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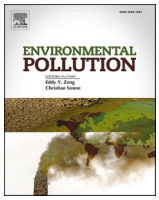

The impacts of pesticide exposure on fish conspecific interactions: A systematic review and meta-analysis

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ABSTRACT

The production of chemical pesticides poses a critical threat to aquatic ecosystems worldwide, with sub-lethal impacts evident at even relatively low concentrations. Historically, ecotoxicologists have ignored an organism's social context when investigating the effects of pesticide exposure and, instead, have tended to focus on individual-level impacts. Recently, however, there has been a growing interest in understanding the impacts of pesticide exposure on social behaviour. Despite this shift, a holistic understanding of how pesticides impact conspecific interactions (i.e., social behaviour towards individuals of the same species) is lacking due to the multitude of behaviours, pesticides and species currently investigated. In this meta-analysis, we examine the effects of pesticide exposure on conspecific interactions in fish by using data collected from 37 studies on 31 pesticides and 11 species. Our results indicate that pesticide exposure generally reduces the expression of conspecific interactions, but it does not affect the variability of responses between individuals. Courtship behaviour was the most impaired, suggesting that pesticide exposure could weaken how matings are partitioned among individuals in a population. Triazoles and organochlorines were the most impactful pesticide classes for mean differences in behaviour, while triazoles and organophosphates had the greatest effects on response variability. These findings indicate that endocrine-disrupting and neurotoxic pesticides can impact fish conspecific interactions, regardless of their chemical class. Unfortunately, there is a large taxonomic bias in the literature, with most studies using zebrafish as a model, which, in turn, provides scope for studies using a broader range of fish species. We found little statistical evidence of publication biases in our dataset and our results were validated by sensitivity analyses. Overall, our synthesis suggests that pesticides broadly reduce the expression of social behaviours, though effects vary across behaviours, pesticide types, and fish species.

1. Introduction

Chemical pollution caused by the continuous production and use of pesticides in agricultural systems is widely regarded as a leading threat to biodiversity (Tang et al., 2021). The increasing human reliance on pesticides has resulted in their detection in aquatic ecosystems globally (Bernhardt et al., 2017; Tang et al., 2021). Consequently, there has been increasing research effort to understand the impacts of pesticides on aquatic ecosystems (Islam et al., 2022; Morrison et al., 2024). To do so, ecotoxicologists routinely use fish species due to their importance in aquatic ecosystems and because of their amenability to laboratory conditions (Choi et al., 2021).

At the concentrations commonly detected in global surface waters, pesticides have been shown to have sublethal effects (Morrison et al., 2024). A sublethal impact garnering considerable interest in ecotoxicology is behaviour due to its critical link with an organism's physiological state (Bertram et al., 2024, 2022; Scott and Sloman, 2004; Wong and Candolin, 2015). Traditionally, ecotoxicologists have focused on the

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impacts of pesticides on individual behaviour by exposing, housing, or testing fish in isolation (Martin and McCallum, 2021; Michelangeli et al., 2022; Pyle and Ford, 2017). However, to fully understand the sublethal impacts of pesticide exposure at the population level and over evolutionary timescales, it is important to consider conspecific interactions—that is, behaviour between individuals of the same species (Boughman et al., 2024; Köhler and Triebskorn, 2013; Michelangeli et al., 2022).

As a result, behavioural ecotoxicologists have recently shifted their focus on the impacts of pesticide exposure to fish conspecific interactions (Morrison et al., 2024), including aggression (Boscolo et al., 2018), collective movement (Shuman-Goodier and Propper, 2016), and courtship (Aulsebrook et al., 2020). However, examining pesticide exposure studies in isolation makes it difficult to capture the broader impacts of pesticides on conspecific interactions across various behaviours, pesticides, species and study methodologies (Morrison et al., 2024). Despite these challenges, no study has systematically evaluated the overall effects of pesticide exposure on fish-conspecific interactions or the extent to which methodological differences influence observed fish responses. These highlighted shortcomings have contributed to the growing demand for more evidence synthesis in behavioural ecotoxicology (Bertram et al., 2022).

Meta-analysis is the statistical aggregation of research results and is a powerful methodology for summarizing evidence on a given topic (Gurevitch et al., 2018). Meta-analysis can, therefore, be used to effectively aggregate research results across different behaviours, pesticides, species and methodologies, investigating how each can contribute to overall observed heterogeneity (Nakagawa et al., 2017). Previous meta-analyses on the effects of pesticides on fish behaviour showed mean decreases in swim speed and activity (Shuman-Goodier and Propper, 2016). More recent work on fish neuromuscular biomarkers suggests that pesticide exposure can also reduce the variability of physiological responses (Santana et al., 2022, 2021). This raises the question of whether pesticide exposure can similarly reduce the variability of behaviours, such as conspecific interactions. This consideration is especially relevant because phenotypic variation is fundamental to the process of natural selection and, thus, has evolutionary consequences (Boughman et al., 2024).

Given the highlighted limitations in our understanding of the impacts of pesticides on fish behaviour due to significant methodological differences among studies, we conducted a phylogenetically controlled meta-analysis. This analysis synthesised the impacts of pesticide exposure on the mean and variability of conspecific interactions and examined whether methodological differences contribute to the observed responses. Our meta-analysis, preregistered at https://osf.io/hdjpq/, aimed to address several predefined objectives. First, we investigated how pesticide exposure affects the mean and variability of fish-conspecific interactions across all studies, specifically whether there is an overall increase or decrease in these measures. Second, we examined the influence of behavioural characteristics, such as the type of behaviour measured and the assays used, on the mean and variability of conspecific interactions. Third, we explored how pesticide characteristics, including the specific pesticides, dosages, exposure durations, and solvents, impact these outcomes. Finally, we assessed how fish characteristics, such as species, source, and sex, influence the mean and variability of conspecific interactions.

2. Methodology

We preregistered the search strings, screening eligibility criteria and planned analyses prior to literature screening (see https://osf.io/hdjpq/). To be transparent on the completeness of reporting we provide a PRISMA-Eco Evo (O'Dea et al., 2021) checklist in Supplementary File 1. The PRISMA checklist was filled in by KM and reviewed by YY. All data, code, model outputs and additional information required to reproduce this study are provided at https://github.com/KyleMorrison99/fish_conspecific_behaviour_MA. We have also provided a detailed markdown file with all code required to reproduce the results https://kylemorrison99.github.io/fish_conspecific_behaviour_MA/. The reporting of the methodology followed MeRIT to improve author contributions' granularity and accountability (Nakagawa et al., 2023a). All additional details relevant to the full literature search, literature screening, data extraction and data analysis can be found in the Supplementary File 2, *Methodology section*.

2.1. Literature search strategy

To find relevant studies on the impacts of pesticide exposure on fish-conspecific interactions, we accessed Scopus, ISI Web of Science Core Collection, and PubMed on March 01, 2024. Additionally, we searched the grey literature using the Bielefeld Academic Search Engine (BASE) and ProQuest. All search strings are provided in full in Supplementary File 2. To augment the database search, KM conducted a backward/forward citation search on 6 relevant reviews already published on the topic (Bertram et al., 2022; Cally et al., 2019; Greer et al., 2019; Köhler and Triebskorn, 2013; Michelangeli et al., 2022; Saaristo et al., 2018; Shuman-Goodier and Propper, 2016; Söffker and Tyler, 2012). KM tested the sensitivity of the search against 10 benchmark papers identified independently of the search process using Google Scholar (Boscolo et al., 2018; Gusso et al., 2020; Hawkey et al., 2021; Jaensson et al., 2007; MacLaren, 2023; Saglio and Trijasse, 1998; Schmidel et al., 2014; Shenoy, 2012; Zaluski et al., 2022; Zhou et al., 2021).

