Methods

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

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Summary

- Meta-analyses enable synthesis of results from globally distributed experiments to draw general 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
illustrate how several key issues can be addressed via a multivariate, hierarchical Bayesian meta-
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 CO$_2$ exchange (SCE, n = 544), representing 100
studies. The MHBM accounted for study duration, climate effects, and covariation among the AB,
BB, and SCE responses to elevated CO$_2$ (eCO$_2$) 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 eCO$_2$ and warming impact ecosystem function.
Predictions identified biomes that may be particularly sensitive to eCO$_2$ or warming, but that are
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.

**Keywords**

Bayesian meta-analysis, climate warming, global change experiments, elevated CO$_2$, hierarchical
model, incomplete reporting, multivariate meta-analysis
Introduction

A plethora of manipulative field experiments have been conducted to evaluate the impacts of various global change factors—e.g., warming, elevated CO$_2$ (eCO$_2$), drought, or nitrogen deposition—on ecosystem structure and functioning of intact or managed ecosystems (e.g., Wu et al., 2011; Dieleman 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, have tested different ranges and combinations of global change factors, and have been performed in diverse environmental contexts. Meta-analyses aim to provide quantitative syntheses of general 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 of, for example, methods used, variables measured and reported, timing of measurements, intensity of measurements (sample sizes)—represents a major challenge for meta-analyses (e.g., Spake & Doncaster, 2017; Gurevitch et al., 2018).

Regardless, meta-analysis techniques are being increasingly applied to evaluate global or broad-scale responses to experimental manipulations of environmental conditions (e.g., Arnqvist & Wooster, 1995; Koricheva & Gurevitch, 2014). Many meta-analyses evaluate response ratios or related metrics (Koricheva & Gurevitch, 2014) of multiple response variables (e.g., above- and belowground biomass, soil carbon and nitrogen, CO$_2$ fluxes) (Wu et al., 2011; Dieleman et al., 2012; Yue et al., 2017a; Song et al., 2019), but they typically treat these variables as independent. The assumption of independent response variables ignores the potential for covarying or coordinated responses (Nakagawa & Santos, 2012), and the fact that individual field experiments may produce data on simultaneously measured variables. While standard multivariate modeling approaches can be leveraged to account for correlations among response variables within a meta-analysis (Nakagawa & Santos, 2012; Komatsu et al., 2019), such multivariate meta-analyses are rare (Nakagawa & Santos, 2012). For example, Pappalardo et al. (2020) reviewed 96 published meta-analyses focused on the ecological impacts of global change or climate change factors; 34 of the 96 studies analyzed multiple 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 eCO$_2$ on soil...
carbon (Hungate et al., 2009), plant biomass (Terrer et al., 2016), or plant C:N:P stoichiometry (Yue et al., 2017a)—it is difficult to fully account for site-level variables that partly explain differences among sites. Even if such meta-analyses do incorporate site-level covariates (e.g., Martin et al., 2018; Falaschi et al., 2019), potentially important covariates are unlikely to be available for each study (Ogle et al., 2013). Such missing information—related to issues of incomplete reporting (Gurevitch & Hedges, 1999; Ogle et al., 2013; Vicca et al., 2018)—often leads the researcher(s) to discard records lacking this information (e.g., Gurevitch & Hedges, 1999; Lajeunesse & Forbes, 2003; Shantz et al., 2016) or to ignore potentially important covariates due to inconsistent reporting across studies (e.g., Vicca et al., 2018).

