2020), only 3% of the meta-analysis studies used a Bayesian approach, and of this subset, only one meta-analysis employed a multivariate model. 97 98 Here, we address this gap by demonstrating a multivariate, hierarchical Bayesian modeling approach 99 that should advance ecological meta-analyses.

100 To illustrate the approach, we use a database on the responses of multiple ecosystem attributes 101 to eCO₂, warming, or their combined effects, which was previously employed to perform a traditional 102 meta-analysis (Dieleman et al., 2012). The full database contains data summaries—treatment means, measures of uncertainty (standard deviations or standard errors), and limited covariates (e.g., duration 103 104 of each study)—from over 150 manipulative experiments, distributed across a range of ecosystem 105 types and climates. While the database contains information on multiple (at least nine) response 106 variables (Dieleman et al., 2012), we focus on a subset of studies that reported aboveground biomass 107 (AB), belowground biomass (BB), and soil CO₂ exchange (SCE). The goal of this study is to describe 108 and demonstrate a hierarchical, multivariate Bayesian meta-analysis approach using these data. We 109 further illustrate the ability of this approach to produce posterior predictions, which can be used to 110 quantitatively inform future experimental studies. We provide annotated code for this analysis and for 111 a more generalized multivariate meta-analysis (accommodating a flexible number of treatment types).

112 **Description**

113 Database of global change manipulation experiments

114 We utilized a database of global change manipulative experiments (hereafter, the GCME database) 115 originally compiled by Dieleman *et al.* (2012). The GCME database contains information on the 116 responses of multiple ecosystem variables-various biomass and carbon pools and fluxes-to 117 elevated CO_2 (eCO₂), warming, or their combination (eCO₂ × warming). The GCME database focuses on experiments that manipulated eCO₂ only, temperature only, or both, with usually two levels each 118 (e.g., ambient ["control"] versus elevated or warmed ["treatment"]). The database includes some 119 studies that implemented watering or fertilization treatments, usually in combination with eCO₂ 120 121 and/or warming. Here, we focused on the eCO₂ and warming treatments, and restricted the data to 122 ambient (control) moisture and nutrient treatments (i.e., no water or nutrient addition). Most of the data-i.e., treatment means, measures of uncertainty, and covariates (e.g., duration of each study)-in 123 the GCME database were extracted from figures or tables in published journal articles, with some data 124 125 obtained directly from researchers. The database as a whole contains information from >150 126 manipulative experiments ("studies"), distributed across multiple ecosystem types and a range of 127 climates.

128 We focused on three key ecosystem response variables: aboveground biomass (AB),

belowground biomass (BB), and soil CO₂ exchange (SCE) (or, "soil respiration"), and thus extracted
a subset of records from the GCME database (many experiments did not report one or more of these
responses). All extracted records are associated with both control and elevated responses, from which
we derived the log-response-ratios (LRR) of AB, BB, and SCE (described below). The number of
studies and number of records ultimately used in this study are summarized in Figure 1 and Table 1,
respectively.

While some (44%) studies provided both mean annual precipitation (MAP) and mean annual temperature (MAT) data, we used WorldClim data (Fick & Hijmans, 2017) aggregated at a 1 km spatial resolution and matched to the site location to obtain a standardized source of MAP and MAT for each study site, representative of the period 1970-2000. Some studies (6 out of 100) were associated with coordinates that resulted in unrealistic climate data when cross-referenced with the WorldClim database (e.g., grid cell dominated by a water body, or potential error in extracted coordinates), and thus their climate data were treated as missing.

142 **Preparing data for the meta-analysis**

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Given the reported sample means (which are positive-valued for all AB, BB, and SCE records), standard deviations, and sample sizes for the control and "treatment" (e.g., elevated or warmed) groups, we computed the log-response-ratio (LRR) and pooled variance (σ^2) for each LRR record *i* (*i* 146 = 1, 2, ..., 1049) based on Hartung et al. (2008) (Chapter 8):

$$LRR_{i} = \log_{e}\left(\frac{\overline{y}_{i}^{T}}{\overline{y}_{i}^{C}}\right)$$
(1)
$$\sigma_{i}^{2} = S_{i}^{*2}\left(\frac{1}{n_{i}^{T} \cdot (\overline{y}_{i}^{T})^{2}} + \frac{1}{n_{i}^{C} \cdot (\overline{y}_{i}^{C})^{2}}\right)$$
(2)
$$S_{i}^{*2} = \frac{1}{n_{i}^{T} + n_{i}^{C} - 2}\left[\left(n_{i}^{T} - 1\right)\left(S_{i}^{T}\right)^{2} + \left(n_{i}^{C} - 1\right)\left(S_{i}^{C}\right)^{2}\right]$$

149 The *T* and *C* superscripts denote the treatment and control groups, respectively; \overline{y} is the sample 150 mean, *n* is the sample size, and *S* is the sample standard deviation. Separate *n* for the treatment and

151 control groups were not readily available in the GCME database, but the number of sample replicates 152 (*n*) was reported. Thus, we assumed $n^T = n^C = n$, and σ^2 in Eqn (2) simplifies to:

$$\sigma_{i}^{2} = \frac{\left(S_{i}^{T}\right)^{2} + \left(S_{i}^{C}\right)^{2}}{2n_{i}} \left(\frac{1}{\left(\overline{y}_{i}^{T}\right)^{2}} + \frac{1}{\left(\overline{y}_{i}^{C}\right)^{2}}\right)$$
(3)

Equations (1)-(3) are commonly employed by both classical and Bayesian meta-analyses. For the 1049 records considered here (Table 1), all of the required quantities (\bar{y} , *n*, and *S*) were reported in the GCME database; when standard errors (*se*) were reported instead of *S*, then (*S*)² was computed as *n*(*se*²). However, it is common to find published studies that do not report *S*, *se*, or *n* (such studies were excluded from the GCME database, (Dieleman *et al.*, 2012)). Ogle et al. (2013; 2014) show how a Bayesian meta-analysis can accommodate incomplete reporting of *S*, *se*, or *n*, and other imputation methods are also available (e.g., Kambach *et al.*, 2020).

