Research Article

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Avian regulation of crop and forest pests, a meta-analysis

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Abstract

BACKGROUND: Birds have been shown to reduce pest effects on various ecosystem types. This study aimed to synthesize the effect of birds on pest abundance, product damage and yield in agricultural and forest systems in different environments. Our hypothesis is that birds are effective pest regulators that contribute to a reduction in pest abundance, enhancement of yield quality and quantity and economic profit, and that pest regulation may depend on moderators such as the type of ecosystem, climate, pest, and indicator (ecological or economic).

RESULTS: We performed a systematic literature review of experimental and observational studies related to biological control in the presence and absence of regulatory birds. We retained 449 observations from 104 primary studies that were evaluated through qualitative and quantitative analyses. Of the 79 studies with known effects of birds on pest regulation, nearly half of the 334 observations showed positive effects (49%), 46% showed neutral effects, and very few (5%) showed negative effects. Overall effect sizes were positive (mean Hedges' $d = 0.38 \pm 0.06$). A multiple model selection retained only ecosystem and indicator types as significant moderators.

CONCLUSION: Our results support our hypothesis that there is a positive effect of avian control of pests for each analyzed moderator and this effect was significant for both ecological and economic indicators. Avian regulation of pests is a potential effective approach for environmentally friendly pest management that can reduce pesticide use regardless of the context of implementation.

Supporting information may be found in the online version of this article.

Keywords: biological control; ecosystem services; natural enemies; pest management; regulating services

1 INTRODUCTION

Millions of tons of pesticides are used yearly to control pests in farmlands and forest systems all over the world.[1,2] However, the use of pesticides has long-term implications for human health, biodiversity,[3–5] soil and water pollution, and the provision of ecosystem services. For instance, pesticides can affect beneficial organisms such as the natural enemies of pests, pollinators, and decomposers.[6] There is a need for environmentally friendly pest management techniques that not only reduce chemical inputs[7] and support efficient production systems,[8] but also contribute to biodiversity conservation and the provision of ecosystem services at different scales.[9–14]

Enhancing the presence of natural enemies, such as birds, can contribute to the sustainable management of pests in agricultural and forest systems.[15–17] The potential role of birds as pest regulators has been demonstrated by individual case studies on several ecosystem types because birds can significantly reduce the population of herbivorous invertebrates, mostly insects.[18–20] For instance, birds reduced infestation by approximately 50% in Costa Rican agroforestry systems[21] and by 33% in alfalfa crops.[22] Some studies based upon bird exclusion in different regions have evidenced the beneficial role of birds in preventing crop damage.[23,24] In herbaceous ecosystems, the presence of migratory birds can reduce grasshopper abundance.[25] Sanz[26] demonstrated the effectiveness of insectivorous birds controlling insects that damage Pyrenean oak (*Quercus pyrenaica*) leaves.

The ability of birds to fly results in high mobility and less sensitivity to barriers, connecting isolated and distant patches.[27] Thus, the capacity of birds to regulate pest populations is particularly important in heterogeneous landscapes (for example,

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agroforestry mosaics), where birds can operate on a broad spatial scale and in a variety of habitats.[28]

Despite this growing body of literature, the ability of birds to regulate agricultural and forest pests seems context dependent. For example, the capacity of insectivorous birds to regulate pests varies with the abundance of invertebrate populations.[29] In this regard, providing artificial nests to attract birds may enhance the population of insectivorous birds[16] and raptors in woody crops,[30] but its effectiveness on pest regulation appears to depend on the ecosystem type and landscape complexity.[31,32] Moreover, regulation intensity varied with climate due to the effect of climate control on predator–prey interactions and fluctuations in insect populations (for example, pest outbreaks).[33] Establishing a sustainable biological control strategy that uses birds as regulatory agents for agricultural and forest pests requires thoughtful quantification of the effect of birds on pest regulation and its context dependency. Furthermore, a range of indicators related to both ecological and economic aspects (for example, prey abundance and yield quality or quantity) must be evaluated to preserve ecological integrity in productive landscapes.[34] Thus, it is relevant and timely to synthesize current knowledge on the effect of birds on pest abundance, product damage and yields, and whether ecosystem, climate, and pest types might modulate this regulatory service.