While classical meta-analysis falls short on accounting for multiple response variables, site-level covariate data, and non-linear responses to global changes, hierarchical Bayesian modeling approaches can accommodate these issues via multivariate model components, even when faced with incomplete reporting (e.g., Nakagawa & Santos, 2012). Bayesian meta-analysis approaches are relatively new in ecology, with recent examples including evaluations of the impacts of multiple global change factors on plant community composition (Komatsu et al., 2019), the competitive abilities of non-native versus native plant species (Golivets & Wallin, 2018), the effects of nutrient loading on mutualism performance (Shantz et al., 2016), and functional traits of multiple species or functional groups (e.g., Lebauer et al., 2013; Ogle et al., 2013; Ogle et al., 2014; Shiklomanov et al., 2020). Komatsu et al. (2019) and Shiklomanov et al. (2020) uniquely employed Bayesian multivariate models to account for potential covariation among multiple responses. However, these studies apparently ignored estimates of uncertainty associated with reported responses, and they did not incorporate incompletely reported covariate data. While these studies represent significant advances towards more flexible and powerful meta-analysis approaches, we are not aware of existing Bayesian 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 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. Here, we address this gap by demonstrating a multivariate, hierarchical Bayesian modeling approach that should advance ecological meta-analyses.
To illustrate the approach, we use a database on the responses of multiple ecosystem attributes to eCO$_2$, warming, or their combined effects, which was previously employed to perform a traditional 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 of each study)—from over 150 manipulative experiments, distributed across a range of ecosystem types and climates. While the database contains information on multiple (at least nine) response variables (Dieleman et al., 2012), we focus on a subset of studies that reported aboveground biomass (AB), belowground biomass (BB), and soil CO$_2$ exchange (SCE). The goal of this study is to describe and demonstrate a hierarchical, multivariate Bayesian meta-analysis approach using these data. We further illustrate the ability of this approach to produce posterior predictions, which can be used to quantitatively inform future experimental studies. We provide annotated code for this analysis and for a more generalized multivariate meta-analysis (accommodating a flexible number of treatment types).

Description

Database of global change manipulation experiments

We utilized a database of global change manipulative experiments (hereafter, the GCME database) originally compiled by Dieleman et al. (2012). The GCME database contains information on the responses of multiple ecosystem variables—various biomass and carbon pools and fluxes—to elevated CO$_2$ (eCO$_2$), warming, or their combination (eCO$_2$ × warming). The GCME database focuses on experiments that manipulated eCO$_2$ only, temperature only, or both, with usually two levels each (e.g., ambient [“control”] versus elevated or warmed [“treatment”]). The database includes some studies that implemented watering or fertilization treatments, usually in combination with eCO$_2$ and/or warming. Here, we focused on the eCO$_2$ and warming treatments, and restricted the data to 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 the GCME database were extracted from figures or tables in published journal articles, with some data obtained directly from researchers. The database as a whole contains information from >150 manipulative experiments (“studies”), distributed across multiple ecosystem types and a range of climates.
We focused on three key ecosystem response variables: aboveground biomass (AB), belowground biomass (BB), and soil CO\textsubscript{2} 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.

### Preparing data for the meta-analysis

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 (\(\sigma^2\)) for each LRR record \(i\) (\(i = 1, 2, \ldots, 1049\)) based on Hartung et al. (2008) (Chapter 8):

\[
LRR_i = \log_e \left( \frac{\bar{y}_T^i}{\bar{y}_C^i} \right)
\]

\[
\sigma_i^2 = S_{i}^{y^2} \left( \frac{1}{n_i^T \cdot (\bar{y}_T^i)^2} + \frac{1}{n_i^C \cdot (\bar{y}_C^i)^2} \right)
\]

\[
S_{i}^{y^2} = \frac{1}{n_i^T + n_i^C - 2} \left[ (n_i^T - 1)(\bar{S}_T^w)^2 + (n_i^C - 1)(\bar{S}_C^w)^2 \right]
\]

The \(T\) and \(C\) superscripts denote the treatment and control groups, respectively; \(\bar{y}\) is the sample mean, \(n\) is the sample size, and \(S\) is the sample standard deviation. Separate \(n\) for the treatment and
control groups were not readily available in the GCME database, but the number of sample replicates
(n) was reported. Thus, we assumed \( n_T = n_C = n \), and \( \sigma^2 \) in Eqn (2) simplifies to:

\[
\sigma^2_i = \frac{\left(S_{iT}^2\right)}{2n_i} + \frac{\left(S_{iC}^2\right)}{2n_i} + \frac{1}{\left(\bar{y}_{iT}^2\right)} + \frac{1}{\left(\bar{y}_{iC}^2\right)}
\]  

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).

