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RESEARCH ARTICLE

Describing posterior distributions of variance components: Problems and the use of null distributions to aid interpretation

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Abstract

1. Assessing the biological relevance of variance components estimated using Markov chain Monte Carlo (MCMC)-based mixed-effects models is not straightforward. Variance estimates are constrained to be greater than zero and their posterior distributions are often asymmetric. Different measures of central tendency for these distributions can therefore vary widely, and credible intervals cannot overlap zero, making it difficult to assess the size and statistical support for among-group variance. Statistical support is often assessed through visual inspection of the whole posterior distribution and so relies on subjective decisions for interpretation.
2. We use simulations to demonstrate the difficulties of summarizing the posterior distributions of variance estimates from MCMC-based models. We then describe different methods for generating the expected null distribution (i.e. a distribution of effect sizes that would be obtained if there was no among-group variance) that can be used to aid in the interpretation of variance estimates.
3. Through comparing commonly used summary statistics of posterior distributions of variance components, we show that the posterior median is predominantly the least biased. We further show how null distributions can be used to derive a *p*-value that provides complementary information to the commonly presented measures of central tendency and uncertainty. Finally, we show how

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these *p*-values facilitate the implementation of power analyses within an MCMC framework.
4. The use of null distributions for variance components can aid study design and the interpretation of results from MCMC-based models. We hope that this manuscript will make empiricists using mixed models think more carefully about their results, what descriptive statistics they present and what inference they can make.

KEYWORDS
hierarchical models, null distribution, permutation, simulations, squidSim, variance

1 | INTRODUCTION

Estimating variance components using mixed-effects models is common in ecology and evolution (Bolker et al., 2009; Dingemanse & Dochtermann, 2013; Harrison et al., 2018). Mixed-effect models are a flexible statistical tool used to study hierarchically structured data, with extensions facilitating quantitative genetic (animal models; Henderson, 1988; Kruuk, 2004) and comparative (meta-analysis and phylogenetic mixed models; Hadfield & Nakagawa, 2010) analyses. Markov chain Monte Carlo (MCMC) algorithms are increasingly used to fit mixed-effects models due to their flexibility and the availability of open-source software (e.g. winBUGS (Gilks et al., 1994), JAGS (Plummer, 2003), MCMCglmm (Hadfield, 2010) and Stan (Stan Development Team, 2022b)). MCMC algorithms are a collection of probabilistic simulation methods for generating observations from designated statistical distributions and are typically implemented within a Bayesian framework (Gelman et al., 2021).

MCMC methods have many advantages. Derived metrics (such as standardized measures of variance like repeatability, heritability and evolvability; Houle, 1992; Nakagawa & Schielzeth, 2010) can be easily estimated using the posterior distributions of their components, propagating uncertainty within and among analyses. In contrast, in a maximum likelihood framework, the methods to estimate the uncertainty of derived metrics (e.g. the delta method) can be laborious and biased with small sample sizes (O'Hara et al., 2008). Data in ecological and evolutionary studies are also commonly non-Gaussian, for example counts (e.g. number of offspring), binary and ratio data (e.g. survival, presence/absence, sex ratio) and categorical data (e.g. colour morphs). The performance of MCMC algorithms in generalized linear mixed-effects models (GLMMs) has been found to be superior in terms of accuracy and precision compared with restricted maximum likelihood (REML) approaches (de Villemereuil et al., 2013; O'Hara & Merilä, 2005). Bayesian methods also allow existing information to be incorporated as a prior distribution, although this has rarely been used in ecological or evolutionary studies (Lemoine, 2019).

Despite these advantages, empiricists face several issues when using MCMC mixed-effect models. Here we focus on the difficulties of describing and interpreting variance estimates and their uncertainty. We highlight two problems, both of which centre around the difficulty of describing the posterior distribution of variance components using summary statistics: (i) finding an appropriate measure of central tendency; and (ii) assessing the statistical support for non-zero among-group variance. These problems arise as variance estimates are constrained to be greater than zero, and so their posterior distributions are often asymmetric.

When describing posterior distributions, we typically present some measure of central tendency alongside some measure of uncertainty (quantile-based intervals or highest posterior density intervals). The posterior mean, median and mode have all been used as measures of central tendency, and recent works have advocated the general use of the posterior median (Gelman et al., 2020; McElreath, 2020). There is, however, no clear guidance on which measure provides an appropriate summary statistic for variance components; in our experience the mode and mean are most commonly reported. When the posterior distribution of a variance component is far away from zero and is symmetric, then the mean, median and mode are approximately equal (Figure 1a) and inferences are robust to the choice of central tendency metric. However, when variances are small (relative to the total variance) and/or sample sizes are small (both common in ecology and evolution), the posterior distributions can be close to zero. As variances are constrained to be greater than zero, these posterior distributions are typically asymmetric and can even be bimodal, with one mode close to zero (e.g. Figure 1b). Consequently, there can be a considerable difference between the mean, median and mode (Figure 1b), making it difficult to draw inferences about the magnitude of the posterior variance estimate.

The use of the posterior mode is often justified as being the closest to the maximum likelihood estimate (MLE) when uninformative priors are used. However, this comparison refers to the joint posterior mode, rather than the marginal mode that is typically estimated and reported. In more complex models, the joint and marginal modes may differ (Held & Sabanés Bové, 2020, section 6.5.4), meaning that the marginal mode and MLE are no longer the same. As shown in Figure S1, the convergence of the posterior mode and MLE also requires the use of uninformative improper priors on the variance, which are generally not advised (Gelman et al., 2021), in part because 'uninformative' priors can be uninformative on one scale but not another (e.g. priors on standard deviation vs. variance). The posterior mode is also hard to estimate; it is typically done using kernel density estimation and different methods may provide quite different estimates (Figure 2), thereby providing another source of hidden ambiguity.

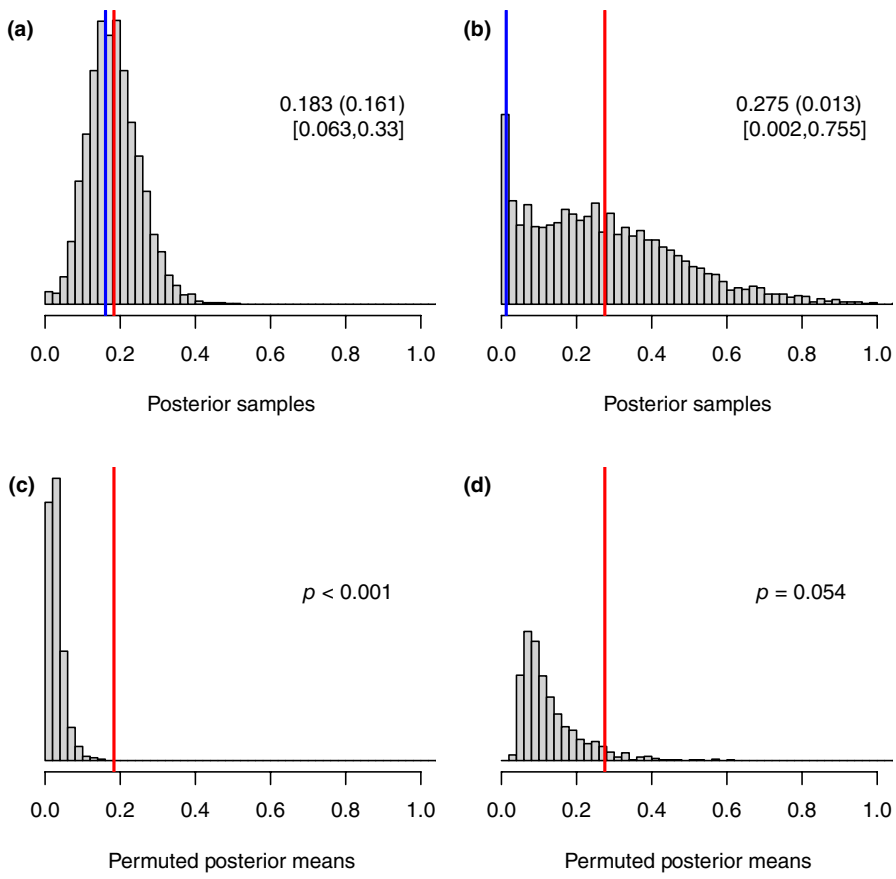

FIGURE 1 Posterior distributions of variance estimates for two different scenarios (a and b) and their respective null distributions (c and d) generated using permutations. Example (a) shows a symmetric posterior distribution far away from zero with close agreement between the posterior mean (red lines) and mode (blue line), while (b) shows an asymmetric posterior distribution close to zero, with clear divergence between the posterior mean and mode. Examples (c) and (d) show null distributions of posterior means generated through permuting the datasets, and corresponding *p*-values, of (a) and (b) respectively. The values given in (a) and (b) correspond to mean (mode) [CRIs]. Both datasets were simulated from Gaussian distributions with among-group variances of 0.2, but with differing sample sizes; (a) with 80 groups and four observations per group; and (b) with 40 groups and two observations per group.