161 Hierarchical, multivariate meta-analysis model description

162 Similar to classical and recent Bayesian approaches, we treated *LRR* and σ^2 (Equations (1) and (3)) as "known" data that we analyzed via a Bayesian meta-analysis model. Again, given that the AB, BB, 163 164 and SCE responses and their associated LRR values may covary at the study level, we simultaneously 165 analyzed these three variables to account for (and estimate) potential covariation among the 166 responses. We also simultaneously analyzed data obtained for all three treatment categories (eCO₂ only, warming only, and $eCO_2 \times warming$), rather than treating these as independent datasets. It is 167 possible that site- and study-level covariates—such as climate and experiment duration—modulated 168 169 the response of AB, BB, or SCE to eCO₂ and/or warming. For example, other studies suggest that experiment duration (e.g., Hungate et al., 2004; Elmendorf et al., 2012; Wang et al., 2014; Mueller et 170 171 al., 2016; Komatsu et al., 2019) and site-level environmental conditions (e.g., He et al.; Elmendorf et al., 2012; Song et al., 2019) affect reported responses to treatment factors. Thus, we accounted for 172 173 potential effects of mean annual precipitation (MAP), mean annual temperature (MAT), their interaction (MAP \times MAT), and experimental duration (Dur) on the reported LRR. 174 175 Our Bayesian meta-analysis model is as follows. First, for record *i*, the likelihood of the LRR

176 data is based on:

| 177 | $LRR_{i} \sim Normal(\mu_{i}, \sigma_{i}^{2})$ | (4) |
|-----|--|----------------|
| 178 | Where <i>LRR</i> and σ^2 are defined in Equations (1) and (3), and treated as "data" or known quan | tities. |
| 179 | Each <i>LRR</i> is essentially "weighted" according to its corresponding variance term, σ^2 . Equation | on (4) |
| 180 | assumes conditional independence—conditional on (or given) the mean response, μ_i , and the | pooled |
| 181 | variance, σ_i^2 —of each variable's computed LRR. We assumed independent likelihoods part | ly |
| 182 | because individual studies (publications) often do not provide information about the covarian | ice |
| 183 | among different response variables, and thus we cannot obtain an analytical estimate of that | |
| 184 | covariance, but we do have estimates of the individual variances, σ_i^2 . However, we accounted | d for |
| 185 | potential correlation among the different response variables at the latent, study level (see Equ | lation |
| 186 | (6)). | |
| 187 | We defined the mean model for the predicted LRR as a linear regression on Dur, MA | P, and |
| 188 | MAT: | |
| 189 | $\mu_{i} = \beta_{\nu(i),s(i),t(i)} + \delta_{\nu(i),t(i)}^{Dur} \cdot Dur_{i} + \delta_{\nu(i),t(i)}^{MAP} \cdot cMAP_{s(i)} + \delta_{\nu(i),t(i)}^{MAT} \cdot cMAT_{s(i)} + \delta_{\nu(i),t(i)}^{Int} \cdot cMAP_{s(i)} + \delta_{\nu($ | (5) |
| 190 | v(i), $s(i)$, and $t(i)$ denote response variable v , study s , and treatment type t associated with rec | ord <i>i</i> , |
| 191 | where, $v = 1$ for AB, $v = 2$ for BB, and $v = 3$ for SEC, and $t = 1$ for eCO ₂ only, $t = 2$ for warm | ning only, |
| 192 | and $t = 3$ for eCO ₂ × warming. The conditional independence assumption, Equation (4), | |
| 193 | accommodates multiple records for a given variable, study, and treatment type; that is, record | ds that |
| 194 | share the same v, s, and t will share the same predicted mean, μ , but they are assumed to be | |
| 195 | conditionally independent given their shared mean. In the model for μ , $\beta_{\nu,s,t}$ represents the stu | udy-level |
| 196 | (latent) LRR for variable v, study s, and treatment type t. The δ parameters represent the effe | ct of Dur, |
| 197 | MAP, MAT, and the MAT×MAP interaction. Note that <i>cMAP</i> and <i>cMAT</i> in Equation (5) rep | oresent |
| 198 | centered values, where $cX = X - mean(X)$, and the mean is computed across all studies. The c | covariate |
| 199 | effects ($\delta_{v,t}$) vary by the covariate of interest (donated by superscripts, e.g., <i>Dur</i> , <i>MAP</i> , <i>MAT</i> , | and Int |
| 200 | (for interaction)), and are estimated for each response variable <i>v</i> and treatment type <i>t</i> . | |
| 201 | We might expect correlation among the three response variables at the study level. So | omewhat |
| 202 | similar to Komatsu et al. (2019), we assigned a multivariate, hierarchical prior to the study-le | evel |
| 203 | effects (β), allowing for potential covariation among the study-level and treatment-type spect | ific AB, |
| 204 | BB, and SCE log-response-ratios: | |
| | | |
| | | |

$$\begin{pmatrix} \boldsymbol{\beta}_{1,s,t} \\ \boldsymbol{\beta}_{2,s,t} \\ \boldsymbol{\beta}_{3,s,t} \end{pmatrix} \sim Normal \begin{pmatrix} \boldsymbol{\beta}_{1,t}^* \\ \boldsymbol{\beta}_{2,t}^* \\ \boldsymbol{\beta}_{3,t}^* \end{pmatrix}, \boldsymbol{\Sigma}_t \end{pmatrix}$$
(6)

206 $\beta_{v,t}^*$ is the overall or global (mean) LRR for variable *v* and treatment type *t*; this quantity is of 207 particular interest, and we evaluated if the corresponding posteriors overlap zero (i.e., significant 208 treatment effect). Σ_t is the 3×3 covariance matrix for treatment type *t* that describes among study 209 variability in the LRR for the different variables (diagonals) and the pairwise correlation among the 210 three study-level response variables (or covariances, off-diagonals), after having accounted for 211 duration and site-level climate.

Following Gelman et al. (2014), we assigned fairly non-informative, standard priors to all remaining parameters, including the δ terms, the β^* terms, and the precision matrices, Σ^{-1} :

$$S_{v,t}^{X} \sim Normal(0,10000)$$

$$\beta_{v,t}^{*} \sim Normal(0,10000)$$

$$\Sigma_{t}^{-1} \sim Wishart(R,3)$$
(7)

Where 10000 in the normal priors is the variance, and *R* is the 3×3 identity matrix; for the superscript on δ , X = Dur, *MAP*, *MAT*, or *Int* as in Equation (5). In this study, the data sufficiently informed the above parameters, but this may not always be the case, and weakly or semi-informative priors may be required (e.g., Lemoine, 2019).