2.2. Literature screening strategy

To screen for relevant literature, KM, supported by ML, MM, SO, RE, GM, JM, AB, and BW, developed a set of eligibility criteria (Fig. s1 for screening flowchart and all inclusion/exclusion criteria). The screening strategy followed a two-step approach: first, studies were screened based on abstract relevance, and second, by full-text relevance. To ensure thorough screening, all literature was reviewed in duplicate with each reviewer blind to the others decision (KM 100 %, ML 23 %, MM 13 %, SO 13 %, RE 13 %, GM 13 %, JM 13 %, AB 12 %). Studies that were either author indicated "Yes" or "Maybe" at the abstract screening stage were included for full-text screening. For inclusion in the meta-analysis, both reviewers had to agree with a "Yes." Conflicts between reviewers at the full text screening stage were resolved through discussion, with a mediator (SN) present if required. All studies rejected at the full-text screening stage were provided with exclusion reasons (Table s2). The literature screening was carried out using the screening software *Rayyan* (Ouzzani et al., 2016). To conduct the screening, we firstly uploaded the deduplicated search records to Rayyan. Then, we conducted title, abstract and keyword screening using the platform's blind abstract screening feature, which hides the reviewers' decisions to minimise bias. Following this, we exported all potentially relevant studies and re-uploaded them into a new Rayyan project for full-text screening. To screen the full texts, each reviewer searched for the full text online and applied the inclusion and exclusion criteria to determine eligibility. After completing both screening stages and reconciling any conflicting decisions, we exported the studies selected for inclusion in the meta-analysis.

2.3. Data extraction

KM extracted data from all relevant studies, with 30 % of the extracted data double-checked (10 % each by YY, GM, and SN). For each study, we extracted a set of predefined variables following the preregistration (https://osf.io/hdjpq/). We have provided descriptions and full definitions of all variables in Supplementary File 2, Section *Data extraction variables*. In short, the extracted variables included behavioural characteristics—such as the behaviours measured (aggression, courtship, social attraction, and collective movement) and the

behavioural assays used (zone, count, entries); pesticide characteristics—including the pesticide used for exposure, its dosage, duration, and the solvent employed; and species characteristics—such as the species exposed, their sex, and the source of the fish. All statistical variables needed to calculate effect size estimates were extracted from text and tables when available. Otherwise, we extracted data from figures using R packages *Shiny Digitise* and *Meta Digitise* (Pick et al., 2019). When raw data or individual points from figures were provided, we calculated means, errors, and sample sizes from the raw data. We imputed standard deviations of effect size estimates when it was missing by using the mean-variance relationship identified (Fig. s14) (Lajeunesse, 2016). To enrich the insights provided during the data extraction we incorporated a systematic evidence map approach to visualise study characteristics (Yang et al., 2025).

2.4. Effect size calculations

We estimated the impacts of pesticides on both the magnitude and variability of conspecific interactions. To measure magnitude and variability we used the response ratio (RR) and the variation ratio (VR), respectively. To approximate normality, both effect size estimates were logarithmically transformed. We defined the two effect size estimates along with their sampling variances as follows:

Response ratio (see Lajeunesse, 2015)

$$lnRR = ln\left(\frac{\bar{x}_{treatment}}{\bar{x}_{control}}\right) + \frac{1}{2}\left(\frac{s^2_{treatment}}{n_{treatment}\ \bar{x}^2_{treatment}} - \frac{s^2_{control}}{n_{control}\ \bar{x}^2_{control}}\right), \quad (1)$$

$$s^2_{lnRR} = \frac{s^2_{control}}{n_{control}\ \bar{x}^2_{control}} + \frac{s^4_{control}}{2n^2_{control}\ \bar{x}^4_{control}} + \frac{s^2_{treatment}}{n_{treatment}\ \bar{x}^2_{treatment}} + \frac{s^4_{treatment}}{2n^2_{treatment}\ \bar{x}^4_{treatment}}, \quad (2)$$

Variation ratio (see Senior et al., 2020)

$$lnVR = ln\left(\frac{s_{treatment}}{s_{control}}\right) + \frac{1}{2}\left(\frac{1}{n_{\text{control}} - 1} + \frac{1}{n_{\text{treatment}} - 1}\right), \quad (3)$$

$$s^2_{\text{lnVR}} = \frac{1}{2}\left(\frac{n_{\text{control}}}{(n_{\text{control}} - 1)^2} + \frac{n_{\text{treatment}}}{(n_{\text{treatment}} - 1)^2}\right), \quad (4)$$

Where $\bar{x}_{treatment}$ and $\bar{x}_{control}$ are the (sample) mean of conspecific interaction for the treatment and control, respectively; $s_{control}$ and $s_{treatment}$. are the (sample) standard deviations (SDs), $n_{control}$ and $n_{treatment}$ are the corresponding sample sizes.

2.5. Statistical modelling summary

All statistical modelling was conducted by KM (checked by SN and YY). To analyse the effect size estimates, we used multi-level meta-analysis models with a sampling variance-covariance matrix (Nakagawa et al., 2023c). The t-distribution was used to compute the test statistics and confidence intervals for the fixed effects, and the restricted maximum likelihood (REML) was used as the model estimator. The constructed models accounted for four types of statistical dependency: 1) the dependency of multiple effect sizes per study, pesticide and species, 2) different levels of phylogenetic relatedness between species, 3) the correlation of errors due to repeated behavioural measurements from the same set of individuals and, 4) multiple treatment groups being compared to a single control group (i.e., shared control between treatments). To quantify heterogeneity (i.e., variance not due to sampling error) we calculated the total heterogeneity I^2_{total}, which indicates the total variance excluding sampling variance. Then, we decomposed the I^2_{total} into the different random effects including between study, between observation, between pesticide and between species (i.e., I^2_{study}, $I^2_{observation}$, $I^2_{pesticide}$ and $I^2_{species}$). Robust-variance estimation was not used because pesticides and species are crossed random effects not nested random effects (Yang et al., 2024). To assess whether effect size estimates were influenced by predefined predictor variables we constructed a series of meta-regression models. The marginal R^2 was used to quantify the proportion of heterogeneity explained by each moderator (Nakagawa and Schielzeth, 2013). We have provided the model parameters for both intercept-only and predictor models in Supplementary File 2.

2.6. Model selection and multi-modal inference

To test the robustness of the results obtained from the predictor models we conducted model selection and multi-model inference (Cinar et al., 2021). This was completed by, fitting 64 models with all possible combinations of predictor variables. We then assessed their AICc values to select the best models whose AICc were <2 units larger than the lowest AICc (Grueber et al., 2011). We then evaluated the importance of the predictor variables by considering all 64 models' Akaike weights. Each of the 64 models had the same random effects structure as the predictor models but were fitted using maximum likelihood rather than REML to allow model comparison (Cinar et al., 2021).

2.7. Publication bias, time lag bias and sensitivity analysis

Publication bias refers to the unequal likelihood of significant findings being published when compared to nonsignificant results, thus creating a bottleneck of underrepresented study findings which, in turn, may potentially lead to unfounded conclusions. We visually inspected the relationship between model residuals and the standard error using funnel plots. This methodology assumes no heterogeneity and, thus, should not be used in isolation. We then performed a multilevel Egger's regression to test the symmetry of the funnel plot using sampling variance as a moderator. Time-lag bias refers to the cases when earlier published studies tend to show larger effect size estimates with smaller sample sizes. To assess the potential time-lag bias, we implemented a multi-level meta-regression with publication year as a moderator. Publication bias is likely only an issue for mean differences because studies did not explicitly test for differences in variability (Yang et al., 2022). Therefore, all publication bias assessments were only conducted for *lnRR*. To further assess the robustness of results, we conducted four sensitivity analyses. We first conducted a leave-one-out cross-validation, where one study, pesticide or species was excluded from the dataset, and the intercept-only model was rerun (see Supplementary File 2 for formulas). Second, we reanalysed the intercept-only model using an alternative variance-covariance matrix under different assumptions about non-independence. Specifically, when it was unclear, we considered two scenarios: assuming that the exposure group comprised the same individuals across different behaviours (resulting in dependent estimates), or assuming they were different individuals (resulting in independent estimates) (Noble et al., 2017). Third, we reanalysed the intercept-only model without the imputed error estimates. Fourth, we conducted an alternative intercept-only analysis using lnCVR instead of lnVR to re-estimate response variability.