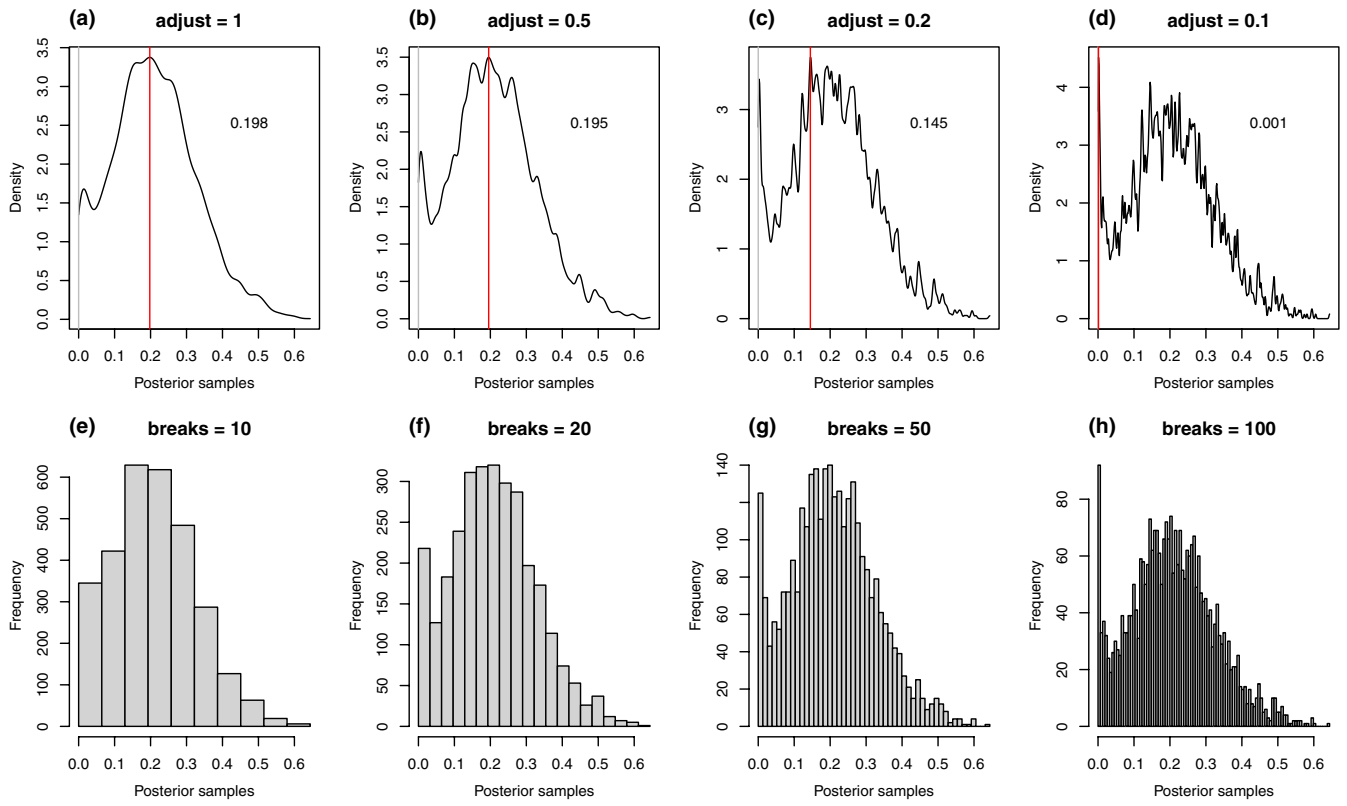

FIGURE 2 The effect of bandwidth choice on the estimation of the posterior mode. Top row shows kernel densities of the same posterior distribution, estimated with different bandwidth scalings, from 1 in (a) to 0.1 in (d) (with intermediate values in (b) and (c)). Red lines and the displayed number show the posterior modes estimated from that scaling. Bottom row (e–h) shows the equivalent histograms for comparison.

Furthermore, the mode requires a larger number of samples in the posterior distribution to be reliably estimated, and will show greater variation between models/chains run on the same dataset (Kruschke, 2015). In contrast, the mean is strongly affected by extreme values, and so by the long tail of an asymmetric distribution.

It is also often important to assess statistical support for among-group variance at a particular level. Typically 95% credible intervals (CRIs) are presented as a measure of uncertainty in parameter estimates derived from MCMC models. As variance components cannot overlap zero, CRIs give no information about the compatibility of the estimates with a null hypothesis (e.g. no among-group variance). Posterior distributions are commonly inspected visually as density plots; a right skewed distribution with a mass near 0 is often assumed to signify that the estimated variance is not different from zero. What is seldom appreciated, however, is that the degree of smoothing that is applied in such plots (via the binning interval or bandwidth) can alter these conclusions. The same distribution can be seen as uni- or bimodal, or peaking at zero or away from zero depending on the degree of smoothing (Figure 2). Such assessments are therefore subjective and lack a proper quantitative basis.

To address this, several metrics for assessing the confidence in a result (such as *p*-values) have been suggested in a Bayesian framework (reviewed in Makowski, Ben-Shachar, et al., 2019). Two of these, region of practical equivalence (ROPE) and Bayes factors, can be used for variance components. The ROPE approach identifies a range of values considered too small to be of any practical relevance (i.e. the ROPE), and quantifies the proportion of overlap between the posterior distribution and the ROPE. This is similar to equivalence testing in a frequentist framework, specifically to the two one-sided tests approach (Lakens et al., 2018). Bayes factors are analogous to frequentist likelihood ratios, comparing different models (e.g. with and without the random effects of interest). Unlike likelihood ratios, they incorporate information from the prior distributions of the parameters into the comparison of the models, and are evaluated using the marginal likelihood rather than at the maximum likelihood. Additionally, Bayesian models can be compared using information criteria which aim to provide out-of-sample prediction accuracy, of which leave-one-out cross-validation (LOO-CV; Browne, 2000; Gelman et al., 2014) has been suggested as the most suitable for complex hierarchical models (Gelman et al., 2021). These metrics (ROPE, Bayes factors and LOO-CV) can be used to provide a measure of statistical support for estimates of variance components, but their implementation is complicated. ROPE requires the definition of a threshold, incorporating further subjectivity into the analysis, while the computation of Bayes factors and LOO-CV can be challenging, and even not implementable in some commonly used programs in ecology and evolution (e.g. MCMCglmm). The use of Bayes factors and LOO-CV is also the topic of active debate (Chandramouli & Shiffrin, 2019; Gelman et al., 2021; Gronau & Wagenmakers, 2019a, 2019b; Navarro, 2019; Vehtari et al., 2019). We address these metrics further in the discussion.

Here, we suggest a complementary method to assess statistical support in mixed-effect models, which compares variance estimates to a null distribution in order to aid statistical inference. This involves creating a distribution of effect sizes that would be expected under the null hypothesis (no among-group variance), and comparing this null distribution with the observed among-group variance. This method has several advantages. Null distributions can be used to generate a *p*-value describing the probability that the observed estimate is as or more extreme than expected under the null hypothesis. Although often criticized through their association with null hypothesis significance testing (NHST; Amrhein et al., 2017, 2019; McShane et al., 2019; Wasserstein & Lazar, 2016), *p*-values have well understood and useful properties. When correctly interpreted, these statistics provide a continuous measure of statistical support, indicating how inconsistent an observed effect size is with a scenario in which there is no among-group variance. In contrast to ROPE, creating null distributions requires no subjective decisions about thresholds and, in contrast to Bayes factors and LOO-CV, they can be implemented using the output from any mixed model.

We present two methods, permutation and simulation, for generating null distributions for variance components. To generate a null distribution using permutation, some feature of the data is randomized to produce a new dataset with the structure of the original dataset, but with no relationship between the response variable and the variable of interest. This randomization is repeated a large number of times to create many different permuted datasets. The same analysis is then carried out on the permuted datasets as on the original dataset, and a test statistic of interest (e.g. the estimate of among-group variance) is used to create a null distribution of test statistics (Figure 1c,d). A (one-tailed) *p*-value can then be derived as the proportion of permuted datasets with a test statistic greater than or equal to the test statistic observed with the real dataset. Permutation tests have already been suggested as an alternative to likelihood ratio tests for frequentist analyses (Fitzmaurice et al., 2007; Samuh et al., 2012), although they are not commonly utilized in ecology and evolution (but see Araya-Ajoy & Dingemanse, 2017; Stoffel et al., 2017). Permutation tests are a subclass of nonparametric tests (Lehmann & Romano, 2005; Pesarin & Salmaso, 2010) and do not rely on specific probability distributions, and so make few assumptions. However, as we show later in the manuscript, datasets can be permuted in several different ways when the data structure is complex, and the consequences of the choices involved in such cases are often not immediately obvious. Simulations provide an alternative method of creating a null distribution. This process is similar to permutation, but instead of generating permuted datasets we can simulate datasets from the observed model parameters (similar to parametric bootstrapping), while setting the variance in question to zero. Again, the same analysis is carried out on the simulated datasets, and the test statistics of interest used to create a null distribution. This simulation method makes more assumptions about the data and model, but allows for more control of the manipulated features of the simulated datasets compared with permutations.

Finally, a crucial part of designing experiments and statistical analyses is assessing the power to detect an effect size of interest. Power is defined as the probability of rejecting the null hypothesis for a given effect size at a specified alpha level. Although power typically relates to NHST and the often criticized alpha level (Amrhein et al., 2017, 2019; McShane et al., 2019; Wasserstein & Lazar, 2016), it remains an important tool for study design regardless of statistical philosophy, by providing a quantitative approach to calculating optimal sample sizes and designing sampling regimes. Power may also provide a more useful metric than precision when considering variance components. As their distributions are bounded at zero, standard errors will always decrease when distributions are close to zero (see Figure S2). However, The concept of power for variance components in MCMC models is not well developed. As null distributions can be used to generate *p*-values, they provide a convenient way of conducting power analysis.