Likely common to many meta-analyses, we are missing some climate (MAP and MAT; 6% of studies) and duration (*Dur*; 4.2% of records) data. However, if we assume reasonable distributions for these covariates, the reported values can be used to inform the parameters of these distributions, which in-turn are used to impute missing covariate values (Ogle *et al.*, 2013). Thus, rather than discarding records with missing covariate data, as would be typical of many classical meta-analyses, we employed simple hierarchical models for the covariate data, providing a mechanism for imputing missing values. Thus, for site *s* or record *i*:

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$$MAP_{s} \sim Normal(\mu_{MAP}, \sigma_{MAP}^{2})$$

$$MAT_{s} \sim Normal(\mu_{MAT}, \sigma_{MAT}^{2})$$

$$Dur_{i} \sim Normal(\mu_{Dur}, \sigma_{Dur}^{2})$$
(8)

We assigned relatively non-informative (wide) normal priors to the global (overall) means (μ 's) and wide uniform priors to the standard deviations (σ 's).

229 Another advantage of the Bayesian approach is the ability to easily obtain posterior 230 distributions for derived quantities (i.e., quantities that are functions of stochastic parameters and 231 potentially observed data) (Hobbs & Hooten, 2015). To illustrate, we obtained the posterior 232 distributions for several derived quantities. To better understand the role of climate context, we 233 evaluated the mean model, Equation (5), at a range of MAP and MAT values that span the climatic 234 characteristics of the GCME studies, standardized for study duration (i.e., for *Dur* = 0 years [start of 235 experiment] and *Dur* = 2.64 years [the average duration across all studies]). We also computed the 236 study-level pairwise correlations in the AB, BB, and SCE log-response-ratios for each treatment type, such that for treatment t and variables v and v' ($v \neq v'$, e.g., for v = AB and v' = BB): 237

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$$\rho_{t,v,v'} = \frac{\Sigma_t(v,v')}{\sqrt{\Sigma_t(v,v)\Sigma_t(v',v')}}$$
(9)

where $\Sigma(v,v')$ is the covariance between variables *v* and *v'*, and $\Sigma(v,v)$ and $\Sigma(v',v')$ are the among study variances of variables *v* and *v'*, respectively, LRR values.

Additionally, we calculated quantities to explore additive, synergistic, and antagonistic effects of the treatments. We obtained the posterior distributions for the predicted study-level LRRs under the eCO₂ × warming treatment *if* the eCO₂-only (t = 1) and warming-only (t = 2) effects are additive (β^{4dd}), and we also calculated the difference ($\Delta\beta$) in the actual eCO₂ × warming effect (t = 3) relative to the predicted additive effect:

$$\beta_{\nu,s,3}^{Add} = \beta_{\nu,s,1} + \beta_{\nu,s,2}$$

$$\Delta\beta_{\nu,s,3} = \beta_{\nu,s,3} - \beta_{\nu,s,3}^{Add}$$
(10)

If the 95% credible interval for $\Delta\beta$ does not contain zero, then this implies that the eCO₂ and warming effects are non-additive. Lajeunesse (2011) provides an alternative method to evaluating an interaction between two different treatment factors (see also, Baig *et al.*, 2015), but application of Equation (10) allows results from both single factor (e.g., eCO₂ only) and multi-factor (e.g., eCO₂ and warming) studies to inform this interaction. All derived quantities (i.e., ρ , β^{4dd} , and $\Delta\beta$) were computed within the Bayesian model to obtain posterior samples of these quantities.

253 The model, Equations (4)-(10), was implemented in JAGS 4.3.0 (Plummer 2003; Plummer 254 2015) using the rjags package (Plummer 2013) in R. Three parallel Markov chain Monte Carlo (MCMC) sequences were run for a pre-defined burn-in of 10⁶ iterations. The sequences were checked 255 for convergence after 10⁶ iterations using the Brooks-Gelman-Rubin diagnostic (Gelman & Rubin, 256 257 1992; Brooks & Gelman, 1998) via the gelman.diag function in the coda package ('rjags') (Plummer 258 et al., 2006) in R. Then, the JAGS model was updated for another 500,000 iterations and every 500th 259 sample was stored to obtain 3,000 relatively independent samples from the three sequences. These samples were used to compute posterior statistics for quantities of interest (e.g., β , β^* , δ , and ρ). 260

261 **Results**

262 Support for the hierarchical, multivariate model

To evaluate model fit, we quantified the ability of our model to replicate the reported ("observed") log-response-ratio (LRR) values (see Chapter 6, Gelman *et al.*, 2014). Across the six different combinations of treatment types (eCO₂-only, warming-only, or eCO₂ × warming) and response variables (AB, BB, and SCE), regressions of predicted (replicated LRR values) versus observed LRR yielded coefficients of determination ranging from $R^2 = 0.14$ (SCE response to eCO₂) to $R^2 = 0.55$ (BB response to eCO₂), with an overall $R^2 = 0.31$ (for all treatment types and response variables combined). See Figures S1 and S2 in Supporting Information.

270 A multivariate approach appears appropriate, especially for AB and BB. The correlation 271 between the study-level AB and BB responses is significantly positive under eCO₂-only (the 95%) 272 credible interval [CI] does not contain zero; Table 2). However, the correlations among study-level AB and BB are not significantly different from zero under warming-only or eCO₂ × warming (Table 273 274 2), partly due to wide CIs, which could reflect the reduced amount of information (fewer records) for these treatment types (Table 1, Fig. 1c,d). After having accounted for treatment type, climate, and 275 276 duration, the SCE response is generally uncorrelated with the AB and BB responses (Table 2). This suggests that a univariate meta-analysis of SCE and a bivariate meta-analysis of AB and BB would 277 278 have been valid in this case, but this was not known *a priori*, and repeating separate univariate and 279 bivariate analyses would not provide further benefits.