2.8. Statistical analysis software

All data analysis was conducted on the R Statistical Environment version 4.2.1 (R Core Team, 2024) using RStudio build 576 (RStudio Team, 2022). The phylogenetically controlled multi-level meta-analysis and meta-regression models were implemented using the *rma.mv* function in the *metafor* package (Viechtbauer, 2010). To infer the phylogenetic relatedness, we constructed a phylogenetic tree using the *Open Tree of Life* implemented using the *rotl* package (Michonneau et al., 2016). The branch length was calculated using the Grafen's method and we implemented using the *ape* package (Paradis and Schliep, 2019). To construct the variance-covariance sampling matrix we use the *vcalc* function in *metafor* assuming a constant variance of $\rho = 0.5$. All

visualisations of the models were constructed using *ggplot2* (Wickham, 2016) and the *orchaRd* 2.0 package (Nakagawa et al., 2023b).

2.9. Deviations from preregistration

While we closely followed our preregistration (see https://osf.io/hdjpq/), we made several minor adjustments and improvements. First, to examine differences in variability between control and treatment groups, we chose *lnVR* as the effect size measure instead of the originally proposed *lnCVR*. We made this selection because the dimensions of the measurements and the true mean-variance relationship are unknown, and *lnVR* clearly demonstrates variation differences irrespective of the mean (Pélabon et al., 2020). Second, although we initially planned to include phylogeny in all models, we ultimately limited its inclusion to intercept-only models based on our findings. Third, to improve our analysis, we introduced additional variables during data extraction and analysis. Specifically, we included two extra columns to indicate whether studies used a control solvent and whether they employed a zone-based or count-based assay. In addition, we added an alternative variance-covariance matrix because cohort identification was often unclear across studies.

3. Results

3.1. Summary of literature

We collected 449 effect sizes from 37 experimental studies involving 31 pesticides and 11 species (Fig. 1a). The behaviours measured in response to pesticide exposure were social attraction (24.6 %, 110 effect size estimates), collective movement (21.2 %, 95 effect size estimates), courtship (20.1 %, 90 effect size estimates) and aggression (34.1 %, 153 effect size estimates) (Fig. 1b). For species characteristics, we found that the most widely studied (73 %, 327 effect size estimates) model species was zebrafish (Fig. 1c). In addition, many studies (51 %, 232 effect size estimates) used fish of both sexes without distinguishing between them (Fig. s3). The fish were most often obtained directly from commercial suppliers (44 %, 197 effect size estimates, Fig. s4). For pesticide exposure characteristics, we found the most common pesticides investigated were deltamethrin (15.4 %, 69 effect size estimates) and atrazine (12.3 %, 55 effect size estimates) (Fig. s5). We found a range of dosages (median = 12 μg/L, 1st quartile = 1 μg/L, 3rd quartile = 500 μg/L; Fig. s6) and durations (median = 336 h, 1st quartile = 96 h, 3rd quartile = 960 h; Fig. s7) were used in the pesticide exposure. Furthermore, many studies did not use a chemical solvent (29.5 %, 132 effect size estimates) or, did not report whether a chemical solvent was used (28.1 %, 125 effect size estimates). However, when a solvent was reported, the most widely used was Dimethyl sulfoxide (DMSO) (31.5 %, 141 effect size estimates) (Fig. s8).

3.2. Overall effect on mean and variability

Pesticide exposure significantly decreased conspecific interactions by 23.4 % on average ($\beta_{lnRR} = -0.2669$, 95 % confidence interval (CI) = [−0.4868, −0.0471], $t_{447} = -2.3862$, $p = 0.0174$; Fig. 2A). In contrast, we found that pesticide exposure tended to not impact the variability of conspecific interactions with a decrease on average of 8.73 % ($\beta_{lnVR} = -0.0914$, CI = [−0.4614, −0.2784], $t_{447} = -0.4857$, $p = 0.6274$; Fig. 2B). The relative data heterogeneity was high for *lnRR* effect size estimates ($I^2_{total} = 97.42$ %) and moderate for lnVR ($I^2_{total} = 70.58$ %). We explored the contribution of all the included random effects for both *lnRR* and *lnVR*. We found that $I^2_{study} = 28.69$ %, $I^2_{observation} = 31.34$ %, $I^2_{pesticide} = 4.34$ % and $I^2_{species} = 33.05$ % for lnRR; whilst $I^2_{study} = 3.24$ %, $I^2_{observation} = 67.34$ %, $I^2_{pesticide} < 0.001$ % and $I^2_{species} = < 0.001$ % for *lnVR*.

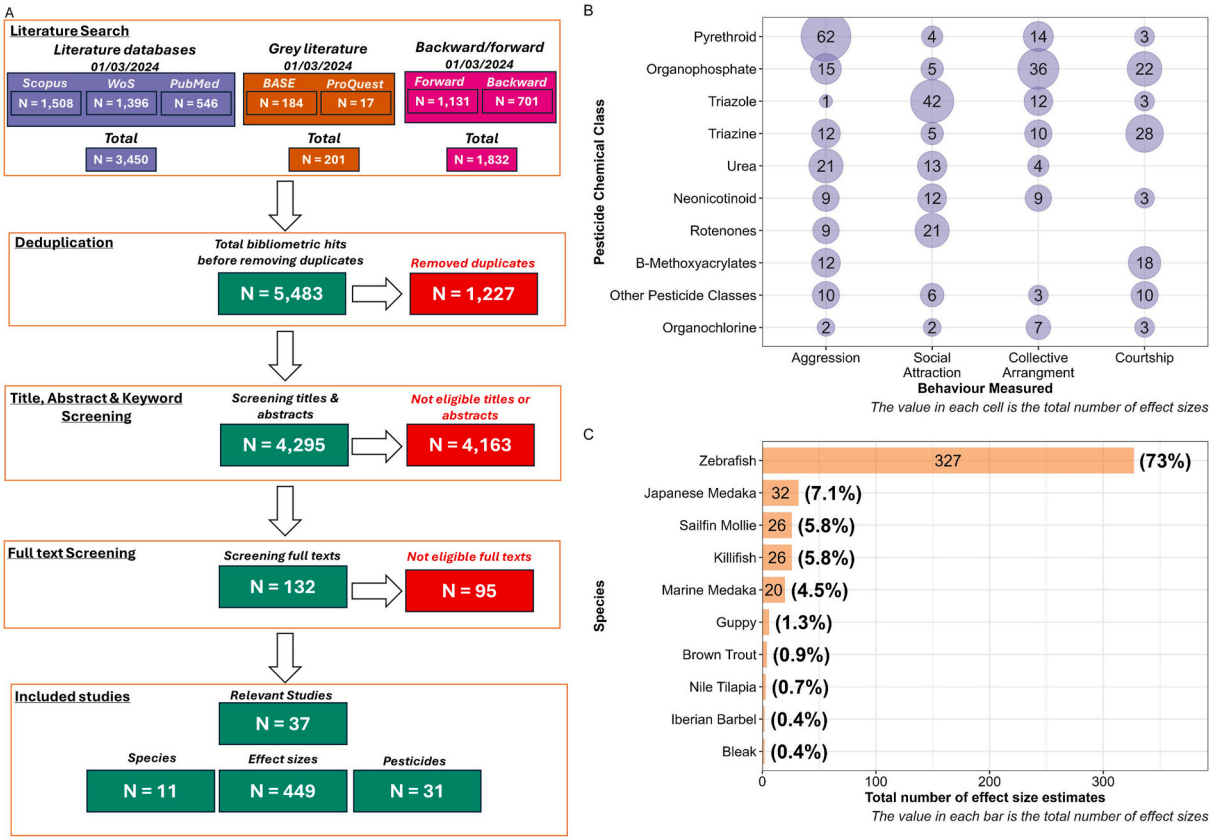

Fig. 1. (A) PRISMA flowchart summarizing the search methods used and the number of studies excluded at each step. (B) a circle plot showing the total number of effect sizes for each pesticide chemical class per behaviour measured. (C) a bar plot showing the total number of effect sizes for each species.