Here, we first compare the metrics of central tendency that are commonly used as summary statistics of posterior distributions of variance components. We then demonstrate the utility of null distributions to generate a complementary *p*-value statistic and aid the interpretation of the variance components, and compare two methods of generating them. Null distributions can provide a continuous, quantitative measure of confidence that the observed variance component is larger than what might be expected under the null hypothesis (no among-group variance), given the data structure and priors used. Importantly, we are not advocating that this approach should replace the presentation and use of effect sizes and CRIs, but rather that it should be used as an additional and complementary statistic. Finally, we show how null distributions can be used to perform power analysis within an MCMC framework.

2 | MATERIALS AND METHODS

All simulations were carried out in R (version 4.1.0; R Core Team, 2022) using the squidSim R package (version 0.1.0; Pick, 2022).

2.1 | Generation of 'observed' datasets

We generated a series of datasets with known parameters, which we will refer to as our 'observed' datasets (to distinguish them from the 'null datasets' in following sections). We first simulated Gaussian data with one hierarchical level and varied the number of observations per group (2 and 4) and the number of groups (20, 40 and 80). We simulated a total variance of 1 and varied the among-group variance (0, 0.1, 0.2 and 0.4; also representing the intra-class correlations [ICCs]/repeatabilities). We simulated every combination of these parameters (24 parameter sets) and for each set we simulated 500 'observed' datasets. Power to detect among-group variance is known to be determined by effect size and sample size both within and among groups. We chose these parameter values and sample sizes to explore scenarios where power is low (Dingemanse & Dochtermann, 2013) to understand the impact on posterior distributions. These sample sizes also correspond to typical experimental designs in behavioural ecology or life history data collected on wild populations (Bell et al., 2009).

We analysed each 'observed' dataset with a linear mixed-effects model specifying group level random effects in a Bayesian framework, using Stan with the rstan package (version 2.21.3; Stan Development Team, 2022a). We specified weakly informative priors on the among-group and residual standard deviations (half-Cauchy distribution with scale 2; a commonly used and recommended prior for variance components (Gelman, 2006)), and ran one chain for each model with 5000 iterations and a warm-up period of 2000 iterations. This ensured an effective sample size in the posterior distribution of the among group variance of >500 across the majority of models (95%). For comparison, we also ran REML models using the lmer function of the lme4 package (version 1.1-29; Bates et al., 2015), the results of which are shown in Figure S3. To ensure that our results were not affected by the choice of the prior, we ran additional models on a subset of the data with a range of different priors (see Supplementary Materials). Changing the prior on the among-group standard deviation did not affect our results, while using uninformative priors on the among-group *variance* led to a concordance between REML estimates and posterior mode, as might be expected (Figure S1).

As a demonstration that our findings hold with more complex data, we additionally simulated Bernoulli (binomial with one observation) and Poisson data. Bernoulli data were simulated with 80 groups and four observations per group. Among-group effects were simulated from a Gaussian distribution on the latent scale, with a mean of 0 and among-group variances of 0 and 0.2, 0.4 and 0.8. The latent scale response variable was then transformed using the inverse logit function to provide the probabilities, and sampled with a Bernoulli process. Poisson data were simulated with 80 groups and two observations per group, with a mean of 2 and a total variance of 0.2 on the latent scale, with among-group variances of 0, 0.02, 0.04 and 0.08 (ICCs of 0 and 0.1, 0.2 and 0.4 on the latent scale). The mean and total variance were chosen based on a literature survey of provisioning data in Pick et al. (2023). We took the exponent of the latent scale response variable to provide expected values, and sampled them with a Poisson process. We simulated 500 'observed' datasets for each variance, and analysed the data using GLMMs as outlined above.

2.2 | Comparison of posterior distribution summary statistics

From the posterior distributions of the among-group variances, we calculated the posterior mean, median and mode, and compared these estimates with the true values.

While calculating the mean and median of the posterior distribution is straightforward, estimating the posterior mode involves some (hidden) assumptions. Typically the mode is estimated using kernel

density estimation, which involves fitting a model to the distribution of posterior samples to estimate a density function. The maximum of this function is then calculated over a series of predicted values, to give the estimated mode. One key parameter in kernel density estimation is the bandwidth, which describes the amount of smoothing and is analogous to the number of breakpoints in a histogram. As shown in Figure 2, with the degree of smoothing can affect where the posterior mode is estimated. To explore this further, we estimated the posterior mode using two bandwidth scalings (0.1 and 1; low and high smoothing respectively), which are the defaults in two commonly used R functions for estimating the mode (MCMCglmm (Hadfield, 2010) and the ggdist and bayestestR packages (Kay, 2022; Makowski, Ben-Shachar, & Lüdecke, 2019) respectively). Further details about the differences between these functions are presented in the Supplementary Materials. In both cases, the kernel density was estimated using the SJ algorithm (Sheather & Jones, 1991), and the mode was estimated using 512 predicted values with a cut-off point at zero.

To compare these different measures of central tendency, we calculated measures of bias, precision and accuracy. Because variance components are limited by 0, deviations from the mean or simulated values will be smaller at smaller effect sizes. To account for this, we also calculated relative measures. We calculated the bias as $\frac{1}{n}\sum\widehat{\theta}_i-\theta$ (where θ is the true value, $\widehat{\theta}_i$ is the model estimate from ith simulation in a parameter set and n is the number of simulations). For the non-zero effect sizes, we also calculated relative bias as $\frac{1}{n}\sum\frac{\widehat{\theta}_i-\theta}{\theta}$, and mean absolute error as $\frac{1}{n}\sum\frac{|\widehat{\theta}_i-\theta|}{\theta}$. Note this is also a relative measure. Mean absolute error is similar to root mean squared error, and combines bias and precision. We also calculated the precision as $1/\sqrt{\frac{1}{n}\sum\left(\widehat{\theta}_i-\overline{\widehat{\theta}}\right)^2}$, and relative precision as $\overline{\widehat{\theta}}/\sqrt{\frac{1}{n}\sum\left(\widehat{\theta}_i-\overline{\widehat{\theta}}\right)^2}$, where $\overline{\widehat{\theta}}$ is the mean of the model estimates across all simulations in a parameter set. Precision is presented in Figure S2.

2.3 | Creation of null distributions and *p*-values

We created null distributions for each 'observed' dataset using two methods to generate 'null datasets'. First, we permuted the 'observed' datasets by shuffling the group indices (IDs) to create 100 new permuted null datasets per 'observed' dataset, in which among-group variance is expected to be zero. Second, we used simulations to create 100 null datasets with the same data structure but no among-group variance for each 'observed' dataset. To determine the value of the residual variance for these simulations, we added together the posterior distributions of the among-group variance and residual variance from the models of each original 'observed' dataset, and used the median of the resulting distributions. This ensured that the total variance in the simulated null datasets was the same as in the 'observed' datasets. The choice of the median for this step should have little consequence, as this derived distribution will be estimated with much less uncertainty and so will be symmetric, meaning that the three measures of central tendency will be equivalent. It is important that any fixed effects, including the intercept, are included in the simulations, especially for GLMMs as the expectations will affect the stochastic variance on the data scale. Each of these null datasets was analysed with the same model as the original 'observed' dataset, and the same parameters (the central tendency estimates of the posterior distribution of the among-group variance) were extracted to create the corresponding null distributions. Although we recommend using null distributions with more samples for empirical studies (e.g. 1000), here we used 100 permutations/simulations for each 'observed' datasets in order to reduce the computational burden (500 simulations for 24 parameter sets is 12,000 Gaussian datasets, each with 100 permutations and 100 simulations). We calculated a *p*-value for each 'observed' dataset, as the proportion of estimates in the null distribution that were higher than the estimate from that 'observed' data. We calculated *p*-values using each central tendency measure, which are compared in Figure S4.

2.4 | Power analysis and comparison with bias and precision

Power is defined as the probability of rejecting the null hypothesis (no among-group variance in this case) for a given effect size and data structure at a specified alpha level (typically 0.05). Although power is typically interpreted in the context of NHST, power can also be seen as a description of the distribution of *p*-values expected for a given effect size and data structure (it is the cumulative density at 0.05 for a given *p*-value distribution). Other descriptions of the *p*-value distribution (e.g. the mean) would be simple functions of the power (Figure S5). We chose to present power as a description of the distribution of *p*-values as it is conceptually well understood and frequently used rather than because of any philosophical alignment with NHST.

Using the 'observed' datasets described above, we compared two ways by which power can be calculated. In both methods, power was calculated for the parameter sets where the true value was greater than zero, as the proportion of 'observed' datasets in which the *p*-value was below a nominal threshold of 0.05. In the first ('full') method, we used the *p*-values generated above, through comparison of the 'observed' datasets with their null distributions from both permutation and simulation approaches. In the second ('reduced') method, we generated *p*-values by using model estimates from the 'observed' datasets with zero among-group variance for each data structure (combination of among- and within-group sample sizes) as a null distribution, against which the estimates from 'observed' datasets simulated with among-group variance could be compared. This method of generating *p*-values is similar to the simulation method of generating null distributions, but uses one null distribution for *all* 'observed' datasets with the same data structure, instead of null distributions for *each* 'observed' dataset. It is therefore massively less computationally intensive for power analyses; exploring power within the parameter space presented here required 12,000 models, rather than 1,212,000.