280 **Posterior estimates of effects parameters**

The global estimates of the LRR for each variable (β^* terms, Equation (6)) suggest that eCO₂ stimulates AB, BB, and SCE relative to ambient levels (Fig. 2a,d,g). Warming effects are not as strong, but the trend is for warming to stimulate AB, BB, and especially SCE (Fig. 2b,e,h). Based on the limited number of studies, eCO₂ × warming led to inconsistent effects on the responses: it increased SCE, tended to reduce BB, but had little to no effect on AB (Fig. 2c,f,i). These global or overall LRR estimates, however, do not reflect variation among sites, or the influence of potential climate drivers and experimental factors (e.g., duration).

288 The covariate effects (δ 's, Equation (5)) are relatively tightly constrained (narrow 95% CIs) 289 for the eCO₂-only and warming-only treatments, but comparatively unconstrained (wide 95% CIs) under $eCO_2 \times warming$ (Fig. 3). These differences in the precision of the δ estimates likely reflect 290 291 differences in sample sizes among the treatment types (Table 1). The duration (Dur) effect was 292 negative for the LRR of BB under eCO₂ (Fig. 3a), AB and SCE under warming (Fig. 3c), and SCE 293 under $eCO_2 \times warming$ (Fig. 3c), indicating that longer exposure to the experimental factor(s) reduced 294 the difference between the control and treatment groups. Conversely, Dur had a positive effect on 295 SCE under eCO₂ (Fig. 3a). The effects of MAP and MAT varied, with a negative effect of MAP on 296 BB under eCO₂ (Fig. 3d) and a positive effect on SCE under warming (Fig. 3e), accompanied by a 297 positive effect of MAT on BB under eCO₂ (Fig. 3g) and negative effects of MAT on AB and BB 298 under warming (Fig. 3h). The MAP × MAT interaction effect was generally non-significant, with the exception of a positive interaction for SCE under eCO₂ (Fig. 3j). 299

300 Incorporation of covariates reveals importance of climate context

To understand how MAP and MAT may govern the responses of interest, within the MHBM model and MCMC routine, we computed the predicted LRR of AB, BB, and SCE under all three treatment types (μ , Eqn (5)), over a range of MAP and MAT values that span the climatic conditions of the study sites. The posterior predictions and uncertainties are visualized in a contour plot (Fig. 4); we focus on a subset of scenarios for illustrative purposes. For example, even though the MAT × MAP interaction was non-significant (Bayesian *p*-value = 0.24) for the AB response to eCO₂ (Fig. 3g),

307 when considering the main effects of MAT (p = 0.17) and MAP (p = 0.12), along with their 308 interaction, interesting non-linear responses emerge (Fig. 4b). The covariate effect estimates (Fig. 3) 309 are based on summaries of their marginal posterior distributions and do not account for posterior 310 correlations between those parameters. The posterior predictions (Fig. 4b-d), however, are simulated based on the joint posterior distribution of the effects parameters. Marginally, none of the climate 311 effects (MAT, MAP, or the MAT \times MAP interaction) are significant for AB under eCO₂, but when 312 313 the LRR of AB under eCO₂ is simulated (to obtain posterior predictions), the posterior simulations 314 account for covariation between the MAT, MAP, and MAT × MAP effects, which results in the non-315 linear response (contours) in Fig. 4b, and a region of significant LRR values (blue shading).

316 The predicted LRR values indicate particular climate regions that are expected to lead to 317 significant effects of eCO₂ (in the absence of warming) on AB (e.g., blue region in Fig. 4b) and SCE (Fig. 4c), and significant effects of warming (in the absence of eCO₂) on SCE (Fig. 4d). The climate 318 319 regions leading to significant responses tend to be broader under eCO₂ (Fig. 4b,c) compared to 320 warming (Fig. 4d), indicating the potential for climate to be a more prominent controller of the AB and/or SCE responses to eCO₂ compared to warming. In particular, eCO₂ is expected to enhance both 321 322 AB and SCE under moderate climates that align with temperate forests, woodlands / shrublands, 323 tropical forest savanna, and temperate grasslands (Fig. 4a,b,c). Warming is expected to enhance SCE 324 under a more restricted climate space characterized by high precipitation and moderate temperatures (e.g., relatively moist temperate forests) (Fig. 4a,d). The effects of eCO₂ and warming on AB and 325 326 SCE are highly uncertain and not well-characterized for biomes defined by more extreme climates 327 (e.g., tundra and subtropical desert; Fig. 4).

328 The effect of climate context is also captured by the study-level LRR estimates. Ignoring climate and duration (as given by β in Equation (5)), the predicted (posterior mean) LRR for AB, BB, 329 and SCE, and their uncertainties (e.g., 95% CI widths), are more similar among studies, for all three 330 331 treatment types (Fig. 2, gray symbols). When we account for climate and duration (based on μ , 332 Equation (5)), greater variability in the estimated study-level LRR values emerges (Fig. 2, colored symbols). The global-level LRR predictions (β^* terms, Equation (6)) are more constrained (narrower 333 CIs) and represent the predicted LRR across all climate and duration conditions represented by the 334 335 studies considered here (triangles, Fig. 2).

336 Additive vs synergistic vs antagonistic treatment effects

337 The Bayesian meta-analysis indicates that the large uncertainty in the combined eCO₂ and warming effects (Fig. 2, Fig. 3) makes it challenging to distinguish the actual effects from an additive response 338 (Fig. 5). For example, the uncertainty in the global estimates of each LRR is fairly large, such that the 339 340 95% CIs tend to overlap the 1:1 line for the actual estimated effect (combined response; vertical CIs, Fig. 5). Conversely, the 95% CIs corresponding to the predicted global *additive* effects are generally 341 342 narrower (horizontal CIs, Fig. 5) and barely overlap the 1:1 line for SCE, but not for AB and BB. This 343 suggests that globally, across all studies, eCO₂ and warming are generally *additive* for AB and SCE 344 with a slight trend towards antagonistic for AB and synergistic for SCE. eCO₂ and warming are generally *antagonistic* for BB, which is also supported by study-level BB estimates (posterior means) 345 346 that all fall below the 1:1 line (Fig. 5). However, given that the vertical 95% CI overlaps the 1:1 line 347 for the global BB response, which reflects the influence of the large uncertainty in the study-level 348 estimates (not shown), this indicates that an additive response cannot be ruled out.