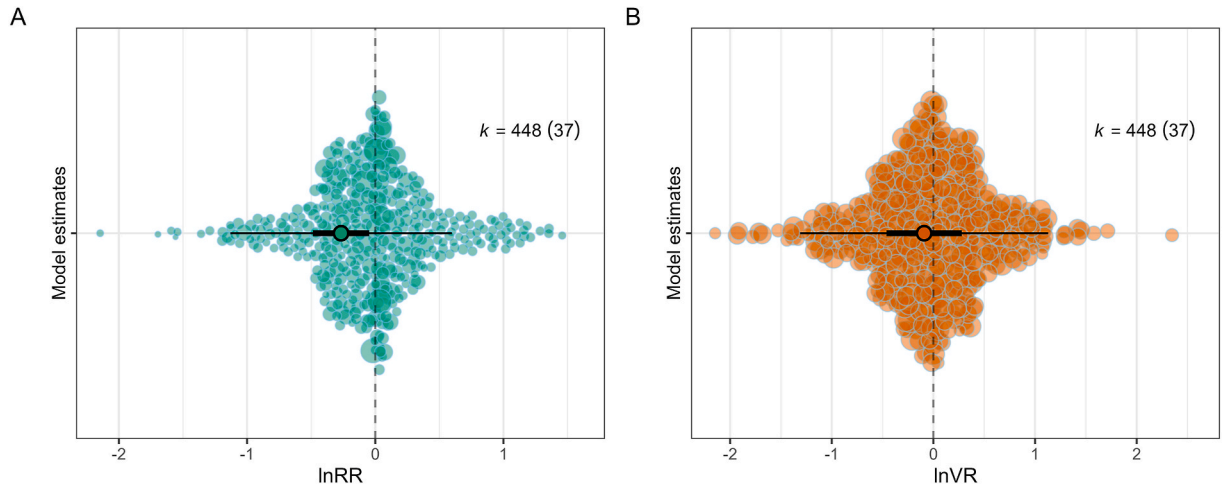

Fig. 2. Impacts of pesticide exposure on fish conspecific interactions. The model estimates the average effects of pesticide exposure on conspecific interactions in fish. (A) shows the mean difference between control and treatment groups on a logarithmic scale (lnRR), where negative values indicate a reduction in conspecific behavioural activity. (B) shows the difference in variances between control and treatment groups, also on a logarithmic scale, where negative values suggest a reduction in the inter-individual variability of conspecific behavioural activity (lnVR). Shorter-thicker whiskers represent 95 % confidence intervals, while longer-thinner whiskers indicate 95 % prediction intervals. 'k' represents the number of effect sizes, and the number of studies is in brackets. Each circle corresponds to an effect size, with its size scaled according to precision (inverse sampling error variance).

3.3. Impacts on conspecific behaviour characteristics

The conspecific interaction measured in response to pesticide exposure played a significant role in moderating the mean and an insignificant role in moderating variability changes (*lnRR*: $F_{4,444} = 7.1848$, $p < 0.0001$, $R^2_{marginal} = 0.07$; *lnVR*: $F_{4,444} = 1.3083$, $p = 0.266$, $R^2_{marginal} = 0.02$). For mean differences, we found that courtship significantly decreased in response to pesticide exposure on average by 34.82 % ($\beta_{lnRR\_courtship} = -0.4280$, CI = [−0.6585, −0.1976], $t_{444} = -3.6501$, $p = 0.003$; Fig. 3A). On the other hand, aggression, sociality and collective movement was not significantly impacted by pesticide exposure ($\beta_{lnRR\_aggression} = -0.1251$, CI = [−0.3531, −0.1030], $t_{444} = -1.0779$, $p = 0.2817$; $\beta_{lnRR\_collective\_behaviour} = -0.1788$, CI = [−0.4183, 0.0607], $t_{444} = -1.4675$, $p = 0.1430$; ($\beta_{lnRR\_sociality} = -0.1530$, CI = [−0.3886, 0.0825], $t_{444} = -1.2768$, $p = 0.2023$; Fig. 3A). For variational differences, we found that none of the behaviours had a significant difference between control and treatment groups ($\beta_{lnVR\_courtship} = -0.1674$, CI = [−0.3718, 0.0370], $t_{444} = -1.6092$, $p = 0.1083$; $\beta_{lnVR\_aggression} = -0.0470$, CI = [−0.2554, −0.1613], $t_{444} = -0.4436$, $p = 0.6476$; $\beta_{lnVR\_collective\_behaviour} = -0.0481$, CI = [−0.2554, 0.1613], $t_{444} = -0.4135$, $p = 0.6794$; $\beta_{lnVR\_sociality} = 0.0743$, CI = [−0.1505, 0.2990], $t_{444} = -0.6493$, $p = 0.5165$; Fig. 3B). There was no significant difference in magnitude or variability between zone-based assays and count-based assays ($\beta_{lnRR\_assay\_contrast} = -0.0235$, CI = [−0.1430, 0.959], $t_{278} = -0.3879$, $p = 0.6984$, Fig. 3C; $\beta_{lnVR\_assay\_contrast} = 0.0523$, CI = [−0.1104, 0.2149], $t_{278} = -0.6328$, $p = 0.5274$, Fig. 3D).

3.4. Impacts of pesticide characteristics

We found no significant differences in mean responses across pesticide classes, but there was a significant difference in response variability (*lnRR*: $F_{14,434} = 1.3108$, $p = 0.1969$, $R^2 = 0.1103$; *lnVR*: $F_{14,434} = 2.0818$, $p = 0.0119$, $R^2 = 0.10$). For mean differences, we found that organochlorines and triazoles significantly decreased interactions with conspecifics ($\beta_{lnRR\_organochlorine} = -0.1674$, CI = [−0.3718, 0.0370], $t_{435} = -2.2570$, $p = 0.0245$; $\beta_{lnRR\_triazole} = -0.5014$, CI = [−0.9188, −0.0841], $t_{435} = -2.3614$, $p = 0.0186$, Fig. 4A). For variability differences, we found that organophosphates and organochlorines led to a significant decrease in variability ($\beta_{lnVR\_organophosphate} = -0.2923$, CI = [−0., 0.4992, −0.0855], $t_{435} = -2.2778$, $p = 0.0057$; $\beta_{lnRR\_triazole} = -0.2512$, CI = [−0.4785, −0.0238], $t_{435} = -2.1709$, $p = 0.0305$, Fig. 4B). For moderating effects of dosage, we found no significant relationship between the dosage of pesticide exposure and the effect on mean or the variability of conspecific interactions ($\beta_{lnRR\_dosage} = -0.0090$, CI = [−0.0254, 0.0074], $t_{423} = -1.0780$, $p = 0.2817$, $R^2_{marginal} = 0.0042$, Fig. 4C; $\beta_{lnVR\_dosage} = -0.0140$, CI = [−0.0323, −0.0042], $t_{423} = -1.5142$, $p = 0.1307$, $R^2_{marginal} = 0.0081$; Fig. 4D). Likewise, for moderating effects of duration we found no significant relationship between duration of pesticide exposure and the mean or the variability of behaviours measured ($\beta_{lnRR\_duration} = -0.0001$, CI = [−0.0002, 0.0001], $t_{446} = -0.8544$, $p = 0.3933$, $R^2_{marginal} = 0.0074$, Fig. 4E; $\beta_{lnVR\_duration} = -0.0112$, CI = [−0.0366, −0.0143], $t_{423} = -0.8625$, $p = 0.3889$, $R^2_{marginal} = 0.0007$; Fig. 4F). We found a weak yet significant difference in mean estimates between studies that used a control solvent and those that did not, but no significant difference in the variability estimates ($\beta_{lnRR\_solvent\_contrast} = 0.1958$, CI = [−0.0670, 0.3247], $t_{320} = 2.9908$, $p = 0.0006$, Fig. 4G; $\beta_{lnVR\_solvent\_contrast} = 0.0893$, CI = [−0.1013, 0.2798], $t_{320} = 0.9218$, $p = 0.3573$, Fig. 4H).

3.5. Species sensitivities and characteristics

Overall, we found that the species of fish did not play a significant role in moderating the impacts on the mean or the variability of response (*lnRR*: $F_{10,438} = 0.9211$, $p = 0.0723$, $R^2 = 0.11$; *lnVR*; $F_{10,438} = 0.9211$, $p = 0.5134$, $R^2 = 0.07$). However, it is important to note, many species are understudied with limited effect size estimates (Fig. 1B). Therefore, confidence intervals are large, and precision is low for most species (Figs. 1C and. 5). In terms of sex of fish, we found no significant difference between female and male fish for both effects on mean and variability ($\beta_{lnRR\_sex\_contrast} = -0.0809$, CI = [−0.2429, 0.0811], $t_{70} = -0.9960$, $p = 0.3227$; $\beta_{lnVR\_sex\_contrast} = 0.1204$, CI = [−0.217 4, 0.4582], $t_{70} = 0.7107$, $p = 0.4797$ Likewise, we did not find a significant difference in the mean or the variance between wild collected fish and laboratory bred/commercially purchased fish ($\beta_{lnRR\_source\_contrast} = -0.4703$, CI = [−1.5404, 05998], $t_{396} = -0.8663$, $p = 0.3873$; $\beta_{lnVR\_source\_contrast} = -0.0490$, CI = [−0.4265, 0.3285], $t_{396} = -0.2560$, $p = 0.7982$).