We were also able to calculate the false positive rate (FPR) for the 'full' method in the same way as power, using the parameter sets where the simulated value was zero. It was pointless to calculate a FPR for the 'reduced' method; by comparing the null distribution with itself, the FPR is, by definition, 5%.

As stated above, posterior distributions are expected to be asymmetric when power is low, which is also when we expect biases in the different measures of central tendency. We therefore examined how well power predicts the relative bias of the different measures of central tendency. During the review process, it was suggested that we could use relative precision to account for the appearance of higher precision in effect sizes near zero. We therefore also compared this metric with power, as it may provide an alternative measure to power for study design.

2.5 | Worked example—Random slopes

Empiricists commonly encounter more complex questions and data structures in their studies than we have presented above. Here we outline a more realistically complex example where the permutation of datasets requires some careful decisions.

Random slope models (where group-specific intercepts and slopes are modelled, also known as random regression) provide a good example of this complexity. We will focus here on generating a null distribution for the estimate of among-group variance in slopes. This estimate is based upon the relationship between the predictor variable and response, the distribution of the response variable across groups and the distribution of the predictor variable within and across groups. This structure provides four ways to generate null distributions via permutation that retain different relationships in the observed dataset (illustrated in Figure S6). The first two are general to variance components, and the second two are specific to random regression models.

1. Permuting the response variable. This is the most unspecific permutation. It retains data structure and breaks all relationships with the response, removing the effects of all random factors and predictors, and allows for testing multiple components at the same time. It is a full null model of all biological processes described by the model.
2. Permuting the group identities. This is a more specific permutation. It breaks the relationship between a specific group and both the response and other predictors, and retains associations between predictors and response (including any other random effects linked to different grouping variables). It will remove the effects of both random intercepts and random slopes associated with the grouping factor in question.
3. Permuting the predictor. This is even more specific, targeting random slopes specifically. It retains the group data structure, but breaks link between predictor and response, and the distribution of the predictor across groups. By breaking the link between predictor and response, there is no relationship that can vary between groups (i.e. random slopes).
4. Permuting the predictor within groups. This is the most specific permutation. It is similar to (3) but retains the distribution of the predictor across groups, while breaking the link between predictor and response within group.

We can also generate null distributions through simulation. Here we have multiple variance components (intercepts and slopes), and so the simulations can either test one component at a time or both together. In this example, we can either simulate no among-group variance in slopes (adding the variance generated by the random slopes to the residual to ensure the same total phenotypic variance), or simulate no variance in either intercepts or slopes (adding the variance generated by both random intercepts and slopes to the residual). We explore these six null distributions using a simulated and a real dataset. They provide a useful contrast between a dataset where we know the true values, and one where the true values are unknown with the potential for greater complexity.

To generate our simulated dataset, we imagined a hypothetical researcher who wants to test whether there is variation among individuals in how temperature affects their body mass. The dataset was simulated with 300 individuals measured four times each. Body mass and temperature were both normally distributed. Temperature was scaled to have a mean of 0 and variance of 1, and has an effect on body mass of 0.2 for the average individual. The simulated among individual variance in the intercepts was 0.2 and the phenotypic variance generated by variation in slopes was 0.1 (with no correlation among random slopes and intercepts), while the residual variance was set to 0.7 to ensure a total phenotypic variance not explained by the average effect of the environment was 1. Formulas to estimate the total phenotypic variance in random slope models can be found in Allegue et al. (2017). There were no systematic differences in the average temperature experienced by the different individuals.

For our real data example, we employed a study on the aggressive response of great tits (*Parus major*) to intruders in a nestbox population in southern Germany (Araya-Ajoy & Dingemanse, 2017). Data were collected over a 6-year period (2010–2015) for all males during their first breeding attempt each year. A male great tit model was presented with a playback song 1 m away from the subject's nest box. Aggression was measured as the minimum distance of the focal male to the model (Araya-Ajoy & Dingemanse, 2014). Territorial intrusions were performed twice during the egg-laying stage and twice during the egg-incubation stage of each focal nest, with males responding, on average, to 2.8 of the 4 intrusions. Males were also sampled across years, with an average of 1.4 reaction norms per male. In total there was 2854 aggression tests performed to 1042 breeding attempts of 679 individuals. Full details are provided in Araya-Ajoy and Dingemanse (2014, 2017).

Both datasets were analysed using random slope mixed-effects models, specifying the environmental predictor (temperature and breeding stage respectively) as a fixed covariate, and random intercepts and environment slopes across individuals. Breeding stage was coded as zero (for egg-laying) versus one (for incubation), and then mean centred and standardized to standard deviation units (Schielzeth, 2010). We generated six null distributions of posterior medians for each dataset (four permutations and two simulations), as outlined above, with which we compared the estimate of among individual variance in slopes from the observed data. Null distributions were generated based upon the analyses of 1000 null datasets. Models were fitted in a Bayesian framework, using Stan with the rstan package (version 2.21.3; Stan Development Team, 2022a). We specified weakly informative priors on the among-group and residual standard deviation. We ran three chains for the models of the simulated and real observed datasets, and a single chain the models for the null datasets, all with 5500 iterations and a warm-up period of 500 iterations.

3 | RESULTS

3.1 | Comparing summary statistics of the posterior distribution

When the simulated among-group variance was zero, all summary statistics were upwardly biased to some extent as the posterior distribution cannot include 0 (Figure 3a; full sampling distributions are shown in Figure S7). Predictably, the posterior mean and median from datasets with zero variance were considerably more upwardly biased than the mode for small sample sizes, with the mean being the most biased. Note that this upward bias was also present in frequentist analyses (see Figure S3), and was not just a feature of Bayesian analyses.

When the simulated among-group variance was non-zero, then the mean, median and mode all appeared to be consistent estimators, in that any bias occurred only at small sample and/or effect sizes. The posterior median generally converged on the simulated value at lower effect and sample sizes (Figure 3b) with a slight tendency to be biased downwards, as compared with the posterior mean, which was upwardly biased, and the posterior mode that was biased towards zero (Figure 3b). Consistent with Figure 2, the bias in the mode depended upon the chosen bandwidth, with the higher smoothing bandwidths showing less bias. We found similar overall patterns in the Poisson and Bernoulli simulations (Figure S8).

In terms of relative precision (Figure 3c), the mean was the most precise estimator, with both estimates of the mode showing considerably lower precision than either median or mean. Similar to the bias, the precision of the different estimators converged as sample size and effect size increased.

In terms of mean absolute error (Figure 3d), a (relative) measure of accuracy that combines bias and precision, the mean and median were very similar, with exception of the lowest sample and effect size combination where the mean was less accurate. The mode was consistently less accurate than the other measures (Figure 3d), although this lower accuracy disappeared at higher sample and effect sizes.

3.2 | Performance of the null distributions

A *p*-value is defined as the probability that an estimate equal to or more extreme than the observed estimate would occur under the null hypothesis (i.e. if the true among-group variance is zero). When the null hypothesis is true, we expect a uniform distribution of *p*-values (we expect 5% of values to be ≤ 0.05, 50% to be ≤ 0.5 etc). When the null hypothesis is false, we expect smaller *p*-values to become more likely, in line with the power we have to detect an effect. We find exactly these patterns when considering the *p*-values generated by null distributions. Both permutation and simulation methods produced a uniform distribution of *p*-values when the simulated among-group variance was zero (Figures 4), and the distributions of *p*-values from both permutation and simulation methods shift towards zero as the sample size and the magnitude of the variance increase (Figure 4). We found similar results in the Bernoulli and Poisson simulations (Figure S9).

Importantly, although the mean, median and mode were often quite different in magnitude (reflecting skew in the posterior distribution), the inference based upon the *p*-values did not differ between the different metrics. There were strong correlations between *p*-values derived with the different central tendency metrics, except when the mode was estimated with less smoothing which produced less consistent *p*-values (see Figures S4 and S10). *p*-values were also strongly correlated between simulation and permutation methods (see Figure S11).