Here, we quantitatively evaluate pest regulation by birds in agricultural and forest systems. For this, we performed a global meta-analysis that included both experimental and observational studies comparing measures related to biological control (pest abundance, product damage, yield, and others) in the presence and absence of regulatory birds. Specifically, we aim to identify: (i) agroecosystem types for which the regulatory effect is maximized; (ii) climate conditions that might be advantageous for pest regulation by birds; (iii) trophic guilds of birds that are beneficial for pest regulation; and (iv) ecological and economic indicators for which the regulatory effect is more effective. We hypothesize that birds are effective pest regulators that contribute to a reduction in pest abundance, enhancement of yield quality and quantity, and economic profit, and that pest regulation may depend on moderators such as the type of ecosystem, climate, pest, and indicator (ecological or economic). The results provide new insights into the avian regulation of pests and determine the moderators that encourage the implementation of environmentally friendly techniques to avoid or reduce pesticide use.

2 MATERIALS AND METHODS

2.1 Database

We performed a systematic literature search of articles published between 1900 and December 2022 using the Web of Science database. The search string was (bird OR avi*) AND (plague OR pest) AND (control OR regulation), which resulted in a total of 1338 records. Of these, 14 were review articles, which were screened for relevant references that rendered 159 additional records. In total, once 26 duplicate records had been deleted, our systematic review considered 1471 primary studies.

For the inclusion of primary studies in our meta-analysis, the articles had to include quantitative measures related to the biological control of pests in both the presence and absence of regulatory birds. Following this rule, 1147 studies were discarded and 324 articles were reviewed in depth (detailed PRISMA flow diagram is given in Supporting Information S1; Figure S1). When essential data for our analyses (for example, dispersal measurements) were not available, we contacted the corresponding authors to ask for that data. If data could not be obtained, articles were excluded from the final analyses. In total, 104 primary articles were used in this study (Supporting Information S1; Figure S2).

We built a database that included 449 measurements (observations) from the 104 primary studies, because some studies included more than one measurement. We extracted variables that measure either pest incidence (for example, pest abundance, pest reduction, pest biomass) and/or economic value (for example, product quality or quantity, net outcome, crop loss) in the presence and absence of birds (a quantification of birds was not considered as very few observations reported this information). The database included mean values, units, sample size and estimated variance of variables of interest in the presence and absence of birds, and 18 columns with relevant information were extracted (Supporting Information S1). If measures were taken multiple times (for example, a four-year experiment that was measured once per year), we considered only the last measure of the response variable. Variables were categorized into two types of indicator of pest regulation (Table 1): (i) ecological (mostly related to pest abundance); and (ii) economic (related to product benefit or damage, yield, and economic impact). Because our meta-analysis included a wide variety of response variables, we classified the relationship between the value of the response variable and pest regulation service as: (i) direct and (ii) inverse (a higher value of the response variable indicates a higher or lower regulation service, respectively; Table 1). The sign of the values of inverse response variables was multiplied by −1 to accurately reflect pest regulation.

We also extracted from each primary study the following information: (i) country; (ii) ecosystem type (natural forest, forest plantation, agroforestry, woody crop, herbaceous crop, and pasture); (iii) climate type (temperate, Mediterranean, or tropical following Köppen-Geiger's classification[35]); (iv) bird guild (insectivorous or raptors); and (v) pest type (invertebrate or vertebrate). The final moderators used to test their effect on avian control of pests were the types of ecosystem, climate and pest, as bird guild and pest type were highly redundant (insectivorous birds predate on invertebrates and raptors mostly predate on vertebrates).

2.2 Data analysis

We performed two types of analysis, namely qualitative (vote counting) and quantitative (meta-analysis). Vote-counting analyses are often critiqued yet they may provide interesting illustrative information such as directional effects, whereas meta-analyses provide robust effect sizes.[36,37]

2.2.1 Qualitative analysis (vote counting)

We performed a qualitative "vote-counting" analysis based on the effect direction following the Light and Smith's procedure.[38] Observations with a positive or negative effect of avian regulation of pests were those for which a statistically significant effect (nominal $p < 0.05$) was reported in or inferred from the primary studies. The effect was deemed neutral if it was not statistically significant, and unknown if no statistical test was reported.[39] Following these criteria, 334 observations extracted from 79 primary studies were retained for vote counting and 115 observations from 38 primary studies were classified as unknown and excluded. We performed chi-squared tests to analyze whether the frequency of observed