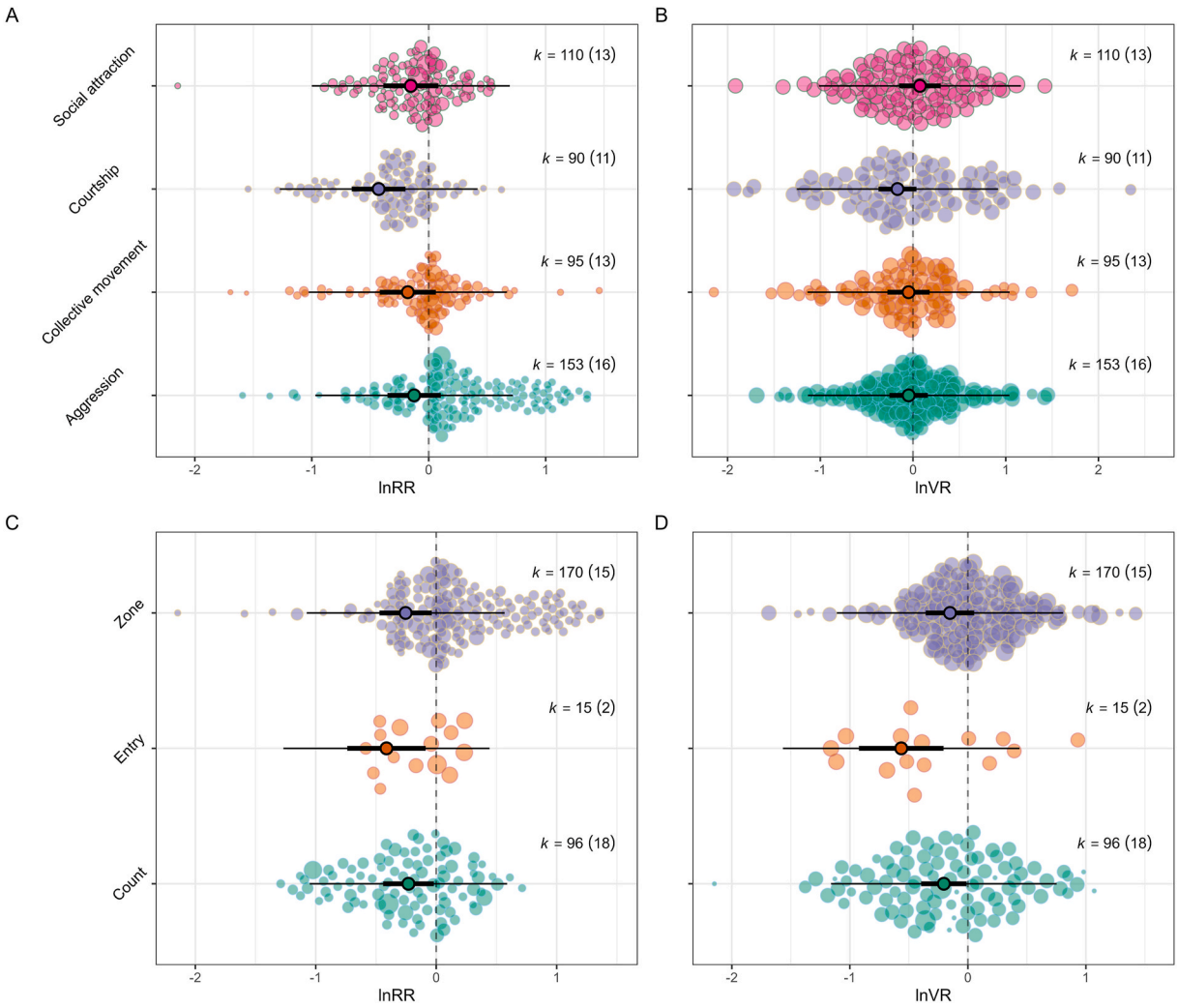

Fig. 3. The moderating effects of behaviour measured: Social Attraction, Courtship, Collective Movement and Aggression on (A) response magnitude of conspecific interaction, and (B) response variability of conspecific interactions, followed by the moderating effects of assay type used: Zone, Entry and Count on (C) response magnitude of conspecific interaction, and (D) response variability of conspecific interactions. The model estimates were obtained using an uni-moderator meta-regression. Refer to Supplementary File 2 for full definitions of all extracted variables. The remaining details are the same as in Fig. 2.

3.6. Model selection and multimodal inference

The model, including all moderators, explained 71.4 % of variation in mean differences and 30.5 % of variation in variability differences. Model selection revealed that the type of behavioural assay was an important moderator for both mean and variability estimates (Fig. 6). The model with the lowest AICc (225.3307) for estimating mean differences included behavioural assay, pesticide chemical class, species and sex of fish and had an 18.7 % probability of being the best model. Whilst the model with the lowest AICc (425.4661) for estimating variability differences included behaviour assay, pesticide chemical class and species, and had a 21.5 % probability of being the best model.

3.7. Publication bias, time-lag bias and sensitivity analysis

We found minimal evidence of publication bias (i.e., no bias towards the publication of significant results) detected by visual inspection of the funnel plot (Fig. s20) and Egger's regression analysis ($\beta_{lnRR\_sampling\_error} = -0.0809$, CI = [−4642, 0.3025], $t_{446} = -0.4145$, $p = 0.6787$; Fig. s21) and we found no time-lag bias in effect sizes over time ($\beta_{lnRR\_publication\_year} = -0.0582$, CI = [−0.0303, 0.1467], $t_{446} = 1.2930$, $p = 0.1967$; Fig. s22). We further investigated the robustness of our results through four sensitivity analyses. Excluding individual studies, species, or pesticides from the models had little influence on the magnitude of results. However, we found that excluding some species or pesticides changed the significance of results (Figs. s23–28). Furthermore, using an alternative variance-covariance structure with a different assumption of non-independence had little impact on the outcomes ($\beta_{lnRR\_alternative\_vcv} = -0.2655$, 95 %, CI = [−0.4839, −0.0470], $t_{447} = -2.3886$, $p = 0.0173$, Fig. s29A; $\beta_{lnVR\_alternative\_vcv} = -0.0799$, 95 %, CI = [−0.2557, −0.00959], $t_{447} = -0.8933$, $p = 0.3722$; Fig. s29B). Last, we found that excluding the imputed error estimates had little influence on the analysis conclusion ($\beta_{lnRR\_no\_imputed} = -0.2460$, 95 %, CI = [−0.4719, −0.0201], $t_{443} = -2.1402$, $p = 0.0329$. Fig. s30A; $\beta_{lnVR\_no\_imputed} = -0.0239$, 95 %, CI = [−0.2986, −0.2509], $t_{443} = -0.1706$, p = 0.8646; Fig. s30B).