3.3 | Power analyses and comparison with bias and precision

When we used the full method of estimating power, both ways of generating null distributions (permutation and simulation) gave very similar results (Figure 5), with marginally higher power for the permutation method. These power estimates were very similar to previous published estimates for frequentist models (Dingemanse & Dochtermann, 2013). When the among-group variances was simulated as zero, these methods displayed the expected FPRs of 5% (black points in Figure 5). The reduced method for estimating power, using the same null distribution for all datasets with an effect size >0 within a particular data structure, generally showed similar power to the other methods (Figure 5). As with the *p*-values, power was not particularly

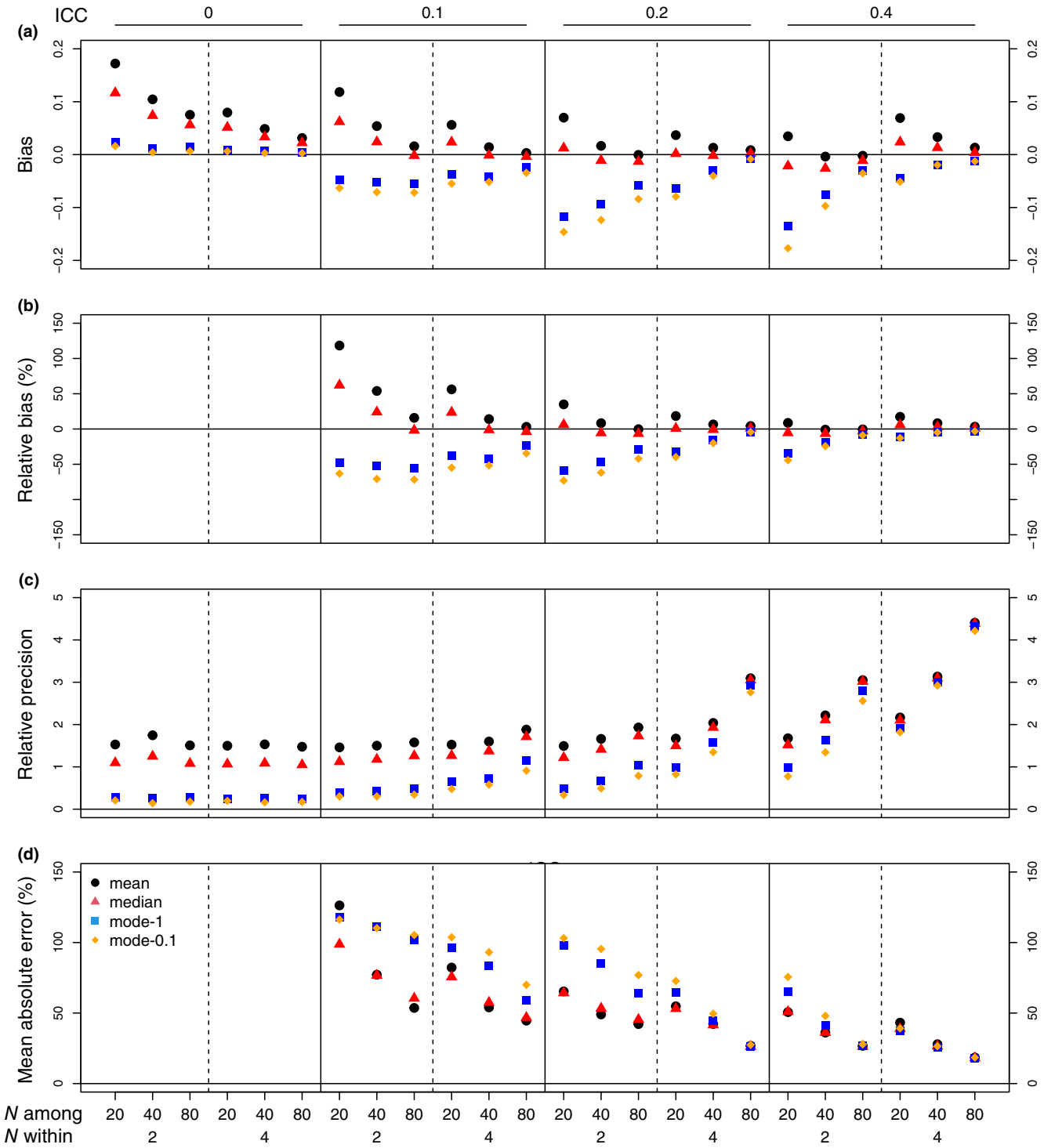

FIGURE 3 Bias (a), relative bias (b), relative precision (c) and mean absolute error (d) of posterior mean, median and mode of variance components from linear mixed-effects models run on data simulated with a Gaussian distribution varying in among group variance (intra-class correlations—0, 0.1, 0.2, and 0.4) and sample size within (2 or 4) and among (20, 40 and 80) groups. Each point is based on the estimates from 500 datasets. Two posterior modes were estimated: mode 1 and mode 0.1 with more and less smoothing respectively (see text for more details). Mean absolute error is also a relative measure, being standardized by the simulated value (see text for more details).

sensitive to the measure of central tendency used, the highest power being seen in the mode with higher smoothing and the lowest power for the mode with the least smoothing (Figure S12).

As shown in Figure 6, relative bias in all measures of central tendency decreased as power increased. This pattern was similar across Gaussian, Poisson and Bernoulli traits. Power was also closely

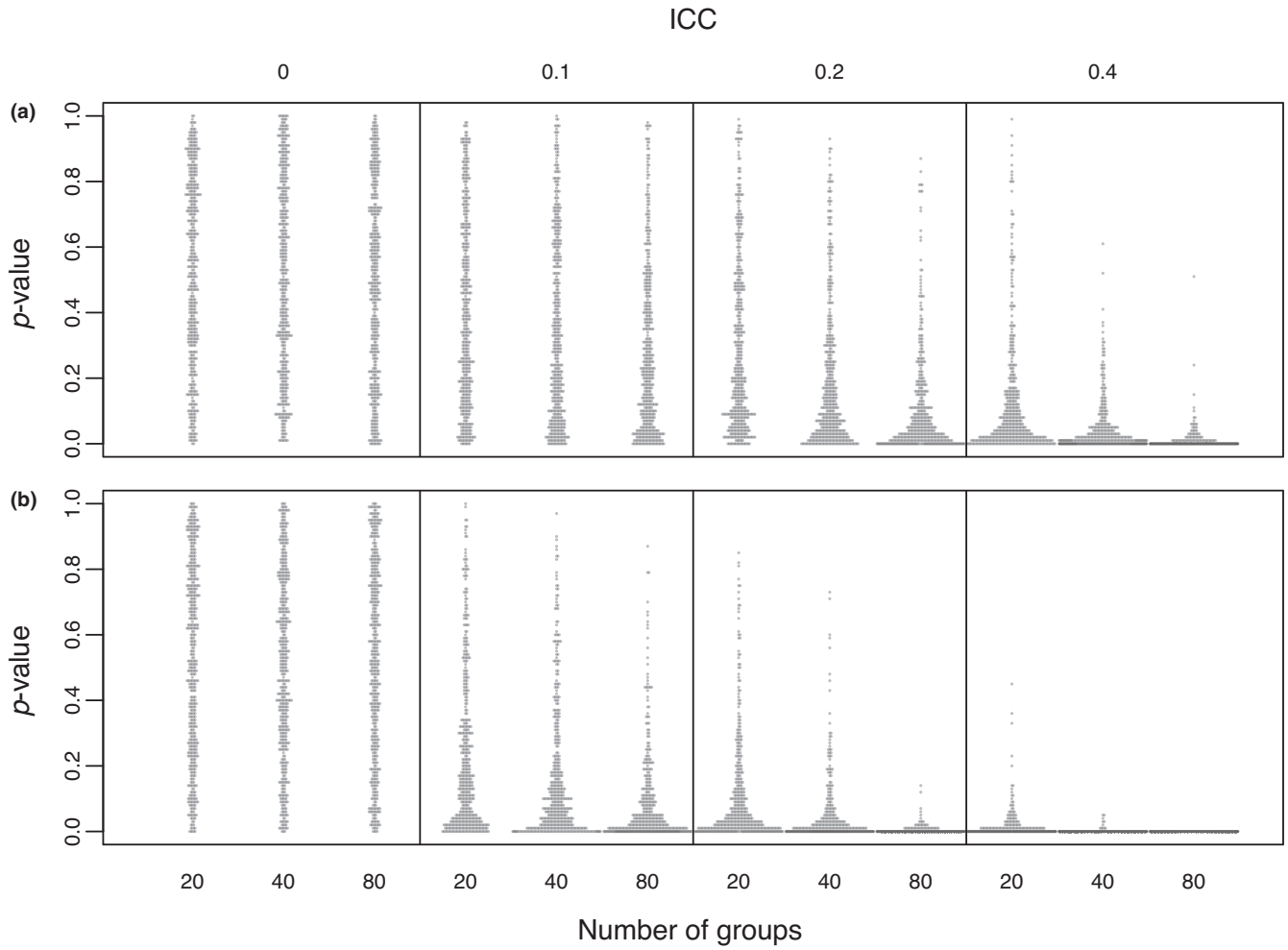

FIGURE 4 Distributions of *p*-values for the among-group variance, estimated used linear mixed-effects models run on data simulated with a Gaussian distribution, varying in among-group variance (intra-class correlations—0, 0.1, 0.2 and 0.4) and sample size among groups (20, 40 and 80), with 500 datasets per combination. *p*-values were estimated using the posterior median and null distributions generated through simulations. (a) shows a within group sample size of 2, and (b) a within group sample size of 4.

related to relative precision (Figure S13) and consequently also to relative bias (Figure S14).

3.4 | Random slope worked example

In both the simulated and real datasets, the different types of null distributions (generated using two simulations and four permutations; Figure S6) provided the same qualitative results, supporting the conclusion that there was among-individual variation in slopes (Figure 7). For both of these datasets, permuting individual identity created null distributions with a larger mean value of random slope variance than the other permutations. Note that these results should be considered in the context of random regression, and may not generalize to other types of model (see Section 4). We therefore generally recommend exploring the particular consequences of different types of permutations for specific datasets where possible, as this may reveal patterns in the data that warrant further exploration.

4 | DISCUSSION

We demonstrate the difficulties of summarizing the posterior distributions of variance estimates from MCMC-based models. We describe different methods for generating null distributions that provide useful complementary information alongside the presentation of central tendency and uncertainty that are generally reported. We also show a way in which null distributions could be used to derive a *p*-value, which is a simple addition to the statistics presented when summarizing a posterior distribution and also facilitates power analysis. Importantly we show that biases in central tendency measures are functions of power.