TABLE 1. Classification of response variables extracted from the primary studies with their most frequent units and effect sign (direct and inverse)

Indicator type	Response variable (number of observations, number of primary studies)	Units	Relation to the provision of effect sign
Ecological	Abundance of invertebrate or vertebrate pest (139, 37)	Mean number, number/ percentage/ proportion of individuals	Inverse
	Pest frequency (3, 7)	Percentage of observations	Inverse
	Pest biomass (2, 14)	Milligrams	Inverse
	Pest density or infestation (13, 37)	Number of individuals per surface	Inverse
	Pest disappearance rate (1, 2)	Proportion of pest remaining	Direct
	Pest survival (2, 4)	Percentage	Inverse
	Trap success (4, 8)	Percentage, individuals trapped per surface	Inverse
	Pest colonization rate (1)	Proportion of product	Inverse
	Pest predation rate/pest reduction/pest consumption (27, 60)	Number of predated individuals, percentage, mean number of individuals	Direct
Economic	Product quality or quantity (abundance of flowers, healthy product). Harvestable product, production, yield, net outcome (21, 52)	Number, Grams, proportion, kg/ha/year	Direct
	Damaged, herbivory rate and infestation of product (fruits, seeds, or leaves), products removed or pecked, crop loss, infested yield (107, 39)	Percentage, mean proportion of damage, proportion, kg ha^{-1}, grams	Inverse
	Economic value of product, monetary value, net outcome, net income (8, 12)	US$ ha^{-1}	Direct
	Costs of inputs (2, 3)	US$ ha^{-1}	Inverse
	Economic loss (1, 3)	US$ ha^{-1}	Inverse

Note: Direct: a higher value of the response variable indicates a higher regulation service. Inverse: a higher value of the response variable indicates a lower regulation service. The numbers of primary studies and observations are shown.

positive, neutral, and negative cases was statistically different from the expected frequency.

2.2.2 *Quantitative analysis (meta-analysis)*

To quantify the direction and magnitude of avian control of pests, we calculated the effect size for 280 observations from 65 primary articles; that is, only those that reported measures of response variables with their corresponding standard deviations and sample sizes in the presence and absence of birds. We used Hedges' *d* value[40] corrected for small samples[36] using the *escalc* function in R.[41] Hedges' *d* is considered the most conservative estimate of effect size and is not affected by differences in variance in paired groups.[42] All effect sizes in this study were estimated based on the response variables provided in published articles. Groups of response variables with a sample size of 20 or more were analyzed separately (pest abundance, $n = 92$; pest density, $n = 30$; product damage, $n = 91$; yield, $n = 21$). Because ecological and economic indicators are notably different in their meaning and measures, meta-analyses for these two types of indicators were performed separately as well.

Mixed models adjusted for meta-analysis[43] were fit to analyze the overall effect of avian regulation, without considering moderators. Also, a null mixed model was adjusted[43] to evaluate the effect of birds on pest control under different moderators, namely ecosystem, climate, pest, and indicator types. Data were analyzed using random effect models for meta-analysis with the *rma.mv* function of the R "metafor" package.[44] Because most of the primary studies rendered several measurements (observations), we used the identity of the primary study as a random effect to account for lack of independence.[43] Akaike's information criteria (AIC), AICc differences (Δ_i) and Akaike weights (w_i) were used to evaluate the effect of moderators on the avian regulation of pests for each step of model selection based on backward elimination.

Mixed models with maximum likelihood estimations of random effects were selected based on significant Cochran's *Q*-test for moderators and for residual heterogeneity.[45] Heterogeneity in effect size among moderator levels was estimated using the statistic Q_M. Statistic I^2 described the percentage variation among primary studies that was due to heterogeneity rather than randomness.[46] Finally, we conducted pairwise comparisons to test for differences between moderator levels.[47]