4. Discussion

In response to evidence that pesticide exposure affects fish behaviour, this study aimed to quantify its overall impact on conspecific interactions and identify how these effects vary between different behaviours, pesticides, and species studied. Here, we conducted a meta-analysis, synthesising evidence from 37 studies involving 31 pesticides and 11 species, offering the first cross-chemical and cross-species quantification of the impacts of pesticide exposure on fish-conspecific

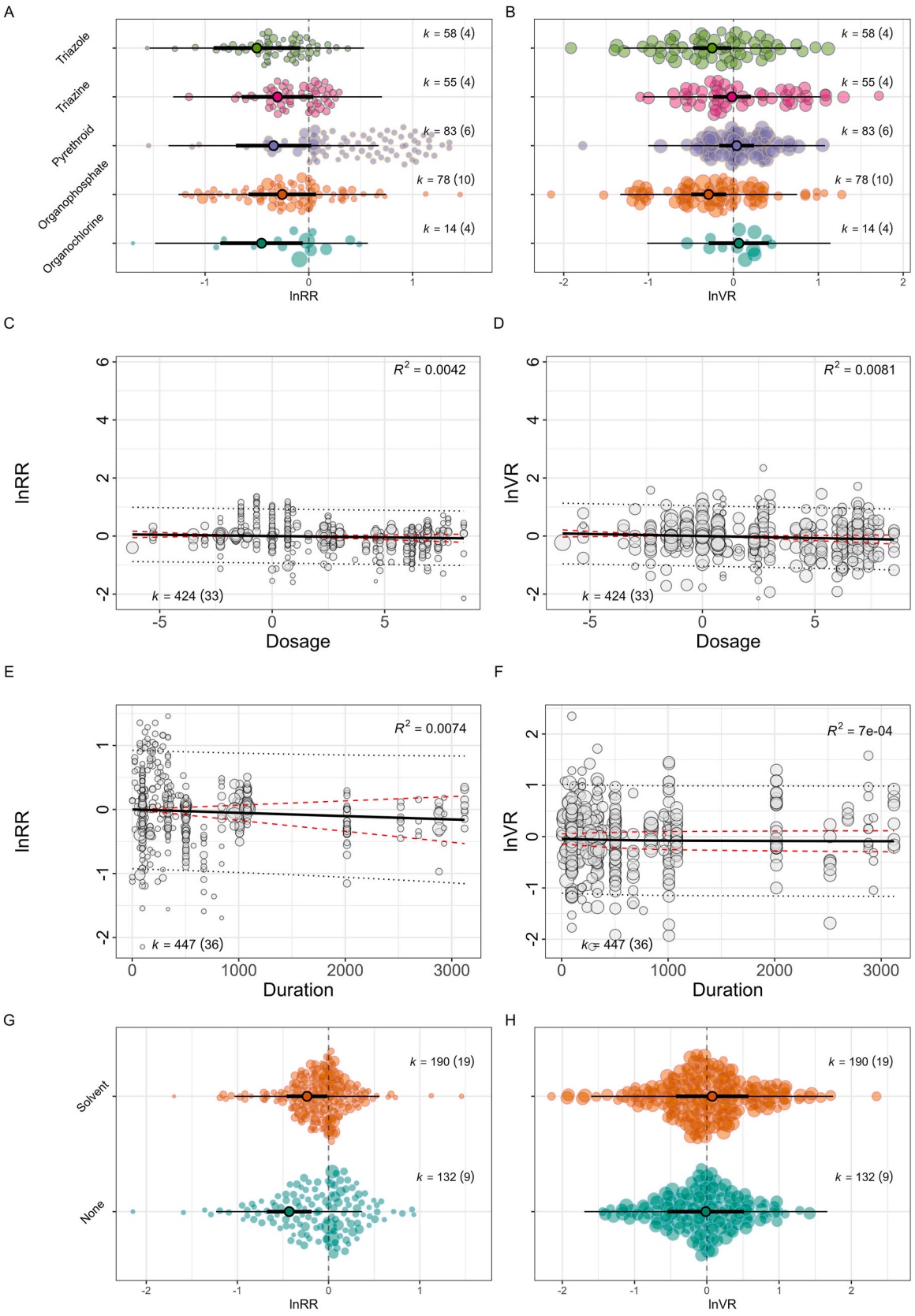

Fig. 4. The moderating effects of pesticide chemical class on (A) response magnitude and (B) response variability in conspecific interactions. Only chemical classes with more than three studies are included here; the complete plot with all chemical classes is available in the Supplementary File 2 (Fig. s18). Following this, we show the (C & D) moderating effects of dosage (ug/L, axis presented on the logarithmic scale) and (E & F) duration (hours) on both the mean and variability of the response. Minimal variance explained by dosage and duration is indicated by the R^2 values. Finally, the moderating effects of solvent use on response magnitude (G) and variability (H) are presented, with separate comparisons for conditions with and without solvents. Model estimates were obtained using univariate moderator meta-regressions. Further details are consistent with those provided in Fig. 2.

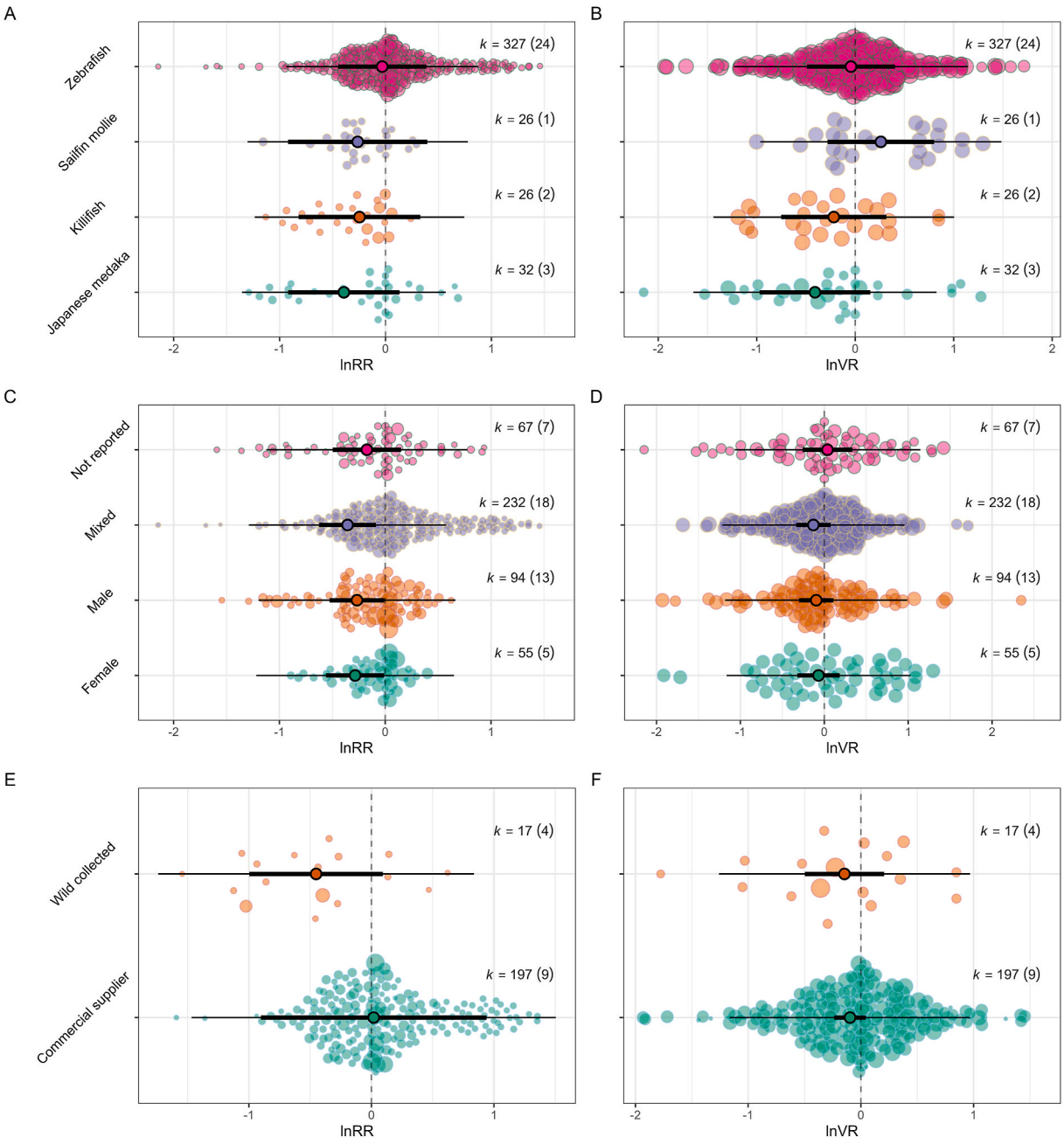

Fig. 5. The moderating effects of species on conspecific interactions, showing (A) response magnitude and (B) response variability. The figure is filtered to include only species with more than 15 effect size estimates; the complete plot, including all species, is provided in the Supplementary File 2 (Fig. s19). Following this, we show the moderating effects of sex on (C) response magnitude and (D) response variability. Finally, we present the moderating effects of fish source type on (E) response magnitude and (F) response variability. Model estimates were obtained using univariate moderator meta-regressions. The remaining details are the same as those in Fig. 2.

interactions. Overall, we found that pesticide exposure significantly reduced fish conspecific interactions by an average of 23.4 %, while the variability of responses was not significantly affected (an 8.73 % change on average). The overall heterogeneity for both the mean and the variability of response was large, and both within-study differences and the study species contributed greatly to this heterogeneity. The sensitivity analysis revealed that the results of the meta-analysis were robust, and little statistical evidence for publication bias in our dataset. This overall decrease in conspecific interactions aligns with other syntheses that have quantified significant declines in fish activity (Shuman-Goodier and Propper, 2016) and neuromuscular function (Santana et al., 2021) due to pesticide exposure. This suggests that impairing behaviour at the muscular control level can reduce fish's ability to perform behaviours, with likely knock-on consequences for their social competence and, hence fitness (Taborsky and Oliveira, 2012).