4.1 | Summary statistics

Our experience in ecology and evolution is that both posterior mean and mode are commonly, but inconsistently, presented without justification. For fixed effect parameter estimates, this is typically

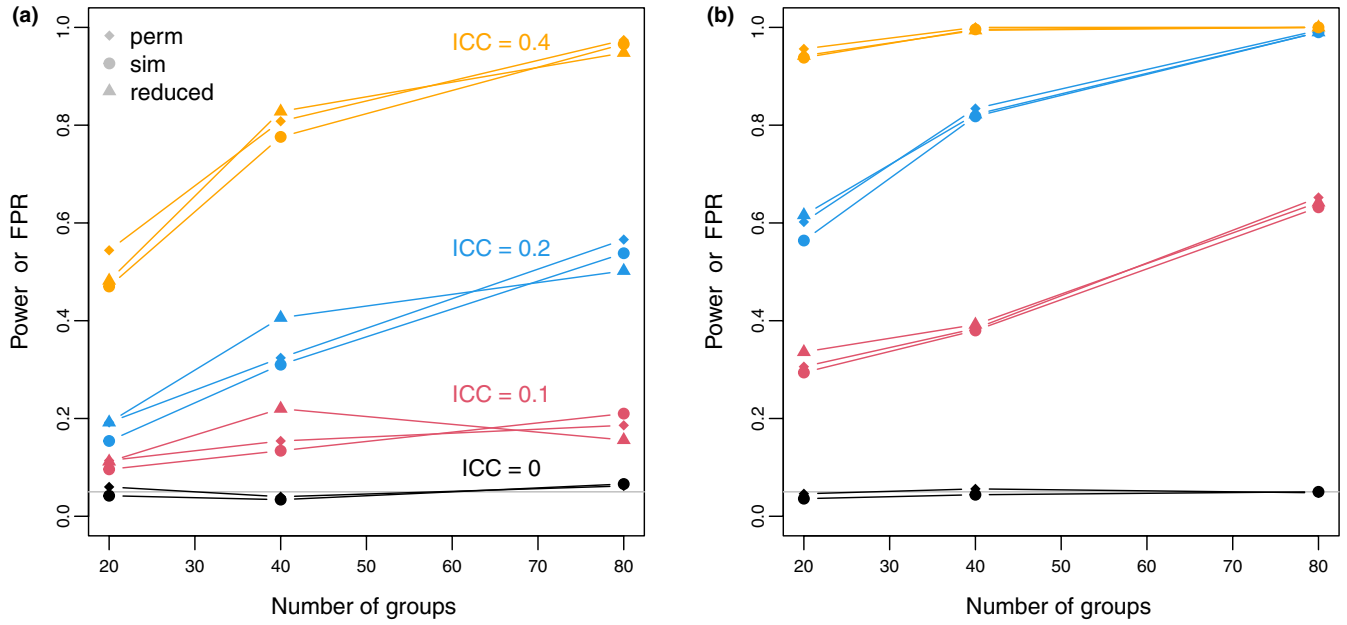

FIGURE 5 Comparisons of power (in colour) and false positive rate (FPR, in black) calculated using permutation (perm), simulation (sim) or a global null distribution (the 'reduced' method in the main text). For each within-group sample size of (a) 2 and (b) 4, we show results for four among-group variances (0 (representing FPR), 0.1, 0.2 and 0.4) and three among-group sample sizes (20, 40 and 80), with 500 datasets per combination. All datasets were simulated with a Gaussian distribution. Power/FPR was calculated using posterior medians.

inconsequential, as the posteriors are usually symmetrically distributed. For estimates of variance components, however, our simulations show that depending upon the underlying parameter value, both mean and mode can show large biases in opposite directions. When posterior distributions were close to zero and there *was* among-group variance, the posterior mode was very biased towards zero, whereas the posterior median and mean performed better. On the other hand, if there was no among-group variance, the mode was the least biased. The mode, however, is more subjective as its estimation depends on the choice of underlying algorithm (results shown here), it requires larger posterior distributions for reliable estimation, and will show greater variation between models/chains (Kruschke, 2015). Unfortunately, the method of mode estimation is rarely justified or even stated in empirical papers. Therefore, we cautiously recommend the presentation of the posterior median, or both median and mean, as a measure of central tendency for variance components. This recommendation is based upon the median being generally less biased than the mean when power is low (Figure 6). Presenting both allows any discrepancy to be seen, which would indicate that the distribution is near to zero and not symmetric, and further emphasize the uncertainty in these measures.

Upward biases in variance components have been seen before when power is low, but the dependence on the choice of the central tendency metric has not been highlighted. For example, Fay et al. (2022) note overestimation of variance components in Bernoulli models, with this overestimation decreasing in size as sample size and effect size increase. Fay et al. (2022) use the posterior mean as a summary statistic, and (as we show in Figure S15) this bias will decrease (although not disappear completely) through the use of a posterior median. This is not just a bias in Bernoulli models, or in fact MCMC models (Figure S3), but a general property of variance components estimated with low power (Figure 6, or low relative precision—Figure S14).

We urge caution in interpreting our results in terms of absolute sample sizes or effect sizes alone. Different types of data and data structures will contain different amounts of information and so vary in power, meaning that the same bias might not result from the same sample size or variance in a different context. GLMMs make this more complex, as similar variances on the latent scale can equate to different variances and so different effect sizes on the expected and observed scales, depending on the link function and the form of stochastic variance (de Villemereuil et al., 2018). For example, we found a comparable range of powers for our Poisson and Bernoulli examples, despite very different simulated variances on the latent scale (0.02, 0.04 and 0.08 vs. 0.2, 0.4 and 0.8 respectively). Similarly, Bonnet and Postma (2015) found very different power to detect the same latent scale variances in Bernoulli and Poisson traits. Given the strong relationship between these biases and power (or relative precision), considering the potential bias in variance estimates in relation to power (or relative precision) may be a productive way forward, as this is comparable across models, distributions, effect and sample sizes.

It is commonly argued that rather than presenting summary statistics, we should present and interpret the whole posterior distribution, typically portrayed using density plots. However, the underlying parameters of the kernel density estimation are not given alongside density plots, meaning the amount of smoothing is unknown. A large degree of smoothing can hide asymmetry and/or bi-modality, and so change inferences. We therefore suggest the use of histograms over density plots in the presentation of posterior distributions, because

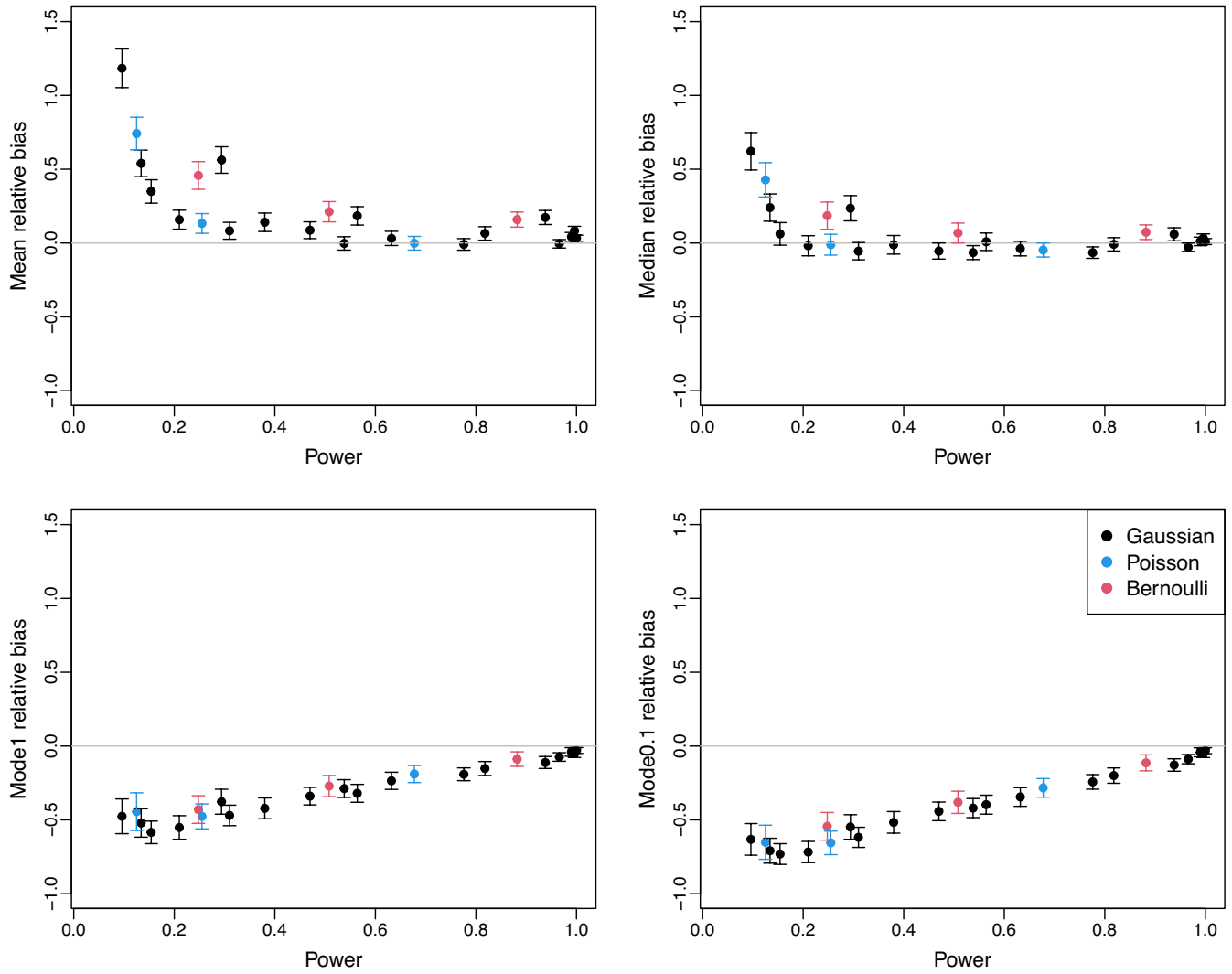

FIGURE 6 Relationships between power and relative bias, the latter being estimated across different measures of central tendency. Power was calculated using null distributions generated using the simulation method and the posterior median. Each point is based on 500 datasets, simulated with either a Gaussian, Bernoulli or Poisson distribution, with varying effect and sample sizes. Mean and 95% confidence intervals of the relative bias are shown.

