Measuring biological generality in meta-analysis: a pluralistic approach to

heterogeneity quantification and stratification

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Abstract

Uncovering general rules enhances the predictive capabilities in ecology and evolution. Meta-analytic approaches play a critical role in this endeavour, examining the extent to which phenomena can be replicated, generalized, and transferred. However, ecologists and evolutionary biologists have largely overlooked the role of meta-analytic heterogeneity in informing generality. To reform this situation, we introduce a pluralistic approach aimed at quantifying and stratifying various heterogeneity metrics, such as I^2, CV, M, and predictive distribution. These metrics offer complementary information, revealing the source, magnitude, and visual representation of heterogeneity. Our analysis of 512 meta-analyses demonstrates that heterogeneity is, on average, ten times larger than statistical noise, contributing to 91% of the observed variance (median $I^2 = 91\%$). This amount of heterogeneity is nearly twice the size of the meta-analytic mean effect (median $CV = 1.8$, $M = 0.6$), indicating substantial total heterogeneity in ecology and evolution. Surprisingly, in half of the cases, focal effects could generalize across studies even with high total heterogeneity by controlling for within-study variation. Our synthesis also visualises empirical distributions of various heterogeneity metrics, potentially serving as new benchmarks for informed interpretation. Our proposed pluralistic approach will accelerate the future quest for general rules via meta-analyses.

Main

Uncovering general patterns holds immense significance in ecology and evolution [1]. This enables scientists, practitioners, and policymakers to transfer findings across diverse systems, taxonomic groups, and spatiotemporal contexts. This pursuit enhances predictive capabilities and facilitates more precise management, intervention, and conservation practices. Ecologists and evolutionary biologists strive to unveil general processes and patterns using a range of approaches [2]. Notably, meta-analytic modelling has emerged as a natural route to assess the generality or context dependence of an effect of interest. By synthesizing a collection of conceptual replications [3], meta-analyses can scrutinize the extent to which inferences drawn from a specific context can be replicated (replication), extended beyond the reference context to a new context of interest (transferred), and extrapolated to the broader target population (generalized) as requested by stakeholders [2,4].

Meta-analyses play a crucial role in evaluating the generality of patterns [3]. Firstly, they quantitatively estimate the population mean effect across studies [5-7], characterising the central tendency of a focal effect. Secondly, they can identify effect modifiers or moderators contributing to context dependence [5] and provide tailored estimates for target contexts [4]. Third, meta-analyses can quantify variability in study outcome, the "heterogeneity" among effect sizes. Without quantifying heterogeneity, it is difficult to interpret both the overall trends and context-specific effects [8]. Heterogeneity can help to indicate the degree of inconsistency, or context dependence, of study findings, with high heterogeneity signalling a need to investigate the drivers of the variation. Lower heterogeneity can indicate high generality. Specifically, the mean effect size is highly transferable across the contexts characterised by the study pool without the need to consider effect modifiers [2]. Until now, the

74 significance of heterogeneity in informing generality has been largely overlooked. Indeed,

75 surveys have revealed that heterogeneity statistics are not routinely reported [7-9].

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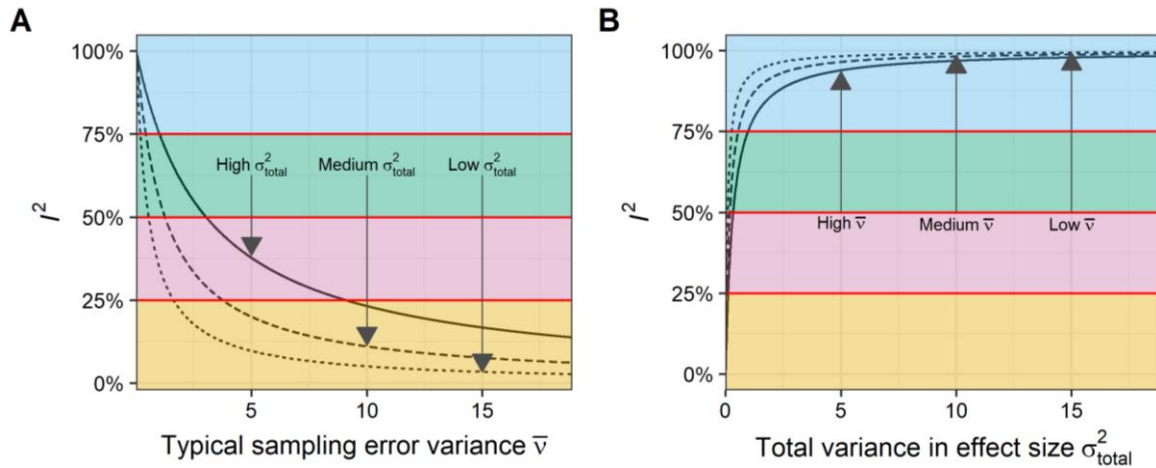
77

78 **Fig. 1:**

79 The interpretation of total I^2 can be ambiguous and can lead to incorrect conclusions about the

80 magnitude of heterogeneity. (A) A large estimated total I^2 value could be due to small sampling error

81 variances $\bar{v}$ (i.e., low statistical noise). (B) On the other hand, a large total I^2 value could also result

82 from a large true heterogeneity. Values of σ^2_{total} and $\bar{v}$ were derived from their empirical distributions

83 based on 512 meta-analyses (see Figs. S1 and S2). Total I^2 values were calculated using Equations 2

84 and 3. High, medium, and low σ^2_{total} (and $\bar{v}$) denote the 25%, 50%, and 75% percentiles of their

85 empirical distributions (Table 1). Three horizontal lines denote the conventional thresholds for the use

86 of I^2 to interpret the magnitude of heterogeneity [10].

87

88 Currently, measuring and interpreting meta-analytic heterogeneity faces two major

89 limitations. First, no single heterogeneity metric provides a holistic interpretation of

90 generality [11].Currently, the I^2 statistic is a popular metric that quantifies the proportion of

91 variance due to differences between effect sizes rather than by statistical noise (i.e., sampling

92 variance) [12,13]. The biological interpretation of I^2, however, is ambiguous [14] because a small

93 absolute heterogeneity can lead to a high I^2 due to small statistical noise (see Fig. 1) [12,14,15]. In

addition, I^2 is a point estimate and cannot reflect the whole distribution of context-specific

effects [16]. Second, meta-analyses typically focus on estimating total heterogeneity only [5],

despite the hierarchical nature of real biological data structures [6,9]. Explicitly decomposing

effect size heterogeneity across hierarchical levels (i.e., stratification) enables a more nuanced

assessment of generality, and helps in identifying contextual factors [5] that drive context

dependence. For example, in a multi-taxon meta-analysis, if stratification of studies by

species yields low heterogeneity at the taxon level, the focal effect still can be generalizable

across taxon (in terms of accounting for within-taxon variation; Fig. 2). This is so, even if the

total heterogeneity remains high [8].
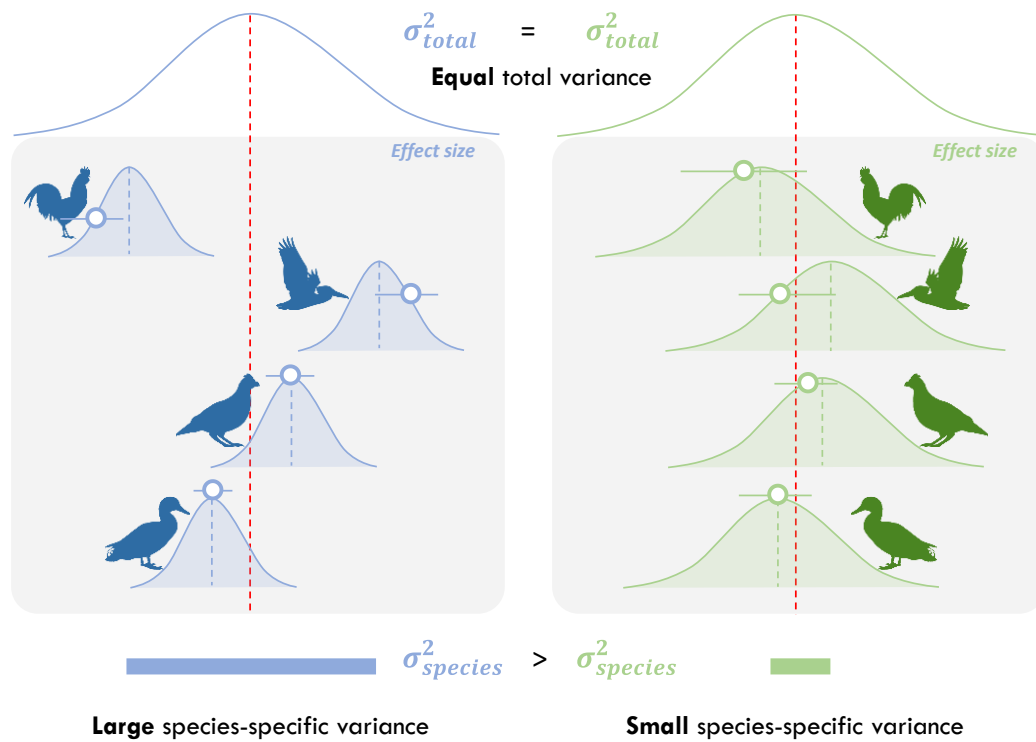
Fig. 2:

A cross-taxa meta-analysis with a high total variance can have a small amount of species-specific

heterogeneity. The focal effect is still possible to be generalizable at the species level. The circles

represent the replication of species-specific effect. The red dashed lines denote the meta-analytic

mean effects. See a real example in **Modelling additional source heterogeneity**.