4.1. Impacts on conspecific behaviour characteristics

We found that pesticide exposure significantly and consistently decreased courtship behaviours in fish. In contrast, aggression, sociality, and collective behaviours exhibited inconsistent changes across studies; some reported increases while others observed decreases, reflecting high heterogeneity in the data (see Fig. 1). The observed reduction in courtship behaviours may result from several mechanisms. First,

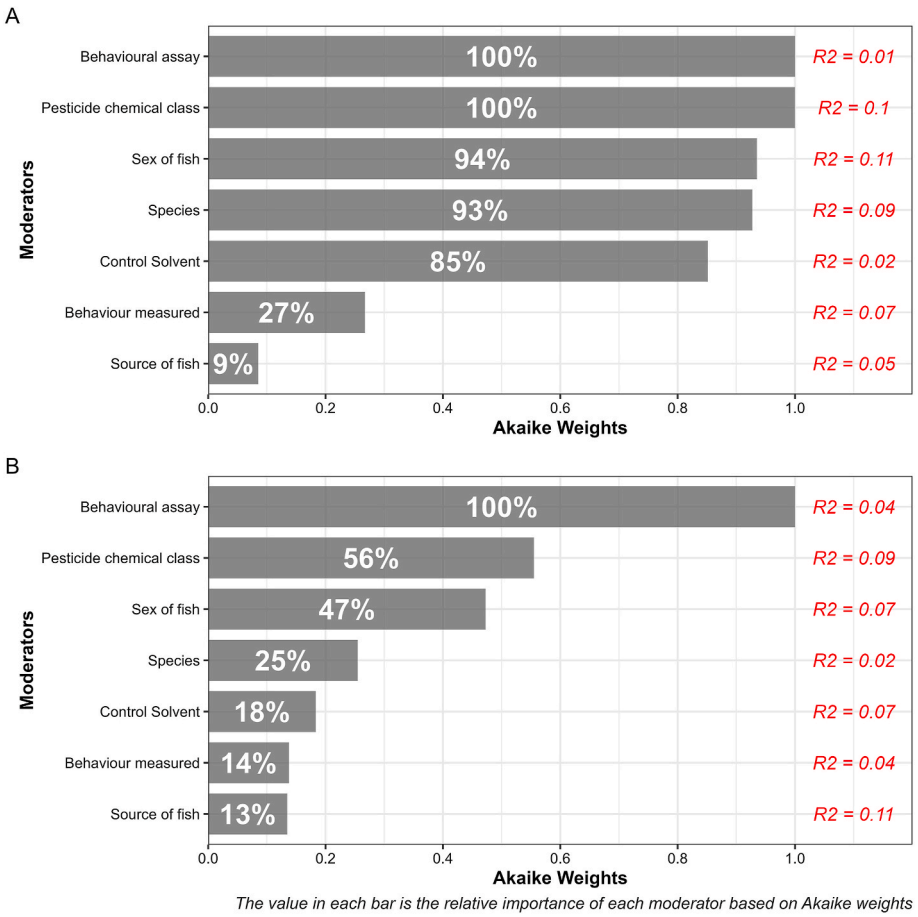

Fig. 6. The relative importance of tested moderator variables based on Akaike weights calculated from the Akaike Information Criterion (AIC) for (A) lnRR and (B) lnVR. The importance of each moderator variable was assessed across 64 candidate models by summing the Akaike weights of all models in which the variable appeared. These Akaike weights approximate the probability that a given model is the best among the candidate set, assuming equal prior probabilities for all models. Additionally, the marginal R^2 which indicates the proportion of variance explained, was estimated using the uni-moderator model with the corresponding moderator variable as the fixed effect.

endocrine-disrupting pesticides, such as organochlorines and organophosphates, can interfere with hormonal functions that regulate reproductive and courtship behaviours (Sárria et al., 2011). For example, organochlorine insecticides, like DDT and its metabolites, can bind to or block hormone receptors—functioning as oestrogen mimics or anti-androgens—which in fishes disrupts normal reproductive endocrine pathways (Martyniuk et al., 2020). Second, pesticide, such as organophosphates, are known to be neurotoxic and can disrupt important neuromuscular transmitters such as acetylcholinesterase (Santana et al., 2021; Shuman-Goodier and Propper, 2016). Acetylcholinesterase inhibition can lead to cholinergic hyperactivation, causing disorientation and irregular swimming (Green and Wheeler, 2013). Based on this, it is plausible that disruption of neuromuscular functions could also be a source of decreased courtship behaviours observed. Third, in addition to these endocrine disrupting and neuromuscular effects, exposure to organophosphate pesticides such as glyphosate has been shown to interfere with sensory processing and cognitive function, further reducing a fish's ability to detect, assess, or respond appropriately to potential mates (Bridi et al., 2017).

The complex impacts of pesticide exposure on fish social attraction and collective movement may be due to reduced activity in response to pesticides. Subsequently, this may decrease social behaviour responses in some contexts (Shuman-Goodier and Propper, 2016), while heightened anxiety may enhance social attraction and collective movement in others (Faria et al., 2021). Similarly, we found that aggression can either increase or decrease under different pesticide exposures. This may be due to pesticides acting antagonistically with androgens or synergistically with oestrogens, which, in turn, may decrease aggression, whereas androgen-synergistic pesticides may increase aggression (Tomkins et al., 2017). Alternatively, these observed behavioural effects could result from neurotoxic impacts, such as disruption of neural circuits involved in aggression, or from other non-endocrine mechanisms such as tissue damage or interference with metabolic pathways that affect energy availability (Rohani, 2023). The observed overall decrease in courtship behaviour suggests that even sublethal concentrations of pesticides can affect the likelihood of exposed individuals successfully attracting mates (Boughman et al., 2024) and may alter how matings are partitioned among individuals in a population (Saaristo et al., 2018; Wong and Candolin, 2015). The multi-directional effects on sociality, collective behaviour, and aggression underscore the complexity of pesticide impacts on fish conspecific interactions. Further, untangling the true adverse outcome pathways between physiological mechanisms and conspecific interactions is challenging, as many pesticides are known to disrupt multiple physiological mechanisms.

4.2. *Impacts of pesticide characteristics*

Our analysis reveals that organochlorine and triazole pesticides exert the most significant detrimental effects on conspecific interactions. Both pesticide classes possess endocrine-disrupting properties and are known to affect the hypothalamic-pituitary-gonadal axis (Martyniuk et al., 2020; Taxvig et al., 2008). This suggests that endocrine-disrupting

chemicals can influence fish-conspecific interactions (Söffker and Tyler, 2012). Similarly, organochlorine pesticides and triazoles are known to cause cholinesterase inhibition, suggesting that disruption of neuromuscular transmitters may have detrimental effects on conspecific interactions (Santana et al., 2021). However, more research is required on a diverse range of chemicals other than pesticides to further investigate the impacts and mechanisms of endocrine-disrupting and neurotoxic chemicals on fish-conspecific interactions (Husak et al., 2009). We also discovered that organophosphates and triazoles can reduce behavioural variability among individual fish, indicating that some pesticides may make fish behaviours more predictable. This finding aligns with previous meta-analyses that reported a reduction in variability of fish physiological biomarkers following pesticide exposure (Santana et al., 2022, 2021). We found that there was high variation in the impacts between different chemical class, emphasising the need for a broad range of pesticides to be studied. Concerningly, we found that some of the most disruptive pesticides, such as the carbamates, remain understudied and, thus, under-represented in this evidence base (see Fig. s18).