Hierarchical, multivariate meta-analysis model description

Similar to classical and recent Bayesian approaches, we treated LRR and \( \sigma^2 \) (Equations (1) and (3)) as
“known” data that we analyzed via a Bayesian meta-analysis model. Again, given that the AB, BB,
and SCE responses and their associated LRR values may covary at the study level, we simultaneously
analyzed these three variables to account for (and estimate) potential covariation among the
responses. We also simultaneously analyzed data obtained for all three treatment categories (eCO2
only, warming only, and eCO2 × warming), rather than treating these as independent datasets. It is
possible that site- and study-level covariates—such as climate and experiment duration—modulated
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
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
potential effects of mean annual precipitation (MAP), mean annual temperature (MAT), their
interaction (MAP × MAT), and experimental duration (Dur) on the reported LRR.

Our Bayesian meta-analysis model is as follows. First, for record \( i \), the likelihood of the LRR
data is based on:
Where $LRR$ and $\sigma^2$ are defined in Equations (1) and (3), and treated as “data” or known quantities. Each $LRR$ is essentially “weighted” according to its corresponding variance term, $\sigma^2$. Equation (4) assumes conditional independence—conditional on (or given) the mean response, $\mu$, and the pooled variance, $\sigma^2$—of each variable’s computed $LRR$. We assumed independent likelihoods partly because individual studies (publications) often do not provide information about the covariance among different response variables, and thus we cannot obtain an analytical estimate of that covariance, but we do have estimates of the individual variances, $\sigma_i^2$. However, we accounted for potential correlation among the different response variables at the latent, study level (see Equation (6)).

We defined the mean model for the predicted $LRR$ as a linear regression on $Dur$, $MAP$, and $MAT$:

$$
\mu_i = \beta_{v(i),s(i),t(i)} + \delta_{v(i),s(i),t(i)}^{Dur} \cdot Dur_i + \delta_{v(i),s(i),t(i)}^{MAP} \cdot cMAP_{s(i)} + \delta_{v(i),s(i),t(i)}^{MAT} \cdot cMAT_{s(i)} + \delta_{v(i),s(i),t(i)}^{Int} \cdot cMAP_{s(i)} \cdot cMAT_{s(i)}
$$

$v(i)$, $s(i)$, and $t(i)$ denote response variable $v$, study $s$, and treatment type $t$ associated with record $i$, where $v = 1$ for AB, $v = 2$ for BB, and $v = 3$ for SEC, and $t = 1$ for eCO$_2$ only, $t = 2$ for warming only, and $t = 3$ for eCO$_2 \times$ warming. The conditional independence assumption, Equation (4), accommodates multiple records for a given variable, study, and treatment type; that is, records that share the same $v$, $s$, and $t$ will share the same predicted mean, $\mu$, but they are assumed to be conditionally independent given their shared mean. In the model for $\mu$, $\beta_{v,s,t}$ represents the study-level (latent) $LRR$ for variable $v$, study $s$, and treatment type $t$. The $\delta$ parameters represent the effect of $Dur$, MAP, MAT, and the MAT$\times$MAP interaction. Note that $cMAP$ and $cMAT$ in Equation (5) represent centered values, where $cX = X - \text{mean}(X)$, and the mean is computed across all studies. The covariate effects ($\delta_{v,s}$) vary by the covariate of interest (donated by superscripts, e.g., $Dur$, MAP, MAT, and Int for interaction), and are estimated for each response variable $v$ and treatment type $t$.

We might expect correlation among the three response variables at the study level. Somewhat similar to Komatsu et al. (2019), we assigned a multivariate, hierarchical prior to the study-level effects ($\beta$), allowing for potential covariation among the study-level and treatment-type specific AB, BB, and SCE log-response-ratios:
\[
\begin{pmatrix}
\beta_{1,v,t} \\
\beta_{2,v,t} \\
\beta_{3,v,t}
\end{pmatrix}
\sim \text{Normal}
\begin{pmatrix}
\beta_{v,t}^* \\
\beta_{v,t}^* \\
\beta_{v,t}^*
\end{pmatrix}, \Sigma_t
\]

(6)

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

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

\[
\delta^X_{v,t} \sim \text{Normal}(0,10000)
\]

\[
\beta^*_{v,t} \sim \text{Normal}(0,10000)
\]

\[
\Sigma_t^{-1} \sim \text{Wishart}(R,3)
\]