although histograms are subject to the same smoothing problems, the degree of smoothing is at least explicit. Alternatively, other plots that explicitly show the raw posterior samples can be used (e.g. beeswarm plots; Figures 4 and 7).

4.2 | Null distributions

The null distribution approaches outlined here are relatively easy to use, although computationally intensive (see Section 4.5). They allow the quantification of confidence that the estimated group-level variance is not simply a consequence of the choice of priors and data structure. Importantly, the *p*-values based upon null distributions are not dependent upon which measure of central tendency is used. Such inferential statistics comparing the observed estimates with the null distributions can provide quantitative measures that can be reported alongside the observed estimates and uncertainty, and provide a useful tool for assessing the probability that variance components are non-zero and thereby supplement visual inspections of posterior distributions, or comparison of posterior mode, median and mean. Furthermore, inferential statistics can serve as an objective and easy-to-communicate assessment of the biological relevance of an estimated variance component to the general public and policy makers, or for the statistical support of non-zero values for derived statistics like heritability, repeatability or evolvability. A common criticism of *p*-values is that they are often misinterpreted. We therefore recommend those using the null distribution approach to acquaint themselves with the relevant literature (useful examples include: Amrhein et al., 2017, 2019; McShane et al., 2019; Wasserstein & Lazar, 2016). Importantly, *p*-values cannot demonstrate the absence of effect, just confidence in difference from the null hypothesis. We believe generating null distributions will help empiricists understand these concepts, as they give a visual representation of what *p*-values signify.

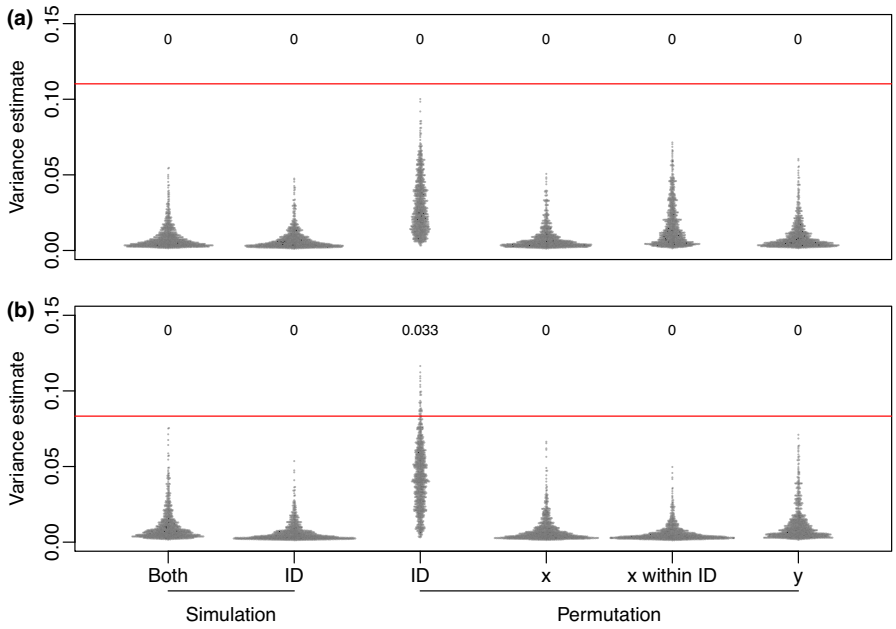

FIGURE 7 Null distributions of posterior medians generated with five different methods (see main text), from (a) a simulated dataset, and (b) a real dataset on aggressiveness in great tits. Red line represents posterior median estimated from original dataset. Values above the points represent the respective *p*-values.

Increasing the complexity of the data structure and model will create more ways to permute datasets. In our random slope examples, we showed how these permutations can become increasing specific to target particular components of the model, from permuting the response to permuting the environmental predictor within individuals. Here, these different permutations led to qualitatively similar results, although whether they always or usually do so would require a much broader set of simulations. Interestingly, permuting individual identity created null distributions with noticeably larger values of random slope variance. We believe this is due to the existence of random slopes generating heterogeneous residuals (i.e. variance in response changed with the environmental predictor) that were confounded with random slope variation in the analyses of the null datasets (similar effects were also shown in Ramakers et al., 2020), whereas the other permutation methods broke up the relationship between the predictor and response. Comparing the results of the different methods of null distributions generation may provide insights that help inform statistical inference or highlight the need for further exploration.

The bulk of the simulations presented here do not directly consider how to assess multiple variance components. In our random slope examples, it made little difference whether we simulated no variance in random slopes and intercepts or just random slopes. However, this may differ between model structures. Generating null distributions for all components at once (e.g. by permuting the response variable, or setting all random effect variances to 0 in simulations) makes the assumption that the different variance components do not affect each other. If this assumption is reasonable (it is typically being made when a given model structure is chosen to be appropriate), then generating null distributions for all components at once would be reasonable. If there is a reason to think that they may affect each other, then null distributions are better generated for each random term at a time.

In some instances, generating a null distribution using permutations may not be possible. For example, in event-history models of survival (where individuals have a sequence of 0/1 (survived/died) for each time point where they are observed), permuting the individual identifiers would fundamentally alter the data structure, meaning that some individuals had multiple deaths. However, this could work in the context of an animal model, where 0s and 1s could be interchanged between individuals, retaining the same structure across individuals, but breaking the link with the pedigree. This demonstrates that the suitability of permutations and how they impact the data structure needs to be carefully assessed on a case-by-case basis. Overall, we are not advocating a specific recipe for permutations—it is likely context and question dependent. We instead advocate a simulation approach at the planning stage to check in advance that the permutation design gives desired properties with your likely data structure.

Generating null distributions through simulation avoids many of the issues with the permutation approach, although it may not account so well for the particularities of each dataset, (e.g. the heteroscedasticity in the random regression examples above). Simulations allow the structure of the data to be fully retained, allow a more fine-scale alternation of the variances in question, and make no additional assumptions than those already made by the statistical model. A simulation approach also simplifies the simultaneous generation of null distributions for multiple variance components while retaining the data structure. Reassuringly, in our random regression examples, the null distributions generated using two simulation methods were similar, and the results were similar to those obtained using the permutation methods. We therefore cautiously recommend the use of this simulation method, as it is the most flexible for complex models.

These null distribution approaches are computationally intensive and the suitability of their application will depend upon the model complexity, the amount of data and the available computational

resources (see Section 4.5). MCMC methods are often used for highly complex problems (e.g. double hierarchical GLMs; Cleasby et al., 2015), where generating a large number of samples for a null distribution may not be an option. The number of samples affects the minimum *p*-value that can be calculated and its precision; a null distribution with 100 samples can have a minimum *p*-value of 0.01 and vary by intervals of 0.01. In addition, stochastic fluctuations in the *p*-value can have a large impact on inference. For this reason, we would recommend a higher number of samples in the null distributions than we used here. We remain neutral to the application of NHST, preferring the use of *p*-values as a continuous measure of statistical support. However, if NHST is employed, researchers must ensure that a large number of samples is used, to prevent inference being based on a handful of rare events. Note that, although not advisable for NHST, we were able to produce meaningful results with 100 simulations, which provided information (although much less reliably) of how incompatible the observed variance was with the range expected under the null hypothesis.

4.3 | Alternative approaches

Use of a *p*-value relies upon the distribution of *p*-values being uniform when the null hypothesis is true, a property that is expected to be invariant to sample size (as we show in Figure 4). *p*-values therefore only provide support against the null hypothesis; they do not provide support for the null hypothesis. In contrast to *p*-values, the ROPE value and Bayes factors aim to additionally assess support for the null hypothesis, and therefore depend upon sample size under both the null and alternative hypotheses. These alternatives are not always simple to implement, and below we outline some potential issues that empiricists may encounter.

The ROPE introduces another source of subjectivity into the analysis through defining an arbitrary threshold. This is not trivial for variance components, as small variances can have large knock-on effects. For example, McFarlane et al. (2015) found that maternal genetic effects accounted for 2% of variation in fitness, which predicted a 56% increase in mean lifetime reproductive success under 10 generations. Bonnet et al. (2022) employed a ROPE approach, using simulations to demonstrate the biological relevance of the thresholds they use. ROPE is often discussed in a context where a cost–benefit analysis can be used to work out the minimum effect size that warrants the use of a particular (e.g. medical) intervention (Kruschke, 2018). While there are clear applications for using ROPE in fields like conservation, where interaction with stakeholders requires thresholds over which decisions are made, for many empiricists, ROPE requires more subjective decisions to be made and justified.