110   Here, we present solutions to the aforementioned limitations, offering pluralistic pathways to

111   biological generality and transferability. We begin by reformulating the concept of

112   heterogeneity within the multilevel meta-analytic model and evaluating commonly used

113   heterogeneity measures. Building on this foundation, we take currently underused

114   heterogeneity metrics and propose new, stratified versions. After introducing the theoretical

115   background, we leverage a big dataset spanning 512 meta-analyses from the fields of ecology

116   and evolutionary biology (cf. [17,18]) to unveil empirical patterns of heterogeneity using these

117   measures and establish meta-scientific evidence on their (in)congruence. Next, we show ways

118   to visualise measures of heterogeneity using predictive distributions. Finally, we provide

119   practical recommendations and a tutorial with R functions for researchers to navigate the

120   complex landscape of heterogeneity (https://yefeng0920.github.io/heterogeneity_guide/). Our

121   synthesis highlights the significance of adopting a pluralistic framework for a comprehensive

122   understanding of meta-analytic findings in ecology and evolutionary biology.

Discerning biological generality

Heterogeneity in multilevel meta-analytic modelling framework

Data used in meta-analyses often exhibit a complex hierarchical structure [5,19], with study identity serving as a typical clustering variable, forming two strata (or more). Ecological and evolutionary meta-analyses typically report around eight effect sizes per study [20]. However, Traditional random-effects meta-analytic approaches do not account for heterogeneity driven by such data stratification [6,7,9], and multi-level meta-analysis is required to model heterogeneity at different strata or multi-levels in a meta-analysis (see **Methods**).

In the simplest multilevel model, the effect size estimate $ES_{[i]}$ is modelled as a combination of the population mean effect or meta-analytic mean effect size μ, random effects at two strata (i.e., between- and within-study levels), and statistical noise:

$$ES_{[i]} = \mu + u_{between[j]} + u_{within[i]} + e_{[i]}, (1)$$

The typical assumptions for Equation 1 is as follows: (i) between-study-level random effect $u_{b[j]}$ follows a normal distribution with mean zero and variance $\sigma^2_{between}$: $u_{between[j]} \sim \mathcal{N}(0, \sigma^2_{between})$, (ii) within-study-level random effect $u_{within[i]}$ follows a normal distribution with mean zero and variance σ^2_{within}: $u_{within[i]} \sim \mathcal{N}(0, \sigma^2_{within})$, and (iii) sampling error $e_{[i]}$ follows a normal distribution with mean zero and variance in effects defined by the sampling variance ($v_{[i]}$) associated with each effect size, i, such that $e_{[i]} \sim \mathcal{N}(0, v_{[i]})$. The assumption of homogeneous variances for the random effects can be relaxed to allow for heteroscedasticity [21]. Similarly, the assumption of independent sampling errors ($e_{[i]}$) can be relaxed to allow for sampling error covariance $v_{[i]}$ [7]. In the following sections, we will elaborate on how to stratify heterogeneity information using Equation 1.

Unstandardised heterogeneity metrics

Cochran's Q is a widely used metric for assessing heterogeneity in meta-analyses [22]. It serves as a test statistic to determine whether the true effects are homogeneous or not, informing a binary decision as to whether the effect sizes come from a common underlying population, or not (i.e., is heterogeneity 'non-zero'?). In contrast, the variance of true effects ($\sigma_{total}^2 = \sigma_{between}^2 + \sigma_{within}^2$) provides a direct measure of absolute heterogeneity. Equation 1 offers a general way to partition the variance of the observed effects into sampling error variance, and that of true effects at different strata, such as between-study ($\sigma_{between}^2$) and within-study strata (σ_{within}^2). By considering additional strata, such as variation in effects among species or geographical locations, the total variance in true effects (σ_{total}^2) can be further decomposed to assess generality at these specific strata (See **Model additional source heterogeneity**). For example, high variation among studies implies lack of generality from one study to another while low variation among species implies effects are similar, on average, across species. Nonetheless, relying solely on such absolute variance may not provide practical intuition regarding the magnitude of heterogeneity. For example, in a meta-analysis with $\sigma_{total}^2 = 1$, it is unclear whether this amount of variance is large and meaningful because absolute variance is not unit-free and not comparable across effect size measure used.

Variance-standardised heterogeneity metrics

The heterogeneity index, I^2 has emerged as the most popular metric as it provides a standardized measure of heterogeneity that accounts for the scale dependence (i.e., unit-free) [10]. I^2 is a variance-scaled heterogeneity metric that measures the proportion of total variance beyond statistical noise [13]. The total I^2 can be computed by dividing the variance in the true effects (σ_{total}^2) by the variance in the observed effects ($\text{Var}[ES_{[i]}]$), as follows:

$$171 \qquad I_{total}^2 = \frac{\sigma_{total}^2}{\text{Var}[ES_{[i]}]} = \frac{\sigma_{total}^2}{\sigma_{total}^2 + \bar{v}}, (2)$$

172 where $\bar{v}$ represents the "typical" sampling error variance. $\bar{v}$ can be computed using different

173 estimators [23,24], with the common one being [13]:

$$174 \qquad \bar{v} = \frac{(k-1)\sum_{i=1}^{k} 1/v_{[i]}}{(\sum_{i=1}^{k} 1/v_{[i]})^2 - \sum_{i=1}^{k} 1/v_{[i]}^2}, (3)$$

175 Within the multilevel modelling framework, the total I^2 can be stratified at different strata

176 [5,24], for example, by estimating I^2 at between-study ($I_{between}^2$) and within-study(I_{within}^2)

177 levels:

$$178 \qquad I_{between}^2 = \frac{\sigma_{between}^2}{\text{Var}[ES_{[i]}]} = \frac{\sigma_{between}^2}{\sigma_{total}^2 + \bar{v}}, (4)$$

$$179 \qquad I_{within}^2 = \frac{\sigma_{between}^2}{\text{Var}[ES_{[i]}]} = \frac{\sigma_{between}^2}{\sigma_{total}^2 + \bar{v}}, (5)$$

180 However, as mentioned earlier, large I^2 values do not necessarily imply a practically relevant

181 amount of heterogeneity (see Fig. 1; also see a case study in **Model additional source of**

182 **heterogeneity**). Statistical noise can sometimes inflate I^2 values, which is a common

183 occurrence in ecology and evolutionary meta-analyses (see **Empirical patterns of**

184 **heterogeneity in ecology and evolution**). Stratified I^2 metrics range from 0 to 100% (but

185 together sum to 100%), providing a clearer intuition of the source of heterogeneity and aiding

186 in assessing the drivers of context dependence at different strata. For example, a I_{within}^2 of

187 90% means within-study variation can account for 90% of heterogeneity, therefore, indicating

188 that within-study level predictors are more likely to drive context dependence. I^2 and its

189 stratified variants can also be transformed into the ratio of the variance of true effect to

190 typical sampling error variance ($\frac{\sigma^2}{\bar{v}} = \frac{I^2}{(1-I^2)}$ or $\log\left(\frac{\sigma^2}{\bar{v}}\right) = logit(I^2)$), which represents

191 heterogeneity as a proportion of the statistical noise (sampling error variance).