349 **Discussion**

350 Key attributes of an MHBM approach

351 We highlight six key attributes of the multivariate, hierarchical Bayesian meta-analysis (MHBM) 352 approach described herein. The first four attributes relate to points (1)-(4), respectively, in Table 3. First, the Bayesian approach can easily accommodate a multivariate model for the response variables 353 354 of interest, which can be extended to more than three response variables. If multiple response 355 variables are measured in the same study, it is possible that they covary. For example, our analysis 356 suggests that the *a priori* assumption of independence among different response variables (e.g., AB 357 and BB in the GCME database) is invalid (Table 2), yet this assumption is regularly employed in 358 classical meta-analyses, including Dieleman et al. (2012) and many recent analyses (e.g., Deng et al., 2020; Hillebrand & Kunze, 2020; Li et al., 2020; Salazar et al., 2020). It is possible that individual 359 360 observations of each response variable are correlated, especially if measured simultaneously or on the 361 same sampling units. Unfortunately, relevant information for quantifying observation-level (or within-362 study) covariance or correlation among multiple response variables is rarely provided in publications

363 (e.g., Jackson et al., 2011; Lin & Chu, 2018). However, we show that one can specify a multivariate 364 model for latent, high-level LLRs, such as study-level values (see also, van Houwelingen et al., 365 2002). Such a model would be appropriate for responses that are either dependent (covary) or independent as the multivariate specification (e.g., normal likelihood used here) allows one to 366 evaluate independence (e.g., correlation coefficients that do not differ significantly from zero). 367 368 Possible disadvantages of specifying a multivariate model include the potential for additional 369 computational costs associated with matrix operations that arise from the multivariate specification, or 370 imputation of missing response values when multiple response variables are aligned (e.g., Jackson et 371 al., 2011; Lin & Chu, 2018).

Second, unreported sample sizes, measures of uncertainty (e.g., S or se), and covariate data are 372 common in ecological meta-analyses (Kambach et al., 2020), and a Bayesian approach can easily 373 374 accommodate simultaneous imputation of such missing information (e.g., Stevens, 2011; Ogle *et al.*, 375 2013). Here, we simply specify likelihoods for the covariate data (e.g., MAP, MAT, and Dur), which 376 serve as priors for the missing values, conditional on the observed (response and covariate) data. This 377 allows us to retain records with missing covariate data, and to propagate uncertainty associated with 378 the missing values. Classical approaches often discard records with missing covariate data (e.g., Lajeunesse & Forbes, 2003; Kambach *et al.*, 2020); in our analysis, this would have only resulted in 379 380 9.4% of the records being discarded, but in other analyses, rates of incomplete reporting can be much 381 higher (e.g., Ogle *et al.*, 2013). The high level of reporting for the GCME database likely reflects 382 initial selection criteria. A more sophisticated model may be required to account for the possibility that data are not missing at random (White *et al.*, 2008), especially for high levels of incomplete 383 384 reporting (e.g., Ogle *et al.*, 2013). In summary, despite a push for comprehensive reporting (Gerstner 385 et al., 2017), incomplete reporting will likely remain a challenge, especially if older studies are 386 included in meta-analyses. Both classical and Bayesian meta-analysis approaches are capable of dealing with missing records via a variety of imputation approaches (Kambach *et al.*, 2020). A fully 387 388 Bayesian approach allows for retention of records with incomplete reporting such that information 389 provided by these records, albeit incomplete, contributes to posterior estimates of study- and global-390 level parameters, covariate effects, variance terms, and other unknown quantities.

391 Third, within the Bayesian meta-analysis, it is straightforward to model the predicted 392 responses (e.g., LRR values) as functions of study- or site-level covariates, or covariates that vary at 393 other levels that are compatible with the data. In this study, the LRR values for AB, BB, and SCE 394 were modeled as functions of site-specific climate and record-level experiment duration; this was not 395 done in the original Dieleman et al. (2012) analysis. The AB and SCE responses to warming and the 396 BB response to eCO₂ are predicted to be largest at the onset of the experiment and decrease with 397 increasing duration, suggesting a time-dependent response to the associated treatment factor. Such 398 duration effects have been reported for individual experiments (e.g., Hungate *et al.*, 2004; Leuzinger 399 et al., 2011; Mueller et al., 2016) and uncovered in formal meta-analyses (Elmendorf et al., 2012; Wang et al., 2014; Komatsu et al., 2019). Conversely, the SCE response to eCO₂ is expected to 400 401 intensify with increasing exposure to eCO₂.

402 Fourth, the Bayesian approach explicitly quantifies uncertainty in all unknown quantities, via 403 the posterior distribution (Gelman et al., 2014). Interval estimates, such as a 95% credible interval 404 (CI), are often used to quantify uncertainty and can lend insight into knowledge gaps. For example, the wide CIs for the study-level LRR for the $eCO_2 \times warming experiments$ (e.g., Fig. 3c, f, i, l) point to 405 the need for more multi-factor studies that manipulate multiple treatment factors (e.g., both eCO₂ and 406 407 temperature). This was also suggested by a classical meta-analysis that was applied only to the eCO₂ 408 × warming records (Dieleman *et al.*, 2012); yet, the Bayesian approach described here provides 409 predictions, and associated uncertainties, for a broad range of climate conditions and biomes that are 410 not represented in the GCME database.

411 Fifth, the Bayesian meta-analysis model can be used to obtain posterior predictions, which can 412 be evaluated to understand the range of potential responses and to further identify information gaps. Such predictions reveal that the effect of eCO₂ on BB and SCE and the effect of warming on all three 413 414 responses (AB, BB, and SCE) depends on climate context, resulting in non-linear responses of AB 415 and/or SCE to eCO₂ (e.g., Fig. 4). In general, most studies in our meta-analysis fall in the middle of 416 the climate space (Fig. 4), where eCO₂ is expected to enhance AB and SCE, and warming is expected to have little or no effect on SCE. However, the climate regions or biomes associated with the 417 418 strongest (most negative or most positive) or most uncertain (leading to non-significant effects) 419 predicted responses are also those that are generally under-represented in manipulative experiments.