Bayes factors can be used to test the 'significance' of parameters in Bayesian mixed-effect models. However, the calculation of Bayes factors is not straightforward. They require large posterior distributions for stable estimation (Schad et al., 2022). They also depend on the marginal likelihoods of the two models which are sensitive to prior specification (Gelman et al., 2021; Navarro, 2019; Schad et al., 2022), even when there is little or no visible effect on the posteriors. Using Bayes factors as a measure of posterior odds also assumes equal probability of the two models, and it is not clear whether this is a reasonable assumption as some would argue that some among-group variance always exists.

Bayesian models can also be compared using information criteria, in particular deviance information criteria (DIC; Spiegelhalter et al., 2002), widely applicable information criteria (WAIC; Watanabe, 2010) and LOO-CV (Browne, 2000; Gelman et al., 2014), which aim to provide out-of-sample prediction accuracy. DIC has several problems which in part come from being based on a point estimate (Plummer, 2008), and provides poor estimates when posterior distributions are not well described by their means (Gelman et al., 2021). WAIC addresses these issues by using the whole posterior. However, some assumptions of WAIC do not hold for hierarchical models with weak priors (Gelman et al., 2014; Millar, 2018). LOO-CV may, therefore, be the most suitable information criteria for this purpose. It is also important whether these information criteria are generated using marginal or conditional likelihoods (Ariyo et al., 2020; Merkle et al., 2019; Millar, 2018)—although the marginal likelihood may be more appropriate for comparing hierarchical models, many software packages only (MCMCglmm) or by default (BUGS, JAGS, Stan) provide the conditional likelihood.

The use of both LOO-CV and Bayes factors for complex models is currently the subject of intense debate. Regardless of the various intricacies of this debate, perhaps a more constraining factor is that Bayes factors and LOO-CV are not implementable in all programs, including those commonly used for variance component estimation in ecology and evolution (i.e. MCMCglmm). Our approach provides an alternative to these methods, which is easily implemented and allows straightforward interpretation.

4.4 | Power analysis and possible alternatives

Power analysis is controversial because of its link to NHST, and the misuse of NHST has been linked to scientific misconduct and the replication crisis (Amrhein et al., 2017, 2019; McShane et al., 2019; Wasserstein & Lazar, 2016). While these criticisms relate to the use of *p*-values *after* data collection and analysis, power analysis is typically conducted *pre*-analysis, and serves a clear purpose in aiding experimental design. Power can also be seen as a description of the distribution of *p*-values expected for a given effect size and data structure. Other descriptions of this distribution (e.g. the mean) would be simple functions of the power (Figure S5), but the common use of this metric makes it more widely understood. One suggested alternative, Type M error (absolute relative bias of significant estimates), also relies upon calculation of *p*-values and an arbitrary alpha value, and is a simple function of power (Gelman & Carlin, 2014). Unlike power, Type M error is affected by the measure of central tendency that is chosen (Figure S16). Another alternative to power is to design studies around a desired

level of precision in estimates. Although this works for unbounded parameters, precision is difficult to interpret for variance components, because it increases as the true value gets closer to zero due to the constraint at zero (see Figure S2). Using relative precision (the inverse of the coefficient of variation of the sampling distribution) avoids this problem. It is strongly related to power (Figure S13), and so optimizing this value may provide an alternative target for planning optimal experimental designs. The relative precision is, however, also highly dependent on the measure of central tendency used. We would therefore suggest that power still provides a suitable metric for designing studies to estimate variance components.

We show two methods of power analysis based upon null distributions. The first (full) method involved generating *p*-values by creating a null distribution for each 'observed' dataset. This method is highly computationally intensive as it involves running a certain number of simulations multiplied by the number of permutations/simulations models, which could realistically be one million models per parameter. Our alternative (reduced) method involved generating *p*-values by comparing the parameter estimates from the 'observed' datasets to a single null distribution for each data structure. While the two methods estimated similar power, the reduced method was massively less computationally intensive (requiring running 2000 models rather than a million for each set of parameters). The disadvantage is that a FPR cannot be calculated.

Even if power is not the intended use, these simulations can still serve an extremely useful purpose before studies are conducted. First, these simulations allow an empiricist to consider the distribution of *p*-values expected under a given effect size and design (power is essentially a description of the shape of this distribution). Second, the null distribution of point estimates can be visualized. Even if an empiricist does not want to calculate a *p*-value, creating a null distribution is a powerful way of considering the distribution of estimates that would be generated with no among-group variance, and would serve to encourage caution in how results that lie within that distribution are interpreted.

4.5 | Computational burden

Null distribution approaches can be computationally intensive. When model complexity and/or sample sizes are high, applying them can take a long time, and may prohibit their use. There are several points in this regard that are worth noting. First, these computational constraints will become increasingly less problematic with advances in computing and software. For example, the introduction of Stan has led to a considerable decrease in computation time for many MCMC models, and the increased availability of computer clusters means that null distribution can be generated in parallel. Second, the mean and median require far lower effective sample size than CRIs to be well estimated (Vehtari et al., 2021). 'Null' models can therefore be run for much shorter times than the original model, as only the mean/median is needed. Third, other metrics are also computationally expensive. For example, the generation of Bayes factors and LOO-CV requires running two models with much larger posterior distributions (one to two orders of magnitude larger; Gronau et al., 2020; Vehtari et al., 2017), followed by additional computationally expensive steps. Finally, our suggested method will be the most efficient for power analysis. Whereas each Bayes factors and LOO-CV require two models with large posteriors, in our method the same null distribution can be used for all simulated datasets with the same data structure, requiring models with much smaller posteriors. Relative precision is even less computationally intensive to generate, but perhaps slightly harder to interpret. Overall, the computational burden of generating a null distribution is perhaps not so high when compared to other alternatives.

There will be cases in which none of these methods (null distributions, Bayes factors or LOO-CV) will be feasible for computational reasons. Are there any less computationally expensive alternatives? The ROPE method provides a clear advantage here as it requires no additional computationally expensive steps to generate, although it may be difficult to apply with variance components. We realized when considering the relative precision as a metric for the sampling distributions that for an individual posterior distribution this metric (mean/SD) is analogous to a *z*-ratio. Interpretation in this context is a little strange, and *z*-ratios are typically used to represent the potential overlap of the uncertainty of a parameter estimate with 0, which cannot occur here. However, this kind of method is used with variance components in frequentist models that report the SEs of the variance components (e.g. when estimating genetic variance/heritability in ASReml (Butler et al., 2017)). Ultimately, we are looking for a usable statistic to describe the support for a difference between the variance component estimate and 0. These metrics would be considerably less computationally intensive to generate than a *p*-value from a null distribution, but may give similar information about the model estimates. Comparing them for individual models shows that this appears to be true; the *z*-ratio correlates strongly with *p*-value (Figure S17a). This statistic (posterior mean/posterior SD) may therefore provide some inferences about the posterior distribution of variance components, although it is much more conservative than a *p*-value generated from null distributions (Figure S17b). While this may provide an interesting solution to the problems of computational power, use of the *z*-ratio requires further exploration before being implemented.

4.6 | Recommendations

1. We advocate using the posterior median as a measure of central tendency for posterior distributions of variance components from MCMC-based models. Our results show that the median is the least biased estimate, but will overestimate variances when power is low. Reporting multiple measures of central tendency allows any asymmetry in the posterior to be made obvious.

2. We advocate reporting of smoothing values in kernel estimation. Kernel density estimation is commonly used for estimating the posterior mode and creating density plots. The parameters used in this estimation are seldom reported, but can have a large impact on interpretation. We advise the reporting of parameters in the kernel density estimation, or the use of more explicit methods of plotting posterior distributions, such as histograms.
3. We recommend using null distributions for inference. Null distributions provide a way of putting the observed parameter estimates into a context expected under an explicitly defined null hypothesis (i.e. no among-group variance). Null distributions can be created in multiple ways, but they are most easily controlled when generated using simulations. As with many aspects of statistical analysis, there are many decisions relating to generating null distributions that may have an affect on the results. Therefore, these methods should be defined pre-analysis, in order to reduce researcher degrees of freedom (Simmons et al., 2011).
4. We also advocate for using a null distribution to estimate power. As well as aiding *post-hoc* inference, null distributions can be used for power analysis. We provide details of a method for doing so that does not present a large computational burden.

AUTHOR CONTRIBUTIONS

Joel Pick, Claudia Kasper, Niels Dingemanse, David Westneat and Yimen Araya-Ajoy conceived the ideas; Joel Pick, Yimen Araya-Ajoy, Holger Schielzeth and Ned Dochtermann designed the methodology; Joel Pick and Yimen Araya-Ajoy ran the simulations; All authors contributed to the interpretation of results; Joel Pick and Yimen Araya-Ajoy led the writing of the manuscript, and all authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.14200.

DATA AVAILABILITY STATEMENT

All code and generated data for the simulated examples are deposited in https://doi.org/10.5281/zenodo.8189617 (Pick & Araya-Ajoy, 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1: Supplementary methods.

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