(7)

Where 10000 in the normal priors is the variance, and \(R\) is the \(3 \times 3\) identity matrix; for the superscript on \(\delta\), \(X = \text{Dur}, \text{MAP}, \text{MAT}\), or \(\text{Int}\) 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 (\(\text{Dur}\); 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 \(i\):

\[
\text{MAP}_s \sim \text{Normal}(\mu_{\text{MAP}}, \sigma^2_{\text{MAP}})
\]

\[
\text{MAT}_s \sim \text{Normal}(\mu_{\text{MAT}}, \sigma^2_{\text{MAT}})
\]

\[
\text{Dur}_i \sim \text{Normal}(\mu_{\text{Dur}}, \sigma^2_{\text{Dur}})
\]

(8)
We assigned relatively non-informative (wide) normal priors to the global (overall) means ($\mu$'s) and wide uniform priors to the standard deviations ($\sigma$'s).

Another advantage of the Bayesian approach is the ability to easily obtain posterior distributions for derived quantities (i.e., quantities that are functions of stochastic parameters and potentially observed data) (Hobbs & Hooten, 2015). To illustrate, we obtained the posterior distributions for several derived quantities. To better understand the role of climate context, we evaluated the mean model, Equation (5), at a range of MAP and MAT values that span the climatic characteristics of the GCME studies, standardized for study duration (i.e., for $Dur = 0$ years [start of experiment] and $Dur = 2.64$ years [the average duration across all studies]). We also computed the 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):

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

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 eCO$_2$ × warming treatment if the eCO$_2$-only ($t = 1$) and warming-only ($t = 2$) effects are additive ($\beta^{add}$), and we also calculated the difference ($\Delta \beta$) in the actual eCO$_2$ × warming effect ($t = 3$) relative to the predicted additive effect:

$$\beta_{v,s,3}^{add} = \beta_{v,s,1} + \beta_{v,s,2}$$

$$\Delta \beta_{v,s,3} = \beta_{v,s,3} - \beta_{v,s,3}^{add}$$

If the 95% credible interval for $\Delta \beta$ does not contain zero, then this implies that the eCO$_2$ 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., eCO$_2$ only) and multi-factor (e.g., eCO$_2$ and warming) studies to inform this interaction. All derived quantities (i.e., $\rho$, $\beta^{add}$, and $\Delta \beta$) were computed within the Bayesian model to obtain posterior samples of these quantities.
The model, Equations (4)-(10), was implemented in JAGS 4.3.0 (Plummer 2003; Plummer 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 $10^6$ iterations. The sequences were checked for convergence after $10^6$ iterations using the Brooks-Gelman-Rubin diagnostic (Gelman & Rubin, 1992; Brooks & Gelman, 1998) via the gelman.diag function in the coda package (‘rjags’) (Plummer et al., 2006) in R. Then, the JAGS model was updated for another 500,000 iterations and every $500^{th}$ 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., $\beta$, $\beta^*$, $\delta$, and $\rho$).

Results

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 (eCO$_2$-only, warming-only, or eCO$_2 \times$ 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 eCO$_2$) to $R^2 = 0.55$ (BB response to eCO$_2$), with an overall $R^2 = 0.31$ (for all treatment types and response variables combined). See Figures S1 and S2 in Supporting Information.

A multivariate approach appears appropriate, especially for AB and BB. The correlation between the study-level AB and BB responses is significantly positive under eCO$_2$-only (the 95% 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 eCO$_2 \times$ warming (Table 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 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 have been valid in this case, but this was not known a priori, and repeating separate univariate and bivariate analyses would not provide further benefits.
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).

The covariate effects (δ's, Equation (5)) are relatively tightly constrained (narrow 95% CIs) for the eCO₂-only and warming-only treatments, but comparatively unconstrained (wide 95% CIs) under eCO₂ × warming (Fig. 3). These differences in the precision of the δ estimates likely reflect differences in sample sizes among the treatment types (Table 1). The duration (Dur) effect was negative for the LRR of BB under eCO₂ (Fig. 3a), AB and SCE under warming (Fig. 3c), and SCE under eCO₂ × warming (Fig. 3c), indicating that longer exposure to the experimental factor(s) reduced the difference between the control and treatment groups. Conversely, Dur had a positive effect on SCE under eCO₂ (Fig. 3a). The effects of MAP and MAT varied, with a negative effect of MAP on BB under eCO₂ (Fig. 3d) and a positive effect on SCE under warming (Fig. 3e), accompanied by a positive effect of MAT on BB under eCO₂ (Fig. 3g) and negative effects of MAT on AB and BB 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).