192

Mean-standardised heterogeneity metrics

Evolutionary biologists and behavioural ecologists are familiar with the variance-scaled metrics such as heritability (h^2) and repeatability (R), which are statistically comparable to the heterogeneity index, I^2. Although less commonly used, there also exists the mean-scaled counterparts, such as evolvability or the coefficient of variation (CV) for additive genetic variance (CV_A) and CV for between-individual variance (CV_B) [25]. In a similar manner, there exists a mean-scaled heterogeneity metric that can provide a standardized measure of heterogeneity, denoted as CV_{total}, that compares the standard deviation σ_t to the magnitude of its population mean (μ) [23]:

$$CV_{total} = \frac{\sigma_{total}}{|\mu|}, (6)$$

CV_t expresses the total heterogeneity as a proportion of the meta-analytic mean effect (or as a percentage of change in the meta-analytic mean effect when multiplied by 100). To provide a more precise quantification of heterogeneity at different strata, we propose stratified versions of CV_t. Under the simplest multilevel model framework (Equation 1), we propose estimating between-study, CV_b, and within-study, CV_w, as follows:

$$CV_{between} = \frac{\sigma_{between}}{|\mu|}, (7)$$

$$CV_{within} = \frac{\sigma_{within}}{|\mu|}, (8)$$

Notably, these mean-scaled variance metrics have the limitation of becoming arbitrarily large as the magnitude of meta-analytic mean effect $|\mu|$ approaches zero [26]. It is this limitation that has probably prevented the widespread adoption of the mean-scaled variance in the field of evolutionary quantitative genetic and animal personality research [25,27].

Variance-mean-standardised heterogeneity metrics

216   To remedy the problems of I^2 and CV_{total} as illustrated above, there is a more robust measure

217   of heterogeneity M_{total} that combines the strengths of mean-scaled and variance-scaled

218   metrics [11]:

$$M_{total} = \frac{\sigma_{between} + \sigma_{within}}{\sigma_{between} + \sigma_{within} + |\mu|}, (9)$$

219

220   Here we propose between-study ($M_{between}$) and within-study (M_{within}) versions by

221   stratifying M_t, which allows for a more precise quantification of heterogeneity at specific

222   strata:

$$M_{between} = \frac{\sigma_{between}}{\sigma_{between} + \sigma_{witin} + |\mu|}, (10)$$

223

$$M_{within} = \frac{\sigma_{within}}{\sigma_{between} + \sigma_{within} + |\mu|}, (11)$$

224

225   M_t and its stratified variants are still standardised measures that quantify the size of

226   heterogeneity relative to the magnitude of meta-analytic mean effect, providing intuitive

227   interpretation. For example, $\sigma_{total} = 0$ leads to $M_{total} = 0$, indicating the population mean

228   effect is fully generalisable, and replicable across different contexts (see a case study in

229   **Model additional source of heterogeneity**). One the other hand, M_{total} and its stratified

230   variants are truncated at one, which overcomes the issue of CV_{total} when the magnitude of

231   meta-analytic mean effect $|\mu|$ approaches zero. Note that there is another mean- and variance-

232   scaled metric, M^2_{total}, where σ_{total} and $|\mu|$ are replaced by their squared values (**Methods**).

233   CV_{total}, M_{total} and M^2_{total} can be all be easily stratified using multilevel meta-analytic

234   models (**Model additional source of heterogeneity**).

235

236   **Empirical patterns of heterogeneity in ecology and evolution**

237   To evaluate empirical patterns in heterogeneity among meta-analytic studies in ecology and

238   evolution, we applied multilevel meta-analytic models (Equation 1) to 512 published meta-

239 analyses [18,28]. For each meta-analysis, we quantified and stratified heterogeneity using I^2_{total},

240 CV_{total}, M_{total}. For I^2_{total}, the 25th, 50th, and 75th percentiles corresponded to 79%, 91%,

241 and 97% I^2_{total}, respectively (Fig. 3), rather than conventional thresholds for interpreting I^2,

242 which typically categorize heterogeneity as small, moderate, or high at 25%, 50%, and 75%

243 I^2_{total}, respectively [10]. This also means, on average, variation in true effect sizes σ^2 was ten

244 times as large as typical sampling error variance ($\frac{\sigma^2}{\bar{v}} = \frac{I^2}{(1-I^2)} = 10$; see Figs. S1 and S2 for

245 empirical distributions of σ^2 and $\bar{v}$) and 91% of them can be attributed to the 'true' biological

246 or methodological differences in research contexts, and thus are theoretically explainable

247 using appropriate predictors.

248

249 While I^2_{total} displayed a left-skewed and single-modal distribution, its stratified counterparts,

250 $I^2_{between}$ and I^2_{within}, demonstrated a right-skewed distribution with multi-modal patterns.

251 There was no consistent trend suggesting one type of stratified heterogeneity consistently

252 outweighed the other across the 512 meta-analyses (Fig. 3). Intriguingly, 47% (242 out of

253 512) of the meta-analyses exhibited smaller between-study level heterogeneity than within-

254 study level heterogeneity ($I^2_{between} < I^2_{within}$; Fig. 4). Within this subset of meta-analyses, the

255 median values for I^2_{total}, $I^2_{between}$ and I^2_{within} were 95%, 21%, and 63%, respectively. It

256 highlights a key finding often overlooked by traditional heterogeneity quantification

257 practices: findings from many meta-analyses with high total heterogeneity can still be

258 generalized at the between-study study level. Such generalization is achievable when

259 replication is defined as the testing of the null hypothesis at the between-study level, and

260 when within-study methodological and biological variations can be adequately accounted for

261 (i.e., within-lab heterogenization [29]) because some meta-analyses have relatively low

262 heterogeneity at the between-study study level.
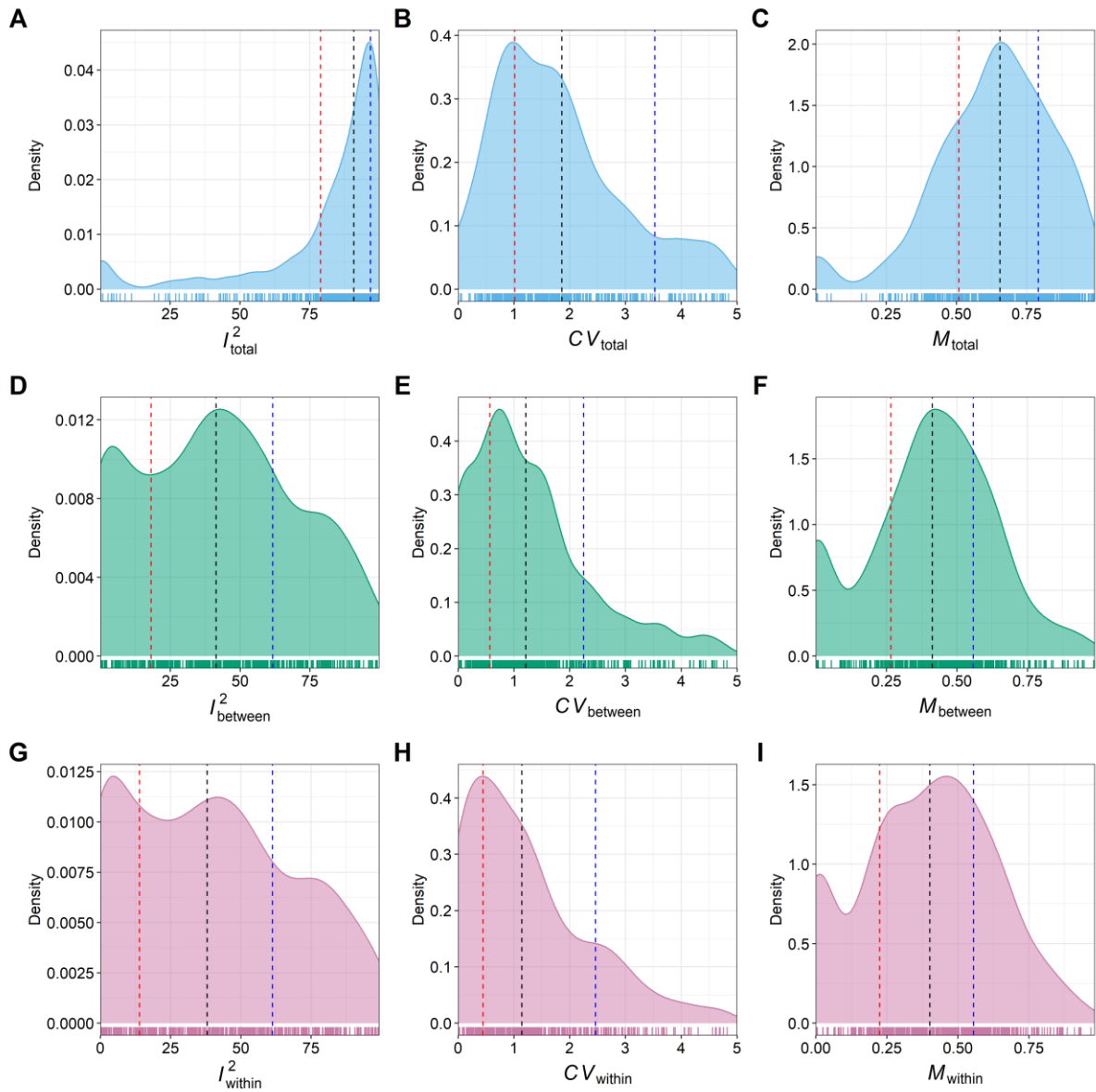
Fig. 3:

The distribution of heterogeneity estimates derived from 512 meta-analyses was systematically

assessed using pluralistic measures and stratified across different strata. Total heterogeneity measures

$(A - C)$: I^2_{total}, CV_{total} and M_{total}. Between-study heterogeneity measures $(D - E)$: $I^2_{between}$,

$CV_{between}$ and $M_{between}$. Within-study heterogeneity measures $(G - I)$: I^2_{wihtin}, CV_{within} and

M_{within}. Three dashed lines correspond to the 25th, 50th, and 75th percentiles, respectively. In panels

B, E, and H, the CV was truncated at five for figure clarity, as very large CV values can be challenging

to interpret when the meta-analytic mean effect is small. For example, the maximum CV observed in

272   the 512 meta-analyses was 106, which was inflated by a small meta-analytic mean effect of 0.03. For

273   the figures without truncation, please refer to Figure S3.

274

275   When the CV_{total} metric was used to quantify heterogeneity, the calculated 25th, 50th, and

276   75th percentiles of CV_{total} values were 1.0, 1.8, and 3.5, respectively (Fig. 3). This means

277   that the standard deviation (in this case, heterogeneity) was, on average, nearly twice that of

278   the meta-analytic mean effect. The distributions of both CV_{total} and its stratified versions,

279    $CV_{between}$, and CV_{within}, displayed a right-skewed pattern with a single-mode. In contrast, the

280   distribution of M_t exhibited a more symmetrical pattern, with the 25th, 50th, and 75th

281   percentiles of M_{total} values being 0.5, 0.6, and 0.8, respectively (Fig. 3), albeit with a minor

282   peak around zero. Notably, stratification analysis revealed that $M_{between}$ and M_{within} had

283   patterns similar to those observed for $CV_{between}$ and CV_{within}. This similarity is expected as

284   they can be mathematically transformed into one another using equations $M_{total} =$

285    $CV_{total}/(1 + CV_{total})$ and $logit(M_{total}) = \log(CV_{total})$. The median values for both

286   CV_{total} and M_{total} across the 512 meta-analyses signify a high amount of heterogeneity,

287   thereby warranting a thorough exploration into the drivers influencing such context

288   dependence. However, stratification of M_{total} also suggests that meta-analyses with high

289   heterogeneity can possess a considerable likelihood of generality at the between-study level,

290   given low $M_{between}$ (as we pointed out above with I^2). On average, there was a median

291    $M_{between} = 0.3$ (SD is 41% of the meta-analytic mean effect) observed in 47% of the meta-

292   analyses (242/512) with smaller $M_{between}$ values compared to M_{within} values (Fig. 4).

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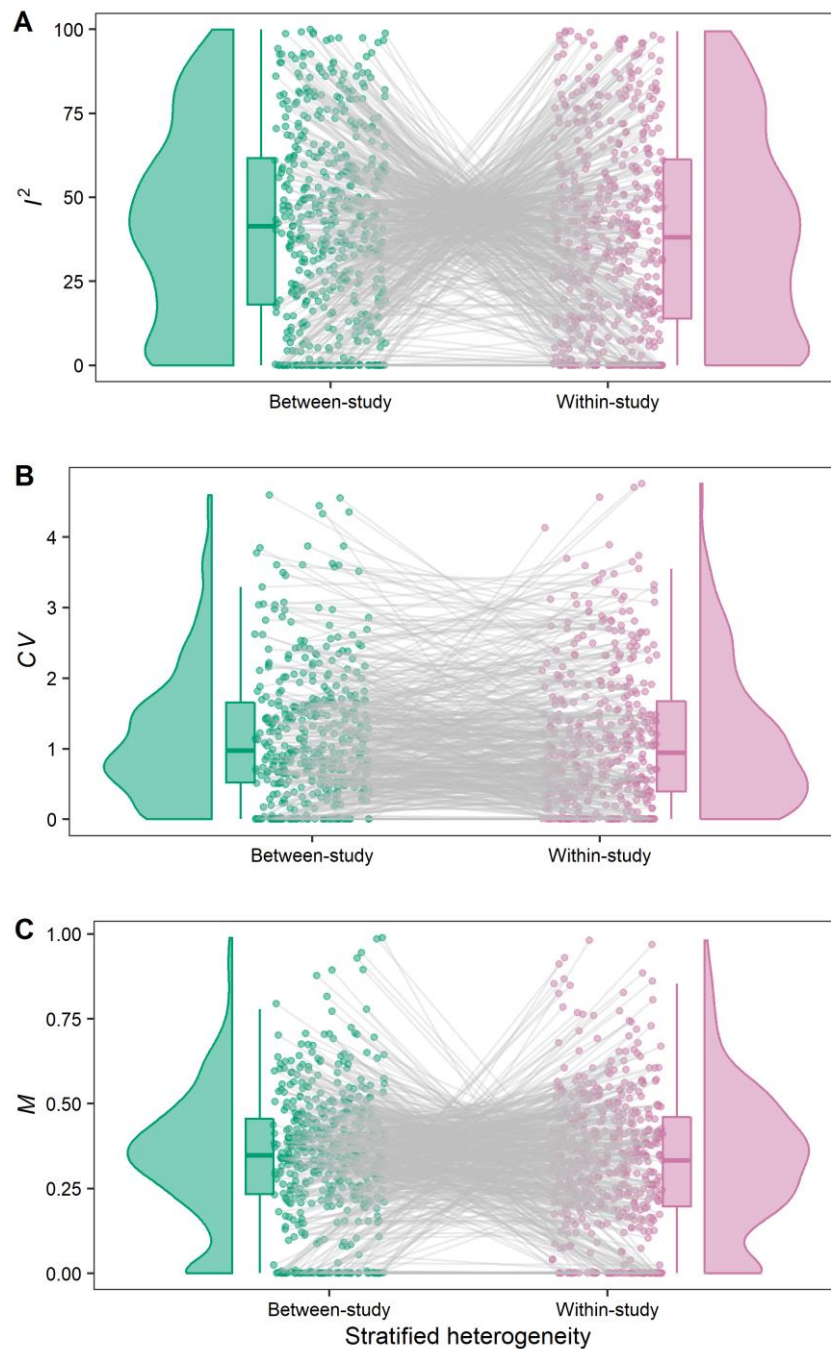
Fig. 4:

Paired comparison of stratified heterogeneity estimates derived 512 meta-analyses for three

heterogeneity metrics (A) I^2, (B) coefficient of variation, CV and (C) M. Heterogeneity was stratified

at both 'between-study' and 'within-study' levels (x-axes). Each point represents an estimate from

each meta-analysis. For panel B, CV has been truncated at five for figure clarity. For the full figures

without truncation, please refer to Figure S4. For other details see Fig. 3.