420 For example, SCE is predicted to be stimulated by warming in wet regions (e.g., temperate 421 rainforests, temperate forests, and tropical forest savanna), but reduced by warming in dry regions 422 (e.g., temperate grassland and subtropical desert) (Fig. 4d). Yet, little data are available for these 423 biomes in the GCME database. This points to the need for more studies in under-represented and 424 potentially sensitive regions (see also, Song *et al.*, 2019), to test the expectation that AB, BB, and 425 SCE responses to eCO₂, warming, or their combination vary among biomes and are governed by 426 climate. Such research bias is not uncommon in meta-analyses, potentially restricting inferences to 427 those ecosystems or biomes that are represented in the meta-analysis (Gurevitch & Hedges, 1999; Lowry et al., 2013). 428

Finally, unlike classical approaches, there are few/no canned software programs for 429 430 implementing Bayesian meta-analyses. However, existing Bayesian software (e.g., JAGS, 431 OpenBUGS, Stan, NIMBLE) can easily implement the Bayesian meta-analysis model described 432 herein. We have provided the code and data from this study, which can be used as a starting point for 433 other meta-analyses. If one is faced with incomplete reporting of standard errors or sample sizes, Ogle 434 et al. (2013) provide theory and code for imputing missing n, S (or se), and other types of information 435 (e.g., categorical covariates), in the context of univariate models for reported sample means (not LRR 436 values), but the imputation procedure is broadly applicable. The ability to impute missing information 437 provides greater flexibility and allows for compilation of more information (more records), versus 438 discarding potentially useful studies because they do no report one or more desired quantities (e.g., 439 Kambach et al., 2020). This will help to ensure that all available information is leveraged from experimental studies to discover general patterns. 440

441 Case study with the GCME database

We briefly compare a few key results from the original, classical meta-analysis reported by Dieleman *et al.* (2012) to those produced by the MHBM approach. Results are generally consistent, but a few potentially important differences emerge. In general, the global effect sizes (LRRs, $\beta_{v,t}^*$ in Equation (6)) followed similar trends among the two analyses such that both produced similar magnitudes of effect sizes (compare Fig. 2 to their Fig. 1), with the exception being the estimated effect size for SCE under eCO₂ and warming. Both indicate that eCO₂ clearly stimulates AB, BB, and SCE, warming

tends to stimulate BB and SCE, and there is comparatively large uncertainty associated with the
combined effect of eCO₂ and warming. Conversely, Dieleman *et al.* (2012) reported that AB was
significantly stimulated by warming and that the combination of eCO₂ and warming significantly
stimulated AB, BB, and SCE; although the mean effect sizes are similar, none of these effects were
significant according to the MHBM. Differences in significance level between the classical approach
and the MHBM approach is not surprising and is consistent with the Bayesian approach providing a
more conservative quantification of uncertainty (e.g., Pappalardo *et al.*, 2020).

455 With respect to the combined effect of eCO_2 and warming, both approaches suggest that, 456 depending on site, eCO₂ and warming can have an additive or slightly antagonistic effect on AB. Moreover, Dieleman et al. (2012) found a general trend for additive effects of eCO₂ and warming on 457 458 multiple ecosystem variables, and given the large uncertainty associated with the study-level 459 estimates produced by the MHBM (Fig. 5), additive effects cannot be ruled out at the study level. This 460 is generally consistent with other studies (Yue et al., 2017b; Song et al., 2019). However, the MHBM 461 also provided global estimates of the combined effects (Fig. 5), whereas the classical analysis only 462 provided study-level estimates, without uncertainty. Based on the global MHBM estimates, there is 463 mild support for a synergistic effect of eCO_2 and warming on SCE (Fig. 5) such that warming can enhance the stimulation of SCE by eCO₂, or vice versa. The MHBM suggests the opposite for BB, 464 465 whereby an overall antagonistic effect emerged. Evidence for additive, synergistic, or antagonistic 466 effects of eCO₂ and warming have implications for interpretation of the underlying mechanisms (e.g., 467 role of nutrient- or water-limitation, leaf area feedbacks, changes in water-use efficiency) and will have consequences for projections of ecosystem responses to future conditions (Dieleman et al., 2012; 468 469 Yue et al., 2017b).

470 Further considerations

We highlight additional considerations relevant to implementing an MHBM approach. First, the
application of an MHBM requires some familiarity with Bayesian methods, but if one has an
understanding of classical meta-analyses and relevant programming languages (e.g., R), it should be
fairly straightforward to specify and implement a Bayesian version of the meta-analysis. Second, a
Bayesian meta-analysis (e.g., MHBM) requires the analyst to explicitly define all equations and

476 underlying assumptions; this may be viewed as a benefit, but can also be challenging for those less 477 familiar with statistical theory, probability distributions, or Bayesian methods. But, there are a myriad 478 of resources (e.g., textbooks) for gaining familiarity in these areas, including, but not limited to 479 Gelman et al. (2014), Gelman and Hill (2007), Hobbs and Hooten (2015), and Kruschke (2014). 480 Third, implementation of a Bayesian meta-analysis model may lead to greater computational 481 challenges relative to a classical approach. The MHBM implemented herein took about 1-hour to 482 complete (i.e., to sample from the posterior), which is relatively fast; but, it is possible that other 483 models could require longer simulation times and/or exhibit convergence issues (Pappalardo *et al.*, 484 2020) that could require additional troubleshooting and/or modification to the model or code (e.g., 485 Ogle & Barber, 2020).

While we use the GCME database (Dieleman et al., 2012) to illustrate the MHBM approach 486 487 for a relatively simple example, we anticipate that incorporation of additional predictor variables 488 could improve model performance and inference. Independent of whether the meta-analysis is 489 implemented in a Bayesian or classical framework, in the example considered here, potentially 490 important predictors include plant functional type, soil characteristics, soil nutrient status, or other 491 environmental conditions. However, many of these variables were not included in the GCME 492 database, and potentially important predictors, such as nutrient availability, are often not reported in 493 the publications from which the target response variables are extracted (Vicca *et al.*, 2018). This 494 further emphasizes the problem of research bias (Gurevitch & Hedges, 1999; Vicca et al., 2018) and 495 the need for comprehensive reporting of results in the primary literature (Gerstner et al., 2017; Kambach et al., 2020), and the more general need for open science and data sharing (Hampton et al., 496 497 2015; Powers & Hampton, 2019).