We analyzed funnel plot asymmetry to evaluate potential publication bias, because small studies (with a low number of samples) can contribute to larger estimate effects and variability.[48] The inverse of variance associated to the effect size was included as a fixed effect in this analysis. The Rosenthal's[49] method was used to calculate the fail-safe number; that is, the number of primary studies needed to change the overall effect of the meta-analysis. We also evaluated the bias associated with publication year, incorporating the year as a fixed effect in the model. We performed a sensitivity analysis to detect potential outliers by calculating hat values of model predictions for each observation.[50,51] All analyses were performed using R version 4.2.1.[41]

3 RESULTS

3.1 Data set description

A total of 449 observations from 104 primary studies conducted in 37 different countries were analyzed by means of vote counting or meta-analysis (32 and 28 countries, respectively, were represented). The data set included observations from Latin America and the Caribbean (22%), Europe and Central Asia (19.8%), East Asia and the Pacific (18.7%), North America (18%), Middle East and Africa (14.9%), and South Asia (6.2%) (Supporting Information S1; Figure S3 and S4). Most observations represented agroforestry systems (30%), woody and herbaceous crops (each 29.3%), natural forests (4.7%), forest plantations (4.2%), and pasture (2.4%). Observations were from tropical (45.2%), temperate (39.2%) and Mediterranean (15.6%) climates. Pest type mostly corresponded to invertebrate pests (87.1%) with only 13% vertebrate pests.

3.2 Directional effect (vote counting) of avian regulation on pests

Half of the 334 observations used for vote counting reported a positive effect of avian regulation on pests, 46.1% reported a neutral effect, and only 4.8% reported a negative effect (Figure 1). The chi-squared test indicated significant differences among the three directional effects ($n = 334$; $\chi^2 = 122.9$; $p < 0.001$). When considered independently, ecosystem ($p < 0.05$), climate ($p < 0.01$), and pest ($p < 0.001$) types also resulted in significant differences (Figure 1; Supporting Information S1; Table S1). Most observations showed a positive or neutral effect, with non-significant differences between them ($n = 318$; $\chi^2 = 0.31$; $p = 0.575$). In addition, there were significant differences between positive and neutral cases in agroforestry ($n = 109$; $\chi^2 = 6.68$; $p = 0.01$), woody crops ($n = 78$; $\chi^2 = 13.13$; $p < 0.001$) and temperate climates ($n = 133$; $\chi^2 = 5.48$; $p = 0.019$; Figure 1).

Analysis of ecological indicators (Table 1) revealed that birds significantly reduced pest abundance in 55.3% of the cases, whereas negative effects were marginal and 42.5% of the observations reported neutral effects (Figure 2; chi-squared test for the three directional effects: $n = 179$; $\chi^2 = 82.3$; $p < 0.001$). Birds had a significant and positive effect on response variables related to economic indicators (Table 1) in nearly half of the cases, whereas negative effects were marginal (Figure 2; chi-squared test for the three directional effects: $n = 155$; $\chi^2 = 47.3$; $p < 0.001$; effects were neutral for half of all observations).

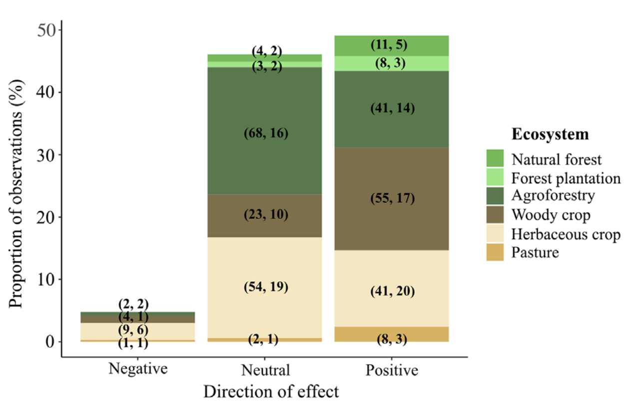

FIGURE 1. Proportion of observations showing the effect direction of avian regulation of pests reported in the primary studies and ecosystem types where data were obtained ($n = 334$). Numbers in parentheses indicate observations and primary articles, respectively, for each ecosystem and effect direction.