300

301   We found only moderate agreement between heterogeneity measured as I^2 and the

302   alternatives (CV_{total}: $r_{spearman} = 0.32$, 95% CI = [0.24, 0.40], M_{total}: $r_{spearman} = 0.33$, 95% CI =

303   [0.25, 0.41]; Fig. 5). In cases of meta-analyses with I^2 larger than 75% or smaller than 25%

304   (identified as large and small heterogeneity by conventional benchmarks [10]), the disagreement

305   between I^2 and CV, as well as I^2 and M, became even more pronounced (Fig. S5 – S7). In

306   contrast, a near-perfect agreement was observed between CV_{total} and M_{total}, as expected

307   ($r_{spearman} = 1$, 95% CI = [0.99, 1]; Fig. 5). Therefore, cross-meta-analysis (meta-scientific)

308   evidence suggests that the heterogeneity source measure I^2 is not consistent with the

309   magnitude measures (CV_{total} and M_{total}) for ecological and evolutionary data. We also found

310   that out of the 512 meta-analyses featuring medium to large I^2_{total} values (>50% based on

311   conventional guidelines), 80 had small CV_{total} (Fig. 5), indicating that more than 20% of the

312   large I^2_{total} values were caused by small sampling errors rather than larger amount of

313   heterogeneity. These findings emphasize the importance of considering multiple metrics to

314   obtain a holistic understanding of heterogeneity in meta-analyses (see **A pluralistic**

315   **framework**).
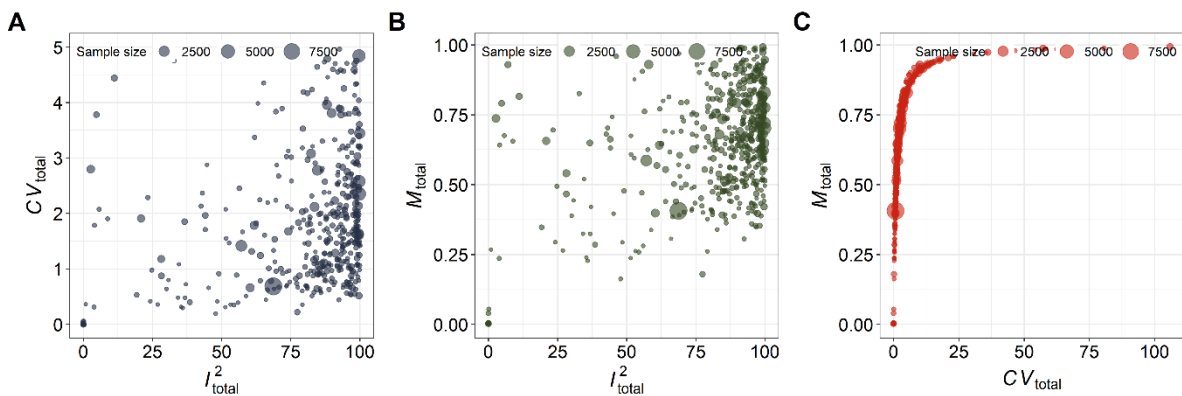
317   **Fig. 5:**

318   Disagreement (or agreement) between different heterogeneity metrics. For other details see Fig. 3.

319   The Spearman correlation estimates ($r_{spearman}$) were: 0.32, 95% CI = [0.24, 0.40] for I^2_{total} and CV_{total},

320   0.33, 95% CI = [0.25, 0.41] for I^2_{total} and M_{total}, and 1, 95% CI = [0.99, 1] for M_{total} and CV_{total}.

Prediction intervals and predictive distributions: visualising heterogeneity

Prediction intervals (PIs) are underreported but insightful in meta-analytic heterogeneity and generality. Surveys have shown that less than one per cent (1/102) of such studies reported Pis [30]). Pis are derived from the definition of σ_t^2 and provide a range within which a future effect size is predicted to fall with a certain probability [14], often 95% (Fig. 6).
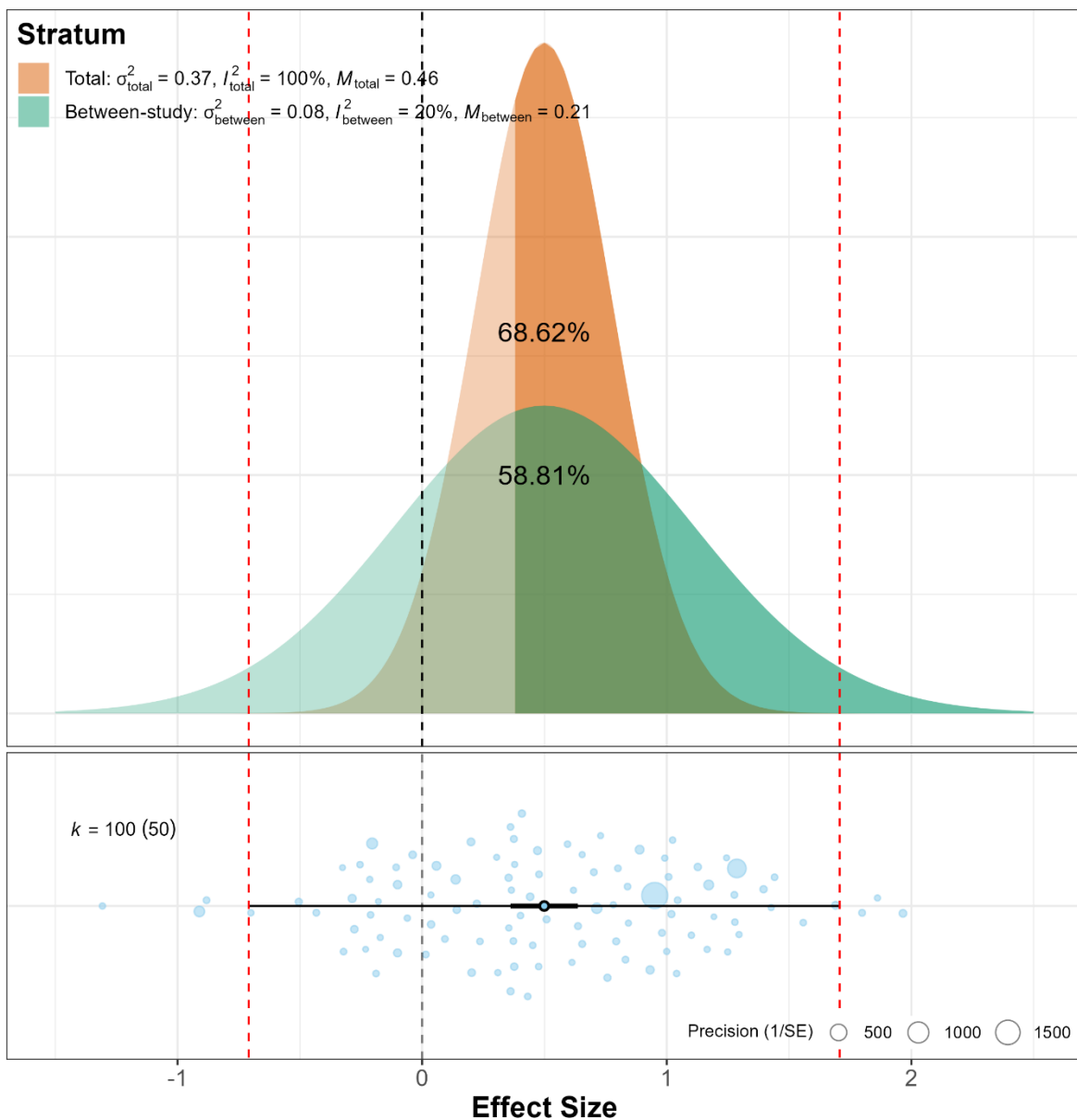
Effect Size

Fig. 6:

Example of how prediction intervals (PIs) combined with 'prediction distributions' (PDs) can be used to understand effect size heterogeneity and generality. Effect size data are simulated assuming two

331   effect sizes were collected from a total of $n = 50$ studies, ($k = 100$), with a $\sigma^2_{between} = 0.1$, $\sigma^2_{within} =$

332   0.6 and an overall meta-analytic mean, u, of 0.5

333   (https://yefeng0920.github.io/heterogeneity_guide/). Red dashed lines are the upper and lower

334   95% PI, black dashed line the 'null' effect. The orchard plot [30] displays the overall meta-analytic

335   mean, 95% confidence interval (CI) and 95% PI. The PDs were constructed using t-distribution with k

336   -1 degrees of freedom, u as location parameter, and total or between-study variance along with

337   sampling variance of around u as scale parameter (see Equation 11). The percentage of effect sizes

338   beyond a given threshold (i.e., the lower 95% CI) are provided.

339

340   For example, consider a conservation intervention with a mean effect size (SMD) of -0.5 and

341   95% PI of [-0.2 to -0.8]. This indicates that 95% of future interventions implemented in are

342   predicted to decrease the conservation outcomes of interest by between 0.2 to 0.8 standard

343   deviations. Unlike the point estimate of heterogeneity, such as σ^2_t, PIs offer an interval to

344   inform the extent to which the focal effect can be generalized [31]. Under Equation 1, 95% PIs

345   can be computed by [7]:

346    $$95\%\text{PI} = \mu \pm t_{0.975}\sqrt{\sigma^2_{between} + \sigma^2_{within} + \text{SE}[\mu]^2}, (11)$$

347   where $t_{0.975}$ denotes the 97.5th percentile of a t-distribution (with $k-1$ degrees of freedom [32],

348   where k is the number of sample size), and SE$[\mu]$ denotes the standard error of the mean

349   effect μ.