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),
when considering the main effects of MAT ($p = 0.17$) and MAP ($p = 0.12$), along with their interaction, interesting non-linear responses emerge (Fig. 4b). The covariate effect estimates (Fig. 3) are based on summaries of their marginal posterior distributions and do not account for posterior 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 effects (MAT, MAP, or the MAT $\times$ MAP interaction) are significant for AB under eCO$_2$, but when the LRR of AB under eCO$_2$ is simulated (to obtain posterior predictions), the posterior simulations account for covariation between the MAT, MAP, and MAT $\times$ MAP effects, which results in the non-linear response (contours) in Fig. 4b, and a region of significant LRR values (blue shading).

The predicted LRR values indicate particular climate regions that are expected to lead to significant effects of eCO$_2$ (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 eCO$_2$) on SCE (Fig. 4d). The climate regions leading to significant responses tend to be broader under eCO$_2$ (Fig. 4b,c) compared to warming (Fig. 4d), indicating the potential for climate to be a more prominent controller of the AB and/or SCE responses to eCO$_2$ compared to warming. In particular, eCO$_2$ is expected to enhance both AB and SCE under moderate climates that align with temperate forests, woodlands / shrublands, tropical forest savanna, and temperate grasslands (Fig. 4a,b,c). Warming is expected to enhance SCE 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 eCO$_2$ and warming on AB and SCE are highly uncertain and not well-characterized for biomes defined by more extreme climates (e.g., tundra and subtropical desert; Fig. 4).

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

The Bayesian meta-analysis indicates that the large uncertainty in the combined eCO$_2$ and warming effects (Fig. 2, Fig. 3) makes it challenging to distinguish the actual effects from an additive response (Fig. 5). For example, the uncertainty in the global estimates of each LRR is fairly large, such that the 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 narrower (horizontal CIs, Fig. 5) and barely overlap the 1:1 line for SCE, but not for AB and BB. This suggests that globally, across all studies, eCO$_2$ and warming are generally additive for AB and SCE with a slight trend towards antagonistic for AB and synergistic for SCE. eCO$_2$ and warming are generally antagonistic for BB, which is also supported by study-level BB estimates (posterior means) that all fall below the 1:1 line (Fig. 5). However, given that the vertical 95% CI overlaps the 1:1 line for the global BB response, which reflects the influence of the large uncertainty in the study-level estimates (not shown), this indicates that an additive response cannot be ruled out.

Discussion

Key attributes of an MHBM approach

We highlight six key attributes of the multivariate, hierarchical Bayesian meta-analysis (MHBM) 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 of interest, which can be extended to more than three response variables. If multiple response variables are measured in the same study, it is possible that they covary. For example, our analysis suggests that the a priori assumption of independence among different response variables (e.g., AB and BB in the GCME database) is invalid (Table 2), yet this assumption is regularly employed in 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 observations of each response variable are correlated, especially if measured simultaneously or on the same sampling units. Unfortunately, relevant information for quantifying observation-level (or within-study) covariance or correlation among multiple response variables is rarely provided in publications.
(e.g., Jackson et al., 2011; Lin & Chu, 2018). However, we show that one can specify a multivariate model for latent, high-level LLRs, such as study-level values (see also, van Houwelingen et al., 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 evaluate independence (e.g., correlation coefficients that do not differ significantly from zero).

Possible disadvantages of specifying a multivariate model include the potential for additional computational costs associated with matrix operations that arise from the multivariate specification, or imputation of missing response values when multiple response variables are aligned (e.g., Jackson et al., 2011; Lin & Chu, 2018).