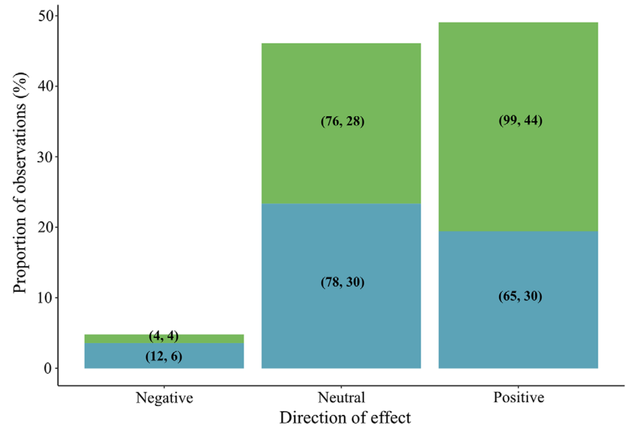

FIGURE 2. Proportion of observations showing the effect direction of avian regulation of pests reported in the primary studies for two types of indicators: ecological (green) and economic (blue). Numbers in parentheses indicate observations and primary articles, respectively, for each indicator type and effect direction.

3.3 Effect size

The overall effect size of avian control on pests was significant and positive (estimated effect size: 0.38 ± 0.06, $p < 0.001$, $n = 280$; Figure 3) and exhibited high heterogeneity among observations ($Q_{\text{Total}} = 1443.27$; df = 279; $p < 0.0001$). This result suggests that most heterogeneity was not explained by sampling error and justifies the inclusion of moderators in the explanatory models. Rosenthal's Fail-Safe analysis showed that 35 940 observations are needed to significantly reduce the direction of the effect size, indicating the robustness of the meta-analysis. Avian control had a positive and significant effect on response variables related to pest abundance (estimated effect size: 0.41 ± 0.08), product damage (estimated effect size: 0.25 ± 0.07), and yield (estimated effect size: 0.32 ± 0.13), but a non-significant effect on response variables related to pest density (Figure 4). The effect of birds on both ecological and economic indicators (separately) of pest regulation was significant and positive (estimated effect sizes: 0.48 $\pm$ 0.08 and 0.25 ± 0.06, respectively; Figures 5 and 6, respectively). Analysis of funnel plot for all meta-analysis performed suggested no bias in reporting of results (Supporting Information S1; Figure S5).

3.4 Effect of moderators

Model selection based on backward elimination retained only two moderators (namely, ecosystem and indicator types; Table 2), suggesting that climate and pest type were irrelevant for avian pest regulation. Avian control had a markedly positive effect in each of the four ecosystem types (Figure 3). There were no significant differences among agroforestry (estimated effect size: 0.29 $\pm$ 0.09), woody crop (estimated effect size: 0.37 ± 0.08) and herbaceous crops (estimated effect size: 0.20 ± 0.10), but there was a significant difference between these three systems and natural ecosystems (estimated effect size: 0.96 ± 0.17). Similarly, pest regulation by birds was positive and significant for both ecological