The lack of an apparent dose–response trend in our results may reflect limitations of the underlying studies. Some of the included studies used pesticide concentrations and exposure durations that likely exceed the threshold for eliciting behavioural effects, meaning even the lowest tested doses can trigger near-maximal behavioural changes (Wolf and Segner, 2023). Under such exposure scenarios, increased dosage is therefore unlikely to yield an additional effect, which may mask any concentration or duration moderating effect. Moreover, there is high variability in toxic potency across pesticide classes, complicating cross-study comparisons. For example, median lethal or effect concentrations in fish can differ by several orders of magnitude among insecticides, herbicides, and fungicides, which obscures consistent trends when pooling data (Delistraty et al., 1998). These factors underscore the need for studies that examine a wider range of sublethal concentrations and exposure times for individual chemicals to detect genuine dose-mediated responses. Therefore, it is important to investigate a broad range of concentrations and durations to identify chemical-specific effect thresholds to quantify true dose and duration-dependant duration behavioural impacts (Sievers et al., 2019).

In terms of control solvents, we surprisingly found that there was a significant difference between studies using a solvent control and those that did not. This indicates that the solvents being used may have an influence on the conspecific interactions being measured and, thus, could mask the impacts of the pesticide exposure. Therefore, control solvents, as well as the concentrations of solvents used, must be carefully selected to ensure they do not influence the outcomes being measured (Bertram et al., 2024). Currently, only one study in the evidence base has included both a true control group and a solvent control group, and no study has examined pesticide exposure in the presence and absence of a solvent. We therefore recommend that solvents be avoided unless necessary and when they are required, researchers should include control groups both with and without the solvent to assess any solvent-related effects and to evaluate the pesticide's impact with and without the added solvent (Green and Wheeler, 2013). Hence, it is important for future studies to consider a broad range of pesticides, as well as study characteristics, such as the solvents used (Bertram et al., 2024).

4.3. Species sensitivities and characteristics

We found that there were no significant differences between species. However, species differences did account moderately for the heterogeneity for both mean and variational differences. Differences in species sensitivity can arise for multiple reasons. First, species vary in their overall frequency or reliance on social behaviours. Species that are more social are therefore expected to be more likely to experience pesticide-induced alterations to their conspecific interactions. Second, species-specific responses to pesticides may be caused by differences in their general sensitivity to environmental change, where some species may be more robust and better physiologically equipped to handle contaminants than others (Nickisch Born Gericke et al., 2022). However, as mentioned previously, the current evidence is based on only a small handful of study species, with most research having been conducted on zebrafish. Therefore, the inability to detect species differences may simply be due to the scant research that has been done on species with a broader range of social behaviour structures.

We did not find differences between males and females in their responses to pesticide exposure. This is despite evidence that the impacts of chemical exposure can be sex-specific in the case of other toxicants (Bertram et al., 2019). This finding may be due to the lack of research investigating pesticide impacts on both males and females without considering potential sex differences, an issue seen in other areas of ecotoxicology (Morrison et al., 2024). However, it is important to maintain environmentally relevant sex ratios in exposure experiments to accurately estimate the impacts of pesticide exposure on wild fish (Ford et al., 2021). Similarly, we did not find differences between wild-caught and laboratory-bred fish despite differences being described for other toxicants (Zuberi et al., 2011). This finding may be due to limited research on wild-caught fish. In this regard, we emphasise the importance of studying the impacts of pesticides on wild-caught fish to accurately represent the genetic diversity, physiology and behaviour of wild fish populations (Ford et al., 2021; Zuberi et al., 2011).

4.4. Research limitations and future opportunities

While we provide an in-depth synthesis of the impacts of pesticides on fish-conspecific interactions, we must acknowledge several limitations in the literature and our study that offer avenues for future research. We found poor reporting of important methodological items such as the sex of fish, their source, and the behavioural assays used (Figs. s3, 4 and 8). Furthermore, the reporting of data elements, such as raw data, code, and sample sizes, was poor. Consequently, we had to extract data primarily from figures, which may introduce small sources of human error. In some cases, sample sizes had to be assumed based on either the lowest value in a range or the number of data points on a graph. We, therefore, echo calls for better reporting of important methodological items (Hitchcock et al., 2018; Morrison et al., 2024; Ricolfi et al., 2024) and support the development of reporting guidelines such as EthoCRED (Bertram et al., 2024). The current evidence base has various gaps that limit the breadth of current understanding and provide opportunities for future research. First, we identified four types of conspecific interactions that have been studied in the pesticide literature to date, namely, courtship, aggression, collective movement and social attraction. However, there still remain many other ecologically important social behaviours that are yet to receive attention in the context of pesticide exposures, such as parental care and cooperative behaviours (Goldberg et al., 2020). Second, there has been a wide range of pesticides investigated in the evidence base but research on some modern pesticides such as the neonicotinoids remains limited (Chung et al., 2023; Liu et al., 2023; Yang et al., 2023). Likewise, we found limited studies investigating the impacts of pesticide mixtures on fish-conspecific interactions (Hawkey et al., 2021). Third, several included studies exclusively tested pesticide concentrations above the behavioural effect threshold, meaning even the lowest doses administered could trigger near-maximal behavioural changes. This methodology likely obscured potential concentration and duration moderating effects, as additional increases in concentration or exposure time would not produce further observable changes under such conditions. Additionally, we were unable to normalise the toxicity across different chemicals, as the effective concentrations required to elicit behavioural changes remain unknown for most pesticides included. Fourth, we found that solvent use was frequently omitted in the evidence base. Furthermore, only one study (Yan et al., 2023) included both a true control and a solvent control, and no study examined pesticide exposure both with

and without a solvent. This made it impossible to separate the effects of the pesticide from those of the solvent. The identified gaps offer promising opportunities for future research on a broader range of conspecific interactions, pesticides, and fish species. They also underscore the importance of investigating various concentrations and exposure durations, as well as carefully considering solvent use (Bertram et al., 2022).

5. Conclusions and boarder implications

In this study, we synthesised the impacts of pesticide exposure on conspecific interactions in fish. Our findings reveal that pesticides generally decrease conspecific social interactions and, most concerningly, reduce courtship behaviours in fish. This reduction in courtship behaviour underscores the importance of considering conspecific social behaviours in ecotoxicology, as sublethal impacts can impact the likelihood of exposed individuals, successfully attracting mates. Beyond our synthesis findings, we identify key gaps in the existing evidence base and suggest areas for improvement within the literature, noting apparent weaknesses in reporting important methodological details and statistics. Collectively, our findings and the highlighted limitations offer direction for policymakers and researchers on the impacts of pesticide exposure.

CRediT authorship contribution statement

Kyle Morrison: Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Gabriel Melhado:** Writing – review & editing, Methodology. **Aneesh P.H. Bose:** Writing – review & editing, Methodology, Funding acquisition. **Rhiannon Eastment:** Writing – review & editing, Methodology. **Malgorzata Lagisz:** Writing – review & editing, Methodology, Conceptualization. **Jack L. Manera:** Writing – review & editing, Methodology. **Marcus Michelangeli:** Writing – review & editing, Methodology, Funding acquisition. **Shiho Ozeki:** Writing – review & editing, Methodology. **Bob B.M. Wong:** Writing – review & editing, Methodology, Funding acquisition. **Yefeng Yang:** Writing – review & editing, Supervision, Methodology, Formal analysis, Conceptualization. **Shinichi Nakagawa:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Declaration of generative AI and AI-assisted technologies in the writing process

In preparing this work, the authors used GPT-4o and GPT-4o1-preview by OpenAI, to improve clarity, readability, and writing flow of human-written drafts. Generative AI was also utilizsd to assist in code annotation. Following the use of these tools, the authors reviewed and edited the content as necessary and take full responsibility for the final publication.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envpol.2025.126353.

Data availability

All data, code, model outputs and additional information required to reproduce this study are provided at https://github.com/KyleMorrison99/fish_conspecific_behaviour_MA.

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