Finally, we return to the utility of the multivariate approach. Application of the MHBM to
synthesizing the AB, BB, and SCE from the GCME database revealed lack of significant correlation
between study-level SCE versus biomass metrics (AB and BB; Table 2). This suggests that a separate,
univariate hierarchical Bayesian meta-analysis could be applied to the SCE records, and a bivariate
model could be applied to the AB and BB records. We argue against this for a few reasons. First, we
do not know *a priori* if such response variables are uncorrelated; this was revealed by the results of
the multivariate model. Secondly, the three response variables share missing covariate data, and it

505 does not make sense to impute those missing values separately, within each individual meta-analysis 506 model. Though, imputation of the missing covariate data could be achieved separately (e.g., Kambach 507 et al., 2020), so that the same imputed values are employed in each meta-analysis. Third, the 508 univariate model(s) would involve simple modifications to the MHBM approach; e.g., Equation (6) would be implemented as a bivariate normal model (for the AB and BB components) and a univariate 509 510 normal model (for SCE), and the prior for the 3×3 covariance matrix in Equation (7) would be 511 modified for a 2×2 covariance matrix (related to the AB-BB bivariate model) and a scalar variance 512 parameter (for the SCE model). All other equations would remain the same. The analyses would then 513 have to be repeated, requiring additional computational time and effort to synthesis the results, but the 514 results and inferences should remain unaffected. Thus, we do not see an advantage of implementing 515 separate models when we already have results from the more general MHBM model. There are situations, however, when an MHBM approach may not be appropriate to begin with, such as cases 516 517 where response variables can *a priori* be assumed to be uncorrelated and when response variable data rarely overlap (e.g., response variable X and Y are rarely/never reported in the same study). In 518 519 summary, the advantages of a Bayesian meta-analysis approach (Table 3) are likely to outweigh the 520 disadvantages, but there are situations where a classical meta-analysis may be preferred, or may help 521 guide the development and implementation of a more flexible Bayesian meta-analysis.

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526 Authors' contributions

- K.O. conceived of the modeling approach, contributed to model implementation, and wrote the
 manuscript. Y.L. prepared data, implemented, coded, and tested the model, and contributed to
 manuscript writing. S.V. provided data, assisted with data preparation, provided feedback on results,
 and contributed to manuscript writing. M.B. contributed to the conceptual development of the
- 531 modeling framework, provided feedback on results, and contributed to manuscript writing.

532 **Data availability**

- 533 All data and code used and described in this study are available on GitHub
- 534 (https://github.com/yliu11/bayesian-meta-analysis).

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Supporting information

Fig. S1. Predicted versus reported ("observed") log-response ratio (LRR) values for each response variable and treatment type.

Fig. S2. Predicted versus reported ("observed") log-response ratio (LRR) values for all records combined.

Figure legends

Fig. 1. Venn diagrams summarizing the number of studies used in the meta-analysis (**a**) across all treatment types, and broken down by treatment type for (**b**) eCO_2 only, (**c**) warming only, and (**d**) $eCO_2 \times$ warming. Focusing on the full dataset used in this study, (**a**) some studies only yield data for 1 of the 3 response variables (e.g., 16 studies only have AB data), whereas others yield data for 2 of the 3 variables (e.g., 24 studies give both AB and BB data), and 19 studies yield data for all 3 responses variables. A "study" represents a specific experimental study, and there may be multiple studies that occur at the same site, but that were not part of the same manipulative experiment. Response variables are aboveground biomass (AB), belowground biomass (BB), and soil CO₂ exchange (SCE). For (**a**), the total number of studies reporting AB, BB, and SCE are 65, 58, and 52, respectively; the total number of studies providing data on more than one response variable. Across all studies, 1049 individual records were used (Table 1).

Fig. 2. Posterior estimates (mean and 95% CI) of the overall (across all sites, triangles, bottom of each panel; β^* , Eqn (5)) and study-specific (small squares) log-response ratios (LRR) for aboveground biomass (AB; **a**, **b**, **c**), belowground biomass (BB; **d**, **e**, **f**), and soil CO₂ exchange (SCE; **g**, **h**, **i**) with respect to elevated CO₂ (eCO₂; left column, **a**, **d**, **g**), warming (middle, **b**, **e**, **h**), and eCO₂ × warming (right, panels **c**, **f**, **i**). The colored squares (AB = green, BB = brown, SCE = blue) denote study-level predictions specific to each site's climate (i.e., μ in Eqn (5) evaluated at each site's mean annual precipitation [MAP] and mean annual temperature [MAT]); the gray symbols in the background represent the study-level LRR under the same climate conditions (i.e., MAP and MAT set to their mean values, giving $\beta_{v,s,t}$ in Eqn (5)). Red arrows point to overall effects that are deemed significantly different from zero (their 95% CI does not contain zero).

Fig. 3. Posterior estimates (mean and 95% CI) of the effects (δ terms) of each covariate (rows) associated with each treatment type (columns). The covariate effects are shown for (a, b, c) study duration, (d, e, f) mean annual precipitation (MAP), (g, h, i) mean annual temperature (MAT), and (j, k, l) the MAP × MAT interaction, for the (a, d, g, i) elevated CO₂ (eCO₂), (g, e, h, k) warming, and

(c, f, i, l) $eCO_2 \times warming treatments$. The dashed horizontal line is the zero line; 95% CIs that do not overlap the zero-line indicate a potentially significant effect of that covariate on the LRR of aboveground biomass (AB, green), belowground biomass (BB, brown), or soil CO₂ exchange (SCE, blue) to the corresponding treatment factor. Bayesian p-values, which are somewhat less conservative than the 95% CIs for evaluating "significance," are indicated with asterisks: $p \le 0.01$ (***), $0.01 (**), and <math>0.05 (*). Note that MAP, MAT, and MAP × MAT effects were not included in the models for AB, BB, and SCE under <math>eCO_2 \times warming$ given data limitations.