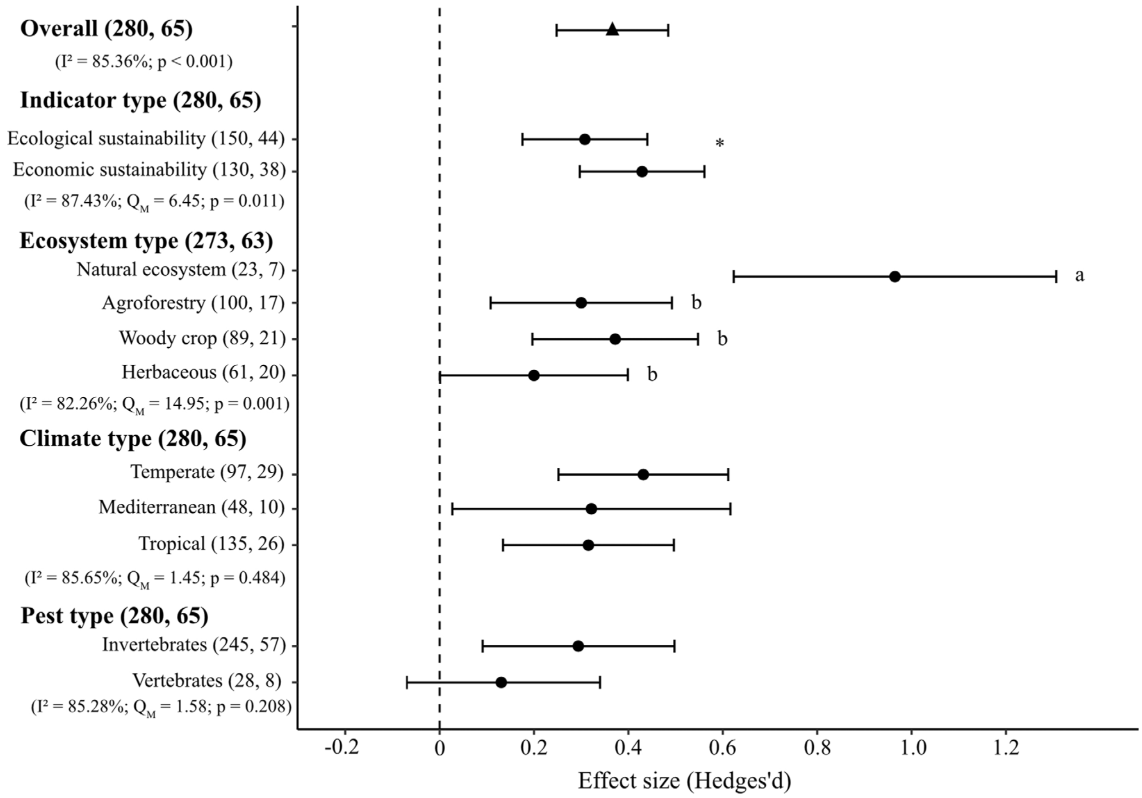

FIGURE 3. Overall effect size (Hedges' *d*; black triangle) and effect size for each group of moderators (black dots). Numbers in parentheses indicate observations and primary studies, respectively, for each category at each level. I^2 is the percentage variation due to heterogeneity, Q_M is the heterogeneity and the *p*-value is the level of significance among effect sizes of factor levels. The black triangle and dots represent mean effect size, and bars represent 95% confidence intervals (CI). A mean effect is significantly different from zero if the 95% CI does not overlap the vertical dashed line. Significant differences between levels of moderators are indicated by asterisks (two levels) and different letters (three levels).

(estimated effect size: 0.30 ± 0.07) and economic indicators (estimated effect size: 0.43 ± 0.06).

Avian control did not differ among temperate (estimated effect size: 0.43 ± 0.09), Mediterranean (estimated effect size: 0.32 ± 0.15), and tropical climate types (estimated effect size: 0.31 ± 0.09). However, avian control differed between pest types according to the analysis of effect size for this moderator (birds did not significantly regulate vertebrate pests [estimated effect size: 0.15 ± 0.18], but regulated invertebrate pests [estimated effect size: 0.31 ± 0.06]; Figure 3).

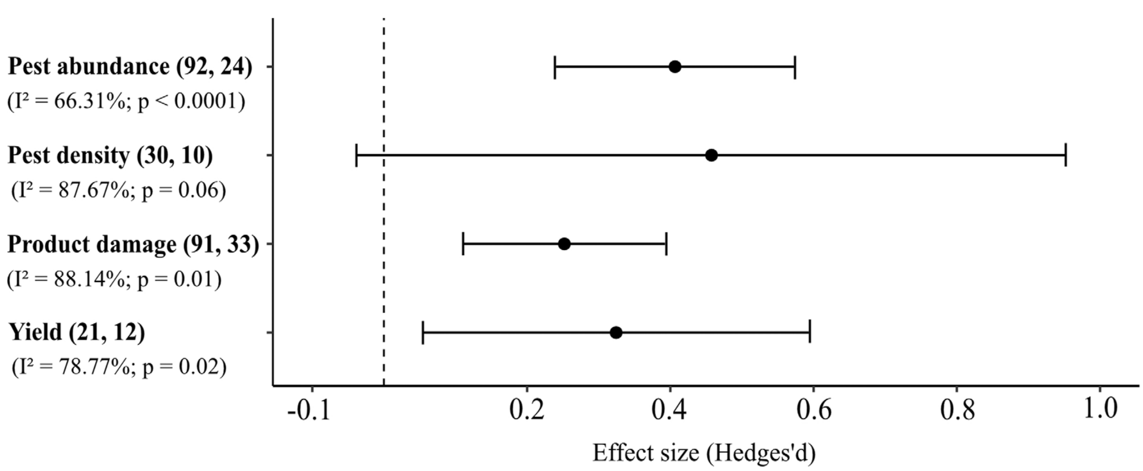

FIGURE 4. Effect of biological control of birds on groups of response variables: pest abundance, pest density, product damage, and yield. Numbers in parentheses indicate observations and primary studies. I^2 is the percentage of variation due to heterogeneity and the *p*-value represents level of significance. Dots represent mean effects size and bars represent 95% confidence intervals (CI). A mean effect is significantly different from zero if the 95% CI does not overlap the vertical dashed line.