Second, unreported sample sizes, measures of uncertainty (e.g., $S$ or $se$), and covariate data are common in ecological meta-analyses (Kambach et al., 2020), and a Bayesian approach can easily accommodate simultaneous imputation of such missing information (e.g., Stevens, 2011; Ogle et al., 2013). Here, we simply specify likelihoods for the covariate data (e.g., MAP, MAT, and Dur), which serve as priors for the missing values, conditional on the observed (response and covariate) data. This allows us to retain records with missing covariate data, and to propagate uncertainty associated with 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 9.4% of the records being discarded, but in other analyses, rates of incomplete reporting can be much higher (e.g., Ogle et al., 2013). The high level of reporting for the GCME database likely reflects 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 reporting (e.g., Ogle et al., 2013). In summary, despite a push for comprehensive reporting (Gerstner et al., 2017), incomplete reporting will likely remain a challenge, especially if older studies are 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 Bayesian approach allows for retention of records with incomplete reporting such that information provided by these records, albeit incomplete, contributes to posterior estimates of study- and global-level parameters, covariate effects, variance terms, and other unknown quantities.
Third, within the Bayesian meta-analysis, it is straightforward to model the predicted responses (e.g., LRR values) as functions of study- or site-level covariates, or covariates that vary at other levels that are compatible with the data. In this study, the LRR values for AB, BB, and SCE were modeled as functions of site-specific climate and record-level experiment duration; this was not done in the original Dieleman et al. (2012) analysis. The AB and SCE responses to warming and the BB response to eCO\textsubscript{2} are predicted to be largest at the onset of the experiment and decrease with increasing duration, suggesting a time-dependent response to the associated treatment factor. Such duration effects have been reported for individual experiments (e.g., Hungate et al., 2004; Leuzinger 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 eCO\textsubscript{2} is expected to intensify with increasing exposure to eCO\textsubscript{2}.

Fourth, the Bayesian approach explicitly quantifies uncertainty in all unknown quantities, via the posterior distribution (Gelman et al., 2014). Interval estimates, such as a 95% credible interval (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\textsubscript{2} × warming experiments (e.g., Fig. 3c,f,i,l) point to the need for more multi-factor studies that manipulate multiple treatment factors (e.g., both eCO\textsubscript{2} and temperature). This was also suggested by a classical meta-analysis that was applied only to the eCO\textsubscript{2} × warming records (Dieleman et al., 2012); yet, the Bayesian approach described here provides predictions, and associated uncertainties, for a broad range of climate conditions and biomes that are not represented in the GCME database.

Fifth, the Bayesian meta-analysis model can be used to obtain posterior predictions, which can be evaluated to understand the range of potential responses and to further identify information gaps. Such predictions reveal that the effect of eCO\textsubscript{2} on BB and SCE and the effect of warming on all three responses (AB, BB, and SCE) depends on climate context, resulting in non-linear responses of AB and/or SCE to eCO\textsubscript{2} (e.g., Fig. 4). In general, most studies in our meta-analysis fall in the middle of the climate space (Fig. 4), where eCO\textsubscript{2} 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 strongest (most negative or most positive) or most uncertain (leading to non-significant effects) predicted responses are also those that are generally under-represented in manipulative experiments.
For example, SCE is predicted to be stimulated by warming in wet regions (e.g., temperate rainforests, temperate forests, and tropical forest savanna), but reduced by warming in dry regions (e.g., temperate grassland and subtropical desert) (Fig. 4d). Yet, little data are available for these biomes in the GCME database. This points to the need for more studies in under-represented and potentially sensitive regions (see also, Song et al., 2019), to test the expectation that AB, BB, and SCE responses to eCO$_2$, warming, or their combination vary among biomes and are governed by climate. Such research bias is not uncommon in meta-analyses, potentially restricting inferences to those ecosystems or biomes that are represented in the meta-analysis (Gurevitch & Hedges, 1999; Lowry et al., 2013).

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

**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 eCO$_2$ and warming. Both indicate that eCO$_2$ 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 eCO\(_2\) and warming. Conversely, Dieleman \textit{et al.} (2012) reported that AB was
significantly stimulated by warming and that the combination of eCO\(_2\) 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 \textit{et al.}, 2020).