350

351   Despite their usefulness, PIs can create the illusion that all effect sizes within the upper and

352   lower intervals are equally likely (Fig. 6; see also [33]). Therefore, statisticians have

353   emphasised the importance of visualising the probability density to accurately capture the

354   likelihood of each effect size within the intervals [34,35]. By considering the entire distribution

355   of true effects while accounting for statistical noise, the predictive distribution (PD) offers a

356   more holistic measure of heterogeneity and generality. In the Bayesian framework, PDs,

357   known as posterior distributions, are a natural part of the process, but even frequentist

358   approaches can adopt PDs (sometimes referred to as "empirical Bayes") to achieve similar

359   aims. An advantage of the PD is its ability to calculate the probability that a true effect size

360   exceeds a biologically or practically meaningful threshold although determining such a

361   threshold usually requires domain-specific knowledge and expertise. The proportion of true

362   effect sizes above a specific threshold could serve as a measure of evidence strength and

363   generality [16]. Consider a case that 69% of effect sizes representing the efficacy of a

364   conservation intervention are predicted to surpass a threshold value representing a practically

365   significant effect (Fig.6, where we assumed the lower confidence limit representing the

366   threshold). If assuming similar configurations of study contexts in the sampled future cases,

367   we can infer that the intervention will achieve this benefit in 69% of future cases, with strong

368   implications for policymaking.

369

370   **Modelling additional sources of heterogeneity**

371   In ecological and evolutionary datasets, complexity often arises from the inclusion of diverse

372   species, temporal, and spatial variations [3]. Such complexity offers a unique opportunity for

373   further disentangling heterogeneity. This can be achieved by embracing a flexible random-

374   effects structure within the multilevel meta-analytic framework [7,9]. To illustrate this, we will

375   show the principles of how to partition heterogeneity in datasets featuring multiple species

376   (similar principles can be applied to those involving different temporal and spatial contexts).

377   In the case of datasets encompassing multiple species, incorporating species-relevant

378   random-effects terms into Equation 1 would lead to the phylogenetic multilevel meta-analytic

379   model [5,36]:

380    $$ES_{[i]} = \mu + u_{species[k]} + u_{phylogeny[k]} + u_{between[j]} + u_{within[i]} + e_{[i]}, \quad (12)$$

381 where $u_{s[k]}$ denotes the non-phylogenetic species random effect, which follows a normal

382 distribution with mean zero and variance $\sigma^2_{species}$; $u_{phylogeny[k]}$ denotes the phylogenetic

383 species random effect, which follows a multivariate normal distribution with mean zero and

384 variance-covariance matrix $\sigma^2_{phylogeny}\boldsymbol{A}$ (where $\sigma^2_{phylogeny}$ is the phylogenetic species

385 variance, and $\boldsymbol{A}$ is phylogenetic correlation matrix based on the distance between species on a

386 molecular-based phylogenetic tree).

387

388 With Equation 12 in hand, the total variance can be stratified at the phylogenetic and non-

389 phylogenetic species level ($\sigma^2_{phylogeny}$ and $\sigma^2_{species}$). Such stratification allows for the

390 assessment of the generality of a focal effect within these strata, as illustrated in the empirical

391 example below. Phylogenetic and non-phylogenetic species-level heterogeneity can be

392 measured using $I^2_{phylogeny}$ and $I^2_{species}$, respectively [5]:

393
$$I^2_{phylogeny} = \frac{\sigma^2_{phypogeny}}{\sigma^2_{phypogeny} + \sigma^2_{species} + \sigma^2_{between} + \sigma^2_{within} + \bar{v}}, (13)$$

394
$$I^2_{species} = \frac{\sigma^2_{species}}{\sigma^2_{phylogeny} + \sigma^2_{sspecies} + \sigma^2_{between} + \sigma^2_{within} + \bar{v}}, (14)$$

395 We derive the alternative stratified version of measures as follows:

396
$$CV_{phylogeny} = \frac{\sigma_{phylogeny}}{|\mu|}, (15)$$

397
$$CV_{species} = \frac{\sigma_{species}}{|\mu|}, (16)$$

398
$$M_{phylogeny} = \frac{\sigma_{phylogeny}}{\sigma_{phylogeny} + \sigma_{species} + \sigma_{between} + \sigma_{within} + |\mu|}, (17)$$

399
$$M_{species} = \frac{\sigma_{species}}{\sigma_{phylogeny} + \sigma_{species} + \sigma_{between} + \sigma_{within} + |\mu|}, (18)$$

400   Furthermore, the predictive distribution also can be stratified at phylogenetic and non-

401   phylogenetic species-level, which provides a visual means to assess the heterogeneity and

402   generality at these strata.

403

404   To illustrate the insights gained through these extended measures, we present an empirical

405   example. We re-analysed a phylogenetic meta-analysis originally conducted by Risely et al.

406   [37]. Our focus centres on a subset of this analysis, specifically examining the impact of

407   infection status on the cost (e.g., movement capacity) of migratory animals. The data and

408   code for replicating all calculations can be found at

409   https://yefeng0920.github.io/heterogeneity_guide/. Our re-analysis yielded three

410   observations. Firstly, I^2_{total} = 97% exceeded the 75th percentile of the empirically derived

411   heterogeneity distribution (Fig. 7 and Table S1). This suggests a high amount of

412   heterogeneity according to the conventional benchmarks [10]. However, when we employed

413   magnitude metrics to measure heterogeneity, they fell below between the 25th and 50th

414   percentiles of the empirically derived heterogeneity distribution (CV_{total} = 1.3 and M_{total} =

415   0.6). This discrepancy was attributed to the small typical sampling variance $\bar{v}$, which was

416   found to be 0.001 in this case, underscoring I^2_{total}'s limitation of relying on $\bar{v}$ to capture

417   relative magnitude of heterogeneity. On the other hand, we emphasise that the proper

418   interpretation of I^2_{total} is to use it to indicate the source of heterogeneity rather than the

419   magnitude, as it represents the variance of the true effect in the context of the variance of the

420   observed effect. For example, I^2_{total} = 97% suggests a heterogeneity can explain most (97%)

421   of the variability in effect size (only 3% is explained by the sampling variance, or the

422   heterogeneity is 32 times larger than that of statistical noise).

423
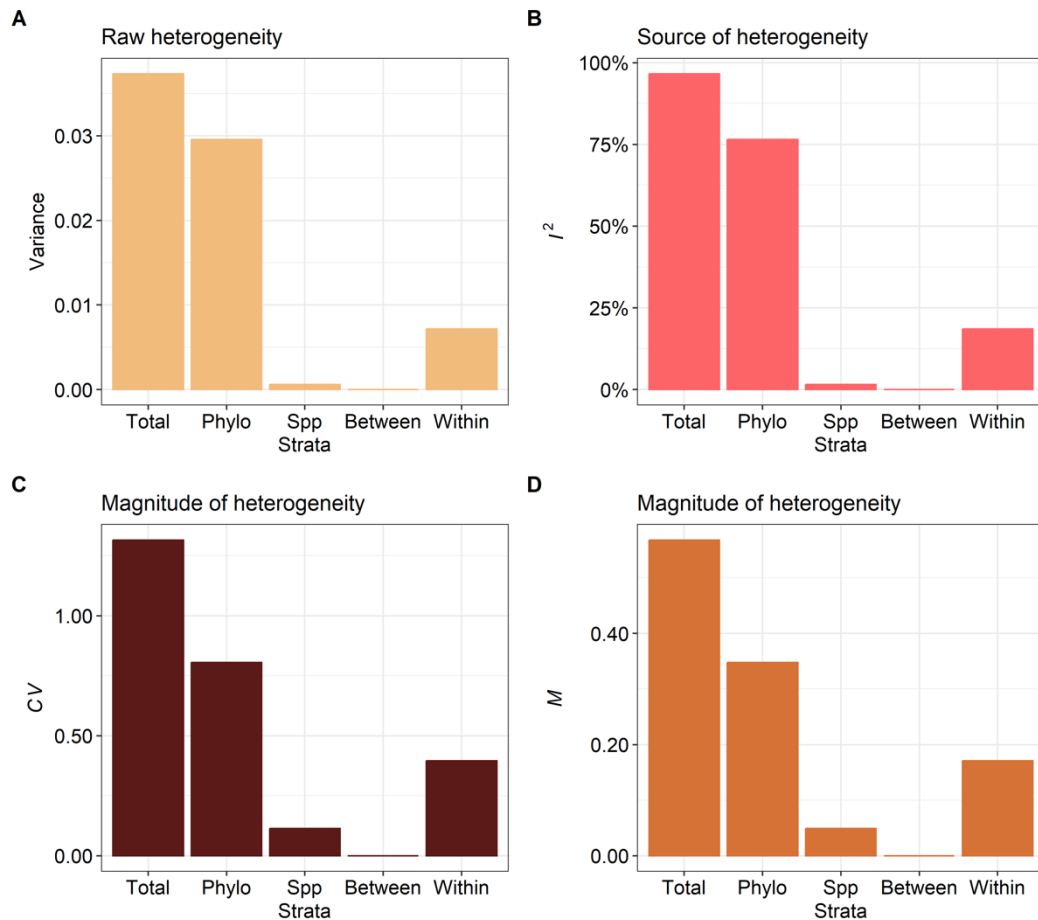
Fig. 7:

Heterogeneity quantification and stratification for multiple metrics. (A) The heterogeneity is quantified using raw variance, (B) source measure I^2, (C) magnitude measure CV, and (D) magnitude measure M, and stratified at phylogenetic (Phylo), non-phylogenetic (Spp), between-study (Between), and within-study (Within) levels. The source measure I^2 sometimes aligns well with the raw variance, as observed in this example (A and B). However, we note that I^2 values can be challenging to interpret as the magnitude of heterogeneity, especially when the typical sampling error variance is extremely small or large. This challenge is often encountered with certain effect size measures, such as the log coefficient of variation ratio (lnCVR), as demonstrated in a real example at https://yefeng0920.github.io/heterogeneity_guide/.

435 Secondly, the estimated mean effect was highly likely to be generalizable and replicable at

436 the between-study- and species-context, if controlling for within-study experimental contexts

437 (e.g., age, sex, outcomes). This is indicated by the stratification analysis that between-study

438 level heterogeneity was extremely low, despite a large heterogeneity according to

439 conventional benchmarks [10]. Traditional meta-analytic practices would overlook these

440 valuable insights, potentially leading to erroneous conclusions. For example, random-effects

441 meta-analysis shows that this dataset has high study-level heterogeneity (I^2_{total} = 96%; Fig. 5

442 and Table S1). However, this amount of heterogeneity was not attributable to the study level

443 but, rather, was mainly explained by the phylogenetic signal ($I^2_{phylogeny}$ = 76%). The

444 stratified version of PD also provided a clearer visual clue that the phylogenetic signal was

445 the primary source of heterogeneity (Fig. 7).

446

447 **A pluralistic framework**

448 Given that different measures offer distinct insights into heterogeneity and generality (Table

449 1), we propose adopting a pluralistic framework to comprehensively assess heterogeneity in

450 ecological and evolutionary meta-analyses. Our recommendations are threefold:

451   (1) Employing multilevel meta-analytic framework: Provided data allow, we strongly

452   advocate for the use of a multilevel meta-analytic framework (Equation 1), as

453   opposed to random-effects meta-analysis, for the modelling and stratification of

454   heterogeneity. Additional random effects can be incorporated into Equation 1 as

455   needed to further dissect heterogeneity. For example, the application of the

456   phylogenetic multilevel meta-analytic model (Equation 12) allows for the

457   disentanglement of species-specific heterogeneity.

458   (2) Quantification and stratification of pluralistic heterogeneity measures: We recommend

459   transparently reporting all variance components, including typical sampling error

460	variances in the main text, supplementary tables, or figures (Figs. 6 and 7 and Table
461	1). As such, pluralistic metrics can be computed using the formula above. I^2, M (with
462	CV being derivable from M), and their stratified versions should be reported as the
463	default measures. PI or PD should also be reported to provide a visual identification
464	of the heterogeneity information. These measures provide complementary
465	information, for example, the source, magnitude, and visual clue of heterogeneity
466	(examples see **Table 1**). We also provide parametric bootstrapping solutions to
467	estimate the uncertainty (e.g., 95%CI) for each of the measures.
468	(3) Check the model parameter identifiability: When models incorporate many random
469	effects, issues of parameter identifiability may arise, wherein unique variance
470	estimates that maximize the likelihood function may not exist (see **Method**) [39].
471	Therefore, we recommend assessing whether variance components are all identifiable
472	through means such as checking profile likelihood, before proceeding with
473	heterogeneity quantification and stratification.
474	(4) Carefully interpret heterogeneity measures: It is crucial to interpret both total and
475	stratified heterogeneity to evaluate variation in effect sizes, aiding in the examination
476	of general rules in the fields of ecology and evolution (see a case study in **Modelling**
477	**additional sources of heterogeneity**). However, neither the conventional benchmarks
478	(25, 50, and 75% as small, moderate and high heterogeneity [10]) nor those of
479	empirically derived distributions (Table 1 and Fig. 3) are currently suitable for
480	informing interpretation. Nevertheless, the empirically derived distribution can be
481	employed to interpret heterogeneity within the context of existing ecological and
482	evolutionary meta-analyses.
483	

484   We argue that ecologists and evolutionary biologists should treat heterogeneity and the meta-

485   analytic mean effect size with equal importance. We provide a user-friendly tutorial equipped

486   with a set of R functions to streamline the qualification, stratification, and interpretation of

487   heterogeneity https://yefeng0920.github.io/heterogeneity_guide/, empowering ecologists and

488   evolutionary biologists to discern generality.

489

490   Table 1

491   Summary of heterogeneity measures, their stratified counterparts, and empirically derived benchmark values. SMD denotes standardised mean

492   difference. lnRR denotes log response ratio. *Zr* denotes Fisher's r-to-z transformed correlation coefficient. 2-by-2 table denotes often

493   dichotomous (binary) effect size measures, such as log odds ratio, log risk ratio. Uncommon measures represent less frequently used effect size

494   measures, such as raw mean difference and regression coefficients.

Types	Metrics	Interpretation and examples	Empirically derived benchmark[1]
Test statistic	Q	Null-hypothesis test. Statistical test of heterogeneity in effect sizes.	Not applicable
Unstandardisation	σ^2	Absolute magnitude measure of heterogeneity. Variance (square of standard deviation) of the meta-analytic mean effect (σ^2_{total}) and its stratification at between- and within-study contexts ($\sigma^2_{between}$ and σ^2_{within}).	25th, 50th, and 75th percentiles (Fig. S1): 0.54, 1.25, 3.03 for SMD; 0.11, 0.27, 0.57 for lnRR; 0.06, 0.12, 0.25 for *Zr*; 1.04, 1.20, 2.51 for the 2-by-2 table; 0.01, 0.04, 0.27 for uncommon measures. The percentiles of typical sampling variance $\bar{v}$ are reported at Fig. S2.
Variance-standardization	I^2	Heterogeneity source measure. Proportion of variance not due to statistical noise. It measures the source of heterogeneity. For example, σ^2_{total} = 95% denotes that 95% of variation is the result of nuisance heterogeneity (i.e., differences in contexts). $\sigma^2_{between}$ = 80% and σ^2_{within} = 15% indicate differences in between-study contexts dominate the heterogeneity, pointing towards between-study level predictors as the likely drivers of context-dependent variation.	25th, 50th, and 75th percentiles (Fig. 3): 79%, 91%, 97% for overall; 78%, 89%, 96% for SMD; 88%, 95%, 99% for lnRR; 73%, 87%, 95% for *Zr*; 71%, 73%, 89% for the 2-by-2 table; 74%, 91%, 98% for uncommon measures.