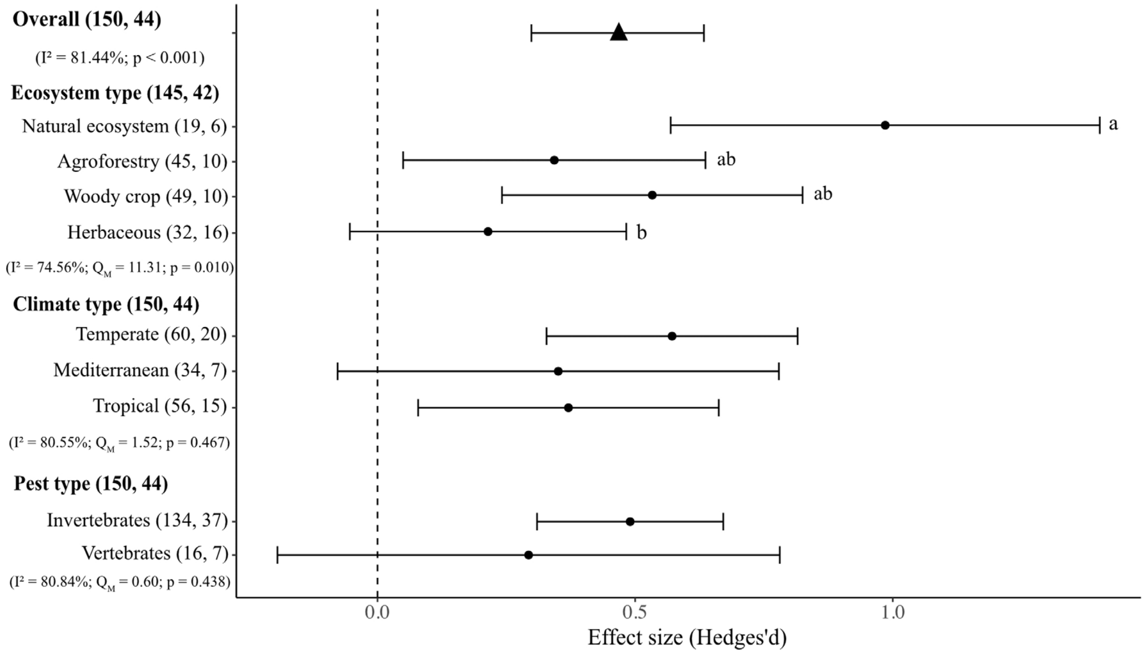

FIGURE 5. Overall effect size (Hedges' *d*; black triangle) and effect size for each group of moderators (black dots) for ecological indicators. Numbers in parentheses indicate observations and primary studies, respectively. I^2 is the percentage of variation due to heterogeneity, Q_M is the heterogeneity, and the *p*-value represents the level of significance among effect sizes. Dots represent mean effect sizes and bars represent 95% confidence intervals (CI). A mean effect is significantly different from zero if the 95% CI does not overlap the vertical dashed line.

All ecosystem types except herbaceous crops exhibited positive and significant ecological indicators of pest regulation (Figure 5). There were significant differences between natural ecosystems (estimated effect size = 0.98 ± 0.21) and herbaceous crops (estimated effect size = 0.21 ± 0.13; Figure 5). Economic indicators of pest regulation did not differ significantly between or among ecosystem, climate, and pest types (Figure 6 and Supporting Information Table S2).