With respect to the combined effect of eCO\(_2\) and warming, both approaches suggest that,
depending on site, eCO\(_2\) and warming can have an additive or slightly antagonistic effect on AB.
Moreover, Dieleman \textit{et al.} (2012) found a general trend for additive effects of eCO\(_2\) and warming on
multiple ecosystem variables, and given the large uncertainty associated with the study-level
estimates produced by the MHBM (Fig. 5), additive effects cannot be ruled out at the study level. This
is generally consistent with other studies (Yue \textit{et al.}, 2017b; Song \textit{et al.}, 2019). However, the MHBM
also provided global estimates of the combined effects (Fig. 5), whereas the classical analysis only
provided study-level estimates, without uncertainty. Based on the global MHBM estimates, there is
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 eCO\(_2\), or vice versa. The MHBM suggests the opposite for BB,
whereby an overall antagonistic effect emerged. Evidence for additive, synergistic, or antagonistic
effects of eCO\(_2\) and warming have implications for interpretation of the underlying mechanisms (e.g.,
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 \textit{et al.}, 2012;
Yue \textit{et al.}, 2017b).

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
underlying assumptions; this may be viewed as a benefit, but can also be challenging for those less familiar with statistical theory, probability distributions, or Bayesian methods. But, there are a myriad of resources (e.g., textbooks) for gaining familiarity in these areas, including, but not limited to Gelman et al. (2014), Gelman and Hill (2007), Hobbs and Hooten (2015), and Kruschke (2014).

Third, implementation of a Bayesian meta-analysis model may lead to greater computational challenges relative to a classical approach. The MHBM implemented herein took about 1-hour to complete (i.e., to sample from the posterior), which is relatively fast; but, it is possible that other models could require longer simulation times and/or exhibit convergence issues (Pappalardo et al., 2020) that could require additional troubleshooting and/or modification to the model or code (e.g., Ogle & Barber, 2020).

While we use the GCME database (Dieleman et al., 2012) to illustrate the MHBM approach for a relatively simple example, we anticipate that incorporation of additional predictor variables could improve model performance and inference. Independent of whether the meta-analysis is implemented in a Bayesian or classical framework, in the example considered here, potentially important predictors include plant functional type, soil characteristics, soil nutrient status, or other environmental conditions. However, many of these variables were not included in the GCME database, and potentially important predictors, such as nutrient availability, are often not reported in the publications from which the target response variables are extracted (Vicca et al., 2018). This further emphasizes the problem of research bias (Gurevitch & Hedges, 1999; Vicca et al., 2018) and 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., 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
does not make sense to impute those missing values separately, within each individual meta-analysis model. Though, imputation of the missing covariate data could be achieved separately (e.g., Kambach et al., 2020), so that the same imputed values are employed in each meta-analysis. Third, the 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 normal model (for SCE), and the prior for the 3×3 covariance matrix in Equation (7) would be modified for a 2×2 covariance matrix (related to the AB-BB bivariate model) and a scalar variance parameter (for the SCE model). All other equations would remain the same. The analyses would then have to be repeated, requiring additional computational time and effort to synthesis the results, but the results and inferences should remain unaffected. Thus, we do not see an advantage of implementing 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 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 summary, the advantages of a Bayesian meta-analysis approach (Table 3) are likely to outweigh the disadvantages, but there are situations where a classical meta-analysis may be preferred, or may help guide the development and implementation of a more flexible Bayesian meta-analysis.
Acknowledgments

This study was motivated by discussions that emerged from a workshop related to “how to improve global change studies and synthesis of results from such studies,” involving input from Christian Körner, Vigdis Vandvik, György Kröel-Dulay, Klaus Larsen, and Josep Peñuelas.

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 modeling framework, provided feedback on results, and contributed to manuscript writing.