Fig. 4. The range of mean annual precipitation (MAP) and mean annual temperature (MAT) considered in this study spans a diversity of **(a)** terrestrial biomes (based on https://github.com/kunstler/BIOMEplot; TR = temperate rainforest). Predicted effects of site-level MAP and MAT on the LRR of **(b)** aboveground biomass (AB) to eCO₂ in eCO₂-only experiments (i.e., under ambient temperatures), **(c)** soil CO₂ exchange (SCE) to eCO₂ in eCO₂-only experiments, and **(d)** SCE to warming in warming-only experiments. Contour lines and associated numerical labels represent the predicted LRR (μ , Eqn (4)), standardized to an initial duration of *Dur* = 0 years (contour plots are nearly identical for an average duration of 2.64 years). Contour lines associated with $\mu > 0$ (solid contour lines) imply that the treatment (eCO₂ or warming) increases AB or SCE relative to the control; $\mu = 0$ (thick blue contour lines) imply that the treatment decreases AB or SCE relative to the control; $\mu = 0$ (thick blue contour lines) implies that the treatment has no effect on AB or SCE. Shaded blue regions indicate that μ (predicted LRR) is statistically different from zero (95% CIs for μ do not contain zero); gray regions indicate lack of significance. Red triangles indicate the location of the study sites in the MAP-MAT climate space (not all sites yielded AB and SCE data). Contour lines are scaled differently in each plot.

Fig. 5. The estimated, combined effect size (log response ratio, LRR) of the $eCO_2 \times$ warming treatment versus the potential additive effect size (LRR based on the sum of the eCO_2 and warming single-factor effect sizes) for the three response variables of interest: aboveground biomass (AB), belowground biomass (BB), and soil CO₂ exchange (SCE). Points (estimates) that fall above, below, or near the 1:1 line indicate synergistic, antagonistic, or additive effects, respectively, of eCO_2 and warming. Small, filled symbols are the site-level estimates (posterior means), and large, open

triangles are the global, overall estimates; the 95% credible intervals (gray whiskers) are shown for the global estimates, but not for the site-level estimates given that they are generally very wide and the majority overlap the 1:1 line.

Tables

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Table 1. Number of individual, univariate log-response ratio (LRR) records, and number of studies producing those records (in parentheses), obtained from the GCME database that were used in the hierarchical Bayesian multivariate meta-analysis model.

| Response | | Treatment type | | |
|-----------|------------------------|----------------|------------------------|------------|
| variable* | eCO ₂ -only | Warming-only | $eCO_2 \times warming$ | Total |
| AB | 127 (42) | 141 (30) | 32 (11) | 300 (65) |
| BB | 122 (46) | 50 (20) | 33 (10) | 205 (58) |
| SCE | 346 (38) | 143 (21) | 55 (10) | 544 (52) |
| Total | 595 (69) | 334 (45) | 120 (18) | 1049 (100) |

A total of 1049 records, obtained from 100 studies, were used in the analysis. See Fig. 1 for the definition of a "study."

* AB = aboveground biomass; BB = belowground biomass; SCE = soil CO₂ exchange.

Table 2. Posterior statistics (median and 95% credible interval [CI]) for the correlation between the study-level AB, BB, and SCE log-response-ratios ($\rho_{t,v,v'}$ in Eqn (9)).

| Treatment type | Response pair | Median | 95% CI |
|--------------------------------|--|--------|-----------------|
| eCO_2 -only ($t = 1$) | AB-BB ($v = 1, v' = 2$) | 0.567 | (0.178, 0.795) |
| | AB-SCE (<i>v</i> = 1, <i>v</i> ' = 3) | -0.286 | (-0.656, 0.231) |
| | BB-SCE ($v = 2, v' = 3$) | -0.274 | (-0.685, 0.312) |
| Warming only $(t = 2)$ | AB-BB ($v = 1, v' = 2$) | 0.330 | (-0.314, 0.781) |
| | AB-SCE ($v = 1, v' = 3$) | -0.074 | (-0.627, 0.595) |
| | BB-SCE ($v = 2, v' = 3$) | 0.260 | (-0.341, 0.738) |
| $eCO_2 \times warming (t = 3)$ | AB-BB ($v = 1, v' = 2$) | 0.035 | (-0.863, 0.825) |
| | AB-SCE (<i>v</i> = 1, <i>v</i> ' = 3) | -0.019 | (-0.771, 0.768) |
| | BB-SCE ($v = 2, v' = 3$) | 0.204 | (-0.706, 0.821) |

Table 3. Summary of the unique attributes of the multivariate Bayesian meta-analysis modeling approach described in this study.

| Attribute | Description* |
|--------------------------------------|--|
| (1) Multivariate components | Implements a multivariate model for the study-level log-response ratios, which explicitly accounts for and estimates covariation among the AB, BB, and SCE responses. That is, since responses such as AB and BB, and potentially SCE, are often measured together in a study (see Fig. 1), it is unrealistic to assume that they are independent of each other, and the multivariate model accounts for such dependence. |
| (2) Retain all records | Retain all records such that records with missing covariate data or incomplete response variable data are not discarded. Missing covariate data are imputed within the model; the missing data are simultaneously "informed" by all observed covariate data and log-response ratio data of all three variables (AB, BB, and SCE), and for all three treatment types. |
| (3) Regression- based approach | Employs a regression-based model for the log-response ratio data that includes the effects of multiple study- or site-specific covariates and their interactions. This allows us to explore how the log-response ratios vary as a function of these potential covariates, which could lend insight into potential non-linearities of the eCO_2 , warming, or combined $eCO2 \times$ warming treatment effects. |
| (4) Uncertainty quantification | Produces a posterior distribution for all quantities of interest (e.g., overall log- response ratios, predicted additive effects of eCO_2 and warming, correlations among AB, BB, and SCE responses, etc.). The posterior distribution explicitly quantifies uncertainty in quantities that we wish to make inferences about, without having to rely on procedures for approximating such uncertainties. |
| (5) Multiple treatment | Simultaneous analysis of the log-response ratio data obtained under different treatment types such that data from studies reporting the effects of eCO_2 -only, |

Ľ Acce are expected to share parameters that describe the overall (global) log-response ratios and the effects of the aforementioned covariates (see (3)).

*AB = aboveground biomass; BB = belowground biomass; SCE = soil CO₂ exchange.



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