		Heterogeneity magnitude measure. Variance expressed as the proportion of the mean effect. It is the measure of the magnitude of heterogeneity in the context of mean effect. For example, $CV_{total} = 1.5$, $CV_{between} = 0.8$, and $CV_{within} = 0.5$ denote that total, between- and within-study variance are 150, 80, and 50% of the mean effect.	25th, 50th, and 75th percentiles (Fig. 3): 1.0, 1.8, 3.5 for overall; 1.1, 2.0, 3.9 for SMD; 1.2, 1.9, 3.5 for lnRR; 0.8, 1.7, 2.9 for Zr; 1.2, 2.2, 2.7 for the 2-by-2 table; 0.7, 1.1, 1.3 for uncommon measures.
Mean-standardization	CV		
Variance-mean-standardization	M	Heterogeneity magnitude measure. Variance expressed as the proportion of the mean effect and a transformation of CV designed with better properties. It is the measure of the magnitude of heterogeneity in the context of mean effect. The interpretation can be eased by back-transformation with $M_{total} = CV_{total}/(1 + CV_{total})$. For example, $CV_{total} = 0.6$, $CV_{between} = 0.5$, and $CV_{within} = 0.4$ denote that total, between- and within-study variance are 150, 100, and 67% of the mean effect.	25th, 50th, and 75th percentiles (Fig. 3): 0.5, 0.7, 0.8 for overall; 0.5, 0.7, 0.8 for SMD; 0.5, 0.7, 0.8 for lnRR; 0.5, 0.6, 0.8 for Zr; 0.5, 0.7, 0.7 for the 2-by-2 table; 0.4, 0.5, 0.6 for uncommon measures.
Visual metric	PI & PD	Heterogeneity visual measure. A plausible interval where a new effect size is predicted to fall with a specified level of probability. It can be used to visually diagnose the heterogeneity and generality of the mean effect. For example, a 95% prediction interval (PI) of [-0.2 to -0.8] indicates that 95% range of future effect sizes are expected in studies with similar contexts. The whole predictive distribution (PD) can be used to derive the probability of a newly observed effect being above a biologically meaningful threshold.	Not applicable

495 [1]The distributions and percentiles could be underestimated if publication bias existed.

496

Methods

Meta-analysis database

The ecological and evolutionary database used in this study were originally compiled by Costello [18], O'Dea [17], and their colleges. They conducted a systematic search for meta-analysis papers published in ecological journals, including those from the Ecological Society of America and journals of the British Ecological Society. Additionally, they supplemented the database with high-profile journals, such as Nature, and Science. Their systematic search yielded 522 meta-analysis datasets. We dropped meta-analysis datasets that could not achieve convergence when fitted to the multilevel model. Convergence could not be reached for ten meta-analysis datasets, even after adjusting key parameters of the iterative methods to maximize the log likelihood function (see below for details). Therefore, our database contained 512 meta-analysis datasets encompassing 17,770 primary studies and 109,495 effect size estimates. On average, each meta-analysis dataset included 240 effect size estimates sourced from 40 studies, with median values of 64 and 23, respectively.

Stratification of hierarchical meta-analytic data

In this section, we elucidate the theoretical background behind employing a three-level meta-analytic approach to stratify datasets characterized by three-level hierarchical structure as outlined above. Note that the stratification of heterogeneity can be further extended to data structures with more than four strata as necessary (see a case study in **Model additional source heterogeneity**). In the first-stage modelling procedure, the true (population) effect size $\mu_{between[j]}$ of j-th study is modelled using a normal distribution with expectation μ and variance $\sigma_{between}^2$, where μ is the population mean effect or overall effect and $\sigma_{between}^2$ denotes the extent to which $\mu_{between[j]}$ deviates from the overall effect μ [24,40]. Moving to the second-stage modelling procedure, the i-th effect size $\mu_{within[i]}$ within j-th study is modelling

522   using a normal distribution with expectation $\mu_{between[j]}$ and variance σ^2_{within}, where σ^2_{within}

523   represents the extent to which within-study effect $\mu_{within[i]}$ deviates from between-study

524   effect $\mu_{between[j]}$[24,40]. In the third-stage modelling procedure, the effect size estimate $ES_{[i]}$ of

525     $\mu_{within[i]}$ is modelled using a normal distribution with expectation $\mu_{within[i]}$ and sampling

526   error variance $v_{[i]}$. This multilevel modelling framework provides a general way to

527   decompose the variance of effect sizes into different strata, for example between- and within-

528   study levels.

529

530   From the implementation perspective, effect size estimate $ES_{[i]}$ is not sequentially modelled

531   through the three-stage process but rather directly modelled from the overarching distribution

532   with an expectation μ and variance-covariance matrix VCV [24,40]:

533
$$\begin{bmatrix} \sigma^2_{between} + \sigma^2_{within} + v_{[1]} & \cdots & \sigma^2_{between} \\ \vdots & \ddots & \vdots \\ \sigma^2_{between} & \cdots & \sigma^2_{between} + \sigma^2_{within} + v_{[k]} \end{bmatrix}, (19)$$

534   The meta-analytic model specified with the variance-covariance matrix VCV is referred to as

535   the multilevel meta-analytic model (Equation 1). VCV can be reparametrized as a compound

536   symmetry random-effects structure within the framework of multivariate meta-analytic model

537   [40,41].

538
$$\begin{bmatrix} \sigma^2_{total} + v_{[1]} & \cdots & \rho\sigma^2_{total} \\ \vdots & \ddots & \vdots \\ \rho\sigma^2_{total} & \cdots & \sigma^2_{total} + v_{[k]} \end{bmatrix}, (20)$$

539   where $\sigma^2_{total} = \sigma^2_{between} + \sigma^2_{within}$ is the total variance in effect sizes and $\rho =$

540     $\sigma^2_{between}/\sigma^2_{total}$ denotes intraclass correlation coefficient. We used the *rma.mv()* function

541   from the *metafor* package [42] to fit all 512 meta-analysis datasets to the three-level meta-

542   analytic model (Equation 1). We employed restricted maximum likelihood (REML) as the

543   variance estimator and the quasi-Newton method as the optimizer to maximize the likelihood

544   function over variance estimation ($\sigma^2_{between}$ and σ^2_{within}), with a threshold of 10^{-8}, a step

545   length of 1, and a maximum iteration limit of 1000. All models successfully converged under

546   these settings. We confirmed the identifiability of variance estimation ($\sigma^2_{between}$ and σ^2_{within})

547   by checking their likelihood profiles. The R code for model fitting can be accessed at the

548   https://github.com/Yefeng0920/heterogeneity_ecoevo.

549

550   **Extended heterogeneity metrics**

551   In addition to CV_{total}, M_{total}, and their stratified counterparts (Equations 6 – 11), we

552   introduce two related heterogeneity measures. CV_{total} has a potential shortcoming that it is

553   not numerically equivalent to the sum of heterogeneity at between- and within-study levels

554   ($CV_{total} \neq CV_{between} + CV_{within}$). This is because the total standard deviation σ_t is not equal

555   to the sum deviations at each stratum ($\sigma_{total} \neq \sigma_{between} + \sigma_{within}$). To address the numerical

556   difference, we propose CV^2_{total}, an analogue to CV_{total}:

557
$$CV^2_{total} = \frac{\sigma^2_{total}}{\mu^2}, (21)$$

558   Similarly, we propose between-study level and within-study level variants ($CV^2_{between}$ and

559   CV^2_{within}):

560
$$CV^2_{between} = \frac{\sigma^2_{between}}{\mu^2}, (22)$$

561
$$CV^2_{wihtin} = \frac{\sigma^2_{within}}{\mu^2}, (23)$$

562   Following the same principle, M^2_{total} can be obtained [11]:

563
$$M^2_{total} = \frac{\sigma^2_{total}}{\sigma^2_{total} + \mu^2}, (24)$$

564   We further propose between-study level (M^2_{total}) and within-study level (M^2_{total}) counterparts

565   as:

566
$$M^2_{between} = \frac{\sigma^2_{between}}{\sigma^2_{total} + \mu^2}, (25)$$

567
$$M^2_{within} = \frac{\sigma^2_{within}}{\sigma^2_{total} + \mu^2}, (26)$$

568   M^2_{total} and its stratified variants ($M^2_{between}$ and M^2_{within}) are re-scaling of CV^2_{total} and its

569   stratified variants ($CV^2_{between}$ and CV^2_{within}). Therefore, they can be converted into each other

570   using simple mathematical relationships, such as ${M^2_{total}}^{-1} = {CV^2_{total}}^{-1} + 1$ or

571    $\text{logit}(M^2_{total}) = \log(CV^2_{total})$.

Data availability

The data needed to reproduce the analyses and figures are archived GitHub repository

https://github.com/Yefeng0920/heterogeneity_ecoevo/tree/main, and will be deposited at

Zenodo after acceptance.

Code availability

The scripts needed to reproduce the analyses and figures are archived GitHub repository

https://github.com/Yefeng0920/heterogeneity_ecoevo/tree/main, and will be deposited at

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Author contributions

YY: Conceptualization; data curation; formal analysis; investigation; methodology; software; visualization; writing – original draft; writing – review and editing. DWAN: Software; visualization; writing – review and editing. RS: Writing – review and editing. AMS: Writing – review and editing. ML: Visualization; writing – review and editing; funding acquisition; supervision. SN: Conceptualization; investigation; methodology; software; validation; writing – review and editing; funding acquisition; supervision. All authors approved the final manuscript.

Competing interests

All authors declare no competing interests.

Additional information

Supplementary materials will be available at the online version.