Data availability

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

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References


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) eCO₂ only, (c) warming only, and (d) eCO₂ × 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 used in the multivariate meta-analysis is 100, which is less than 65 + 58 + 52 = 175 due to many (75) 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; , 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 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) elevated CO₂ (eCO₂), (g, e, h, k) warming, and

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(c, f, i, l) eCO$_2$ × 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 CO$_2$ 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 ≤ 0.01 (**), 0.01 < p ≤ 0.05 (**), and 0.05 < p ≤ 0.1 (*). Note that MAP, MAT, and MAP × MAT effects were not included in the models for AB, BB, and SCE under eCO$_2$ × 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 eCO$_2$ in eCO$_2$-only experiments (i.e., under ambient temperatures), (c) soil CO$_2$ exchange (SCE) to eCO$_2$ in eCO$_2$-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 µ > 0 (solid contour lines) imply that the treatment (eCO$_2$ or warming) increases AB or SCE relative to the control (ambient); contour lines associated with µ < 0 (dashed contour lines) imply that the treatment decreases AB or SCE relative to the control; µ = 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$_2$ × 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 CO$_2$ 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

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.

<table>
<thead>
<tr>
<th>Response variable*</th>
<th>Treatment type</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>eCO(_2)-only</td>
<td>Warming-only</td>
<td>eCO(_2) × warming</td>
<td>Total</td>
<td></td>
</tr>
<tr>
<td>AB</td>
<td>127 (42)</td>
<td>141 (30)</td>
<td>32 (11)</td>
<td>300 (65)</td>
<td></td>
</tr>
<tr>
<td>BB</td>
<td>122 (46)</td>
<td>50 (20)</td>
<td>33 (10)</td>
<td>205 (58)</td>
<td></td>
</tr>
<tr>
<td>SCE</td>
<td>346 (38)</td>
<td>143 (21)</td>
<td>55 (10)</td>
<td>544 (52)</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>595 (69)</td>
<td>334 (45)</td>
<td>120 (18)</td>
<td>1049 (100)</td>
<td></td>
</tr>
</tbody>
</table>

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 CO\(_2\) 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)).

<table>
<thead>
<tr>
<th>Treatment type</th>
<th>Response pair</th>
<th>Median</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>eCO₂-only ((t = 1))</td>
<td>AB-BB ((v = 1, v' = 2))</td>
<td>0.567</td>
<td>(0.178, 0.795)</td>
</tr>
<tr>
<td></td>
<td>AB-SCE ((v = 1, v' = 3))</td>
<td>-0.286</td>
<td>(-0.656, 0.231)</td>
</tr>
<tr>
<td></td>
<td>BB-SCE ((v = 2, v' = 3))</td>
<td>-0.274</td>
<td>(-0.685, 0.312)</td>
</tr>
<tr>
<td>Warming only ((t = 2))</td>
<td>AB-BB ((v = 1, v' = 2))</td>
<td>0.330</td>
<td>(-0.314, 0.781)</td>
</tr>
<tr>
<td></td>
<td>AB-SCE ((v = 1, v' = 3))</td>
<td>-0.074</td>
<td>(-0.627, 0.595)</td>
</tr>
<tr>
<td></td>
<td>BB-SCE ((v = 2, v' = 3))</td>
<td>0.260</td>
<td>(-0.341, 0.738)</td>
</tr>
<tr>
<td>eCO₂ (\times) warming ((t = 3))</td>
<td>AB-BB ((v = 1, v' = 2))</td>
<td>0.035</td>
<td>(-0.863, 0.825)</td>
</tr>
<tr>
<td></td>
<td>AB-SCE ((v = 1, v' = 3))</td>
<td>-0.019</td>
<td>(-0.771, 0.768)</td>
</tr>
<tr>
<td></td>
<td>BB-SCE ((v = 2, v' = 3))</td>
<td>0.204</td>
<td>(-0.706, 0.821)</td>
</tr>
</tbody>
</table>
Table 3. Summary of the unique attributes of the multivariate Bayesian meta-analysis modeling approach described in this study.

<table>
<thead>
<tr>
<th>Attribute</th>
<th>Description*</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1) Multivariate components</td>
<td>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.</td>
</tr>
<tr>
<td>(2) Retain all records</td>
<td>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.</td>
</tr>
<tr>
<td>(3) Regression-based approach</td>
<td>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 eCO$_2$ × warming treatment effects.</td>
</tr>
<tr>
<td>(4) Uncertainty quantification</td>
<td>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.</td>
</tr>
<tr>
<td>(5) Multiple treatment factors</td>
<td>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, warming-only, or eCO$_2$ × warming treatments are analyzed together because they...</td>
</tr>
</tbody>
</table>
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.