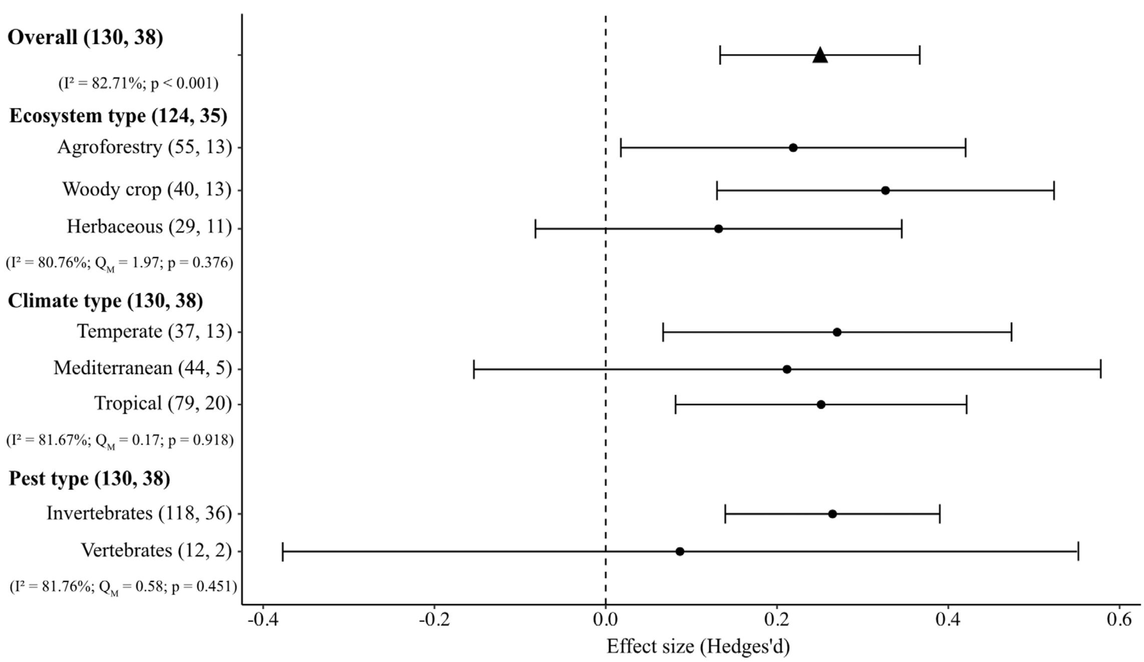

FIGURE 6. Overall effect size (Hedges' *d*; black triangle) and effect size for each group of moderators (black dots) for economic indicators. Numbers in parentheses indicate observations and primary studies, respectively. I^2 is the percentage of variation due to heterogeneity, Q_M is the heterogeneity, and the *p*-value is the level of significance among effect sizes. Dots represent mean effect size and bars represent 95% confidence intervals (CI). A mean effect is significantly different from zero if the 95% CI does not overlap the vertical dashed line.

TABLE 2. Model selection based on backward elimination of moderator variables that may explain avian control of pests

Model	AIC	AiCc	ΔAICc	w_i
ECOSYSTEM + INDICATOR TYPE + (1| STUDY)	686.83	687.14	0.00	0.54
ECOSYSTEM + PESTS + INDICATOR TYPE + (1| STUDY)	688.16	688.59	1.45	0.26
CLIMATE + ECOSYSTEM + INDICATOR TYPE + (1| STUDY)	690.76	691.30	4.16	0.07
ECOSYSTEM + (1| STUDY)	691.99	692.22	5.08	0.04
CLIMATE + ECOSYSTEM + PESTS + INDICATOR TYPE + (1| STUDY)	692.11	692.79	5.65	0.03
ECOSYSTEM + PESTS + (1| STUDY)	692.98	693.29	6.15	0.02
INDICATOR TYPE + (1| STUDY)	695.21	695.30	8.16	0.00
PESTS + INDICATOR TYPE + (1| STUDY)	696.12	696.27	9.13	0.00
CLIMATE + ECOSYSTEM + PESTS + (1| STUDY)	696.76	697.31	10.17	0.00
CLIMATE + PESTS + INDICATOR TYPE + (1| STUDY)	697.95	698.26	11.12	0.00
1 + (1|STUDY)	700.29	700.34	13.2	0.00

Abbreviations: AIC, Akaike's information criterion; and AICc, corrected Akaike's information criterion; ΔAICc, relative difference in AICc values from the model with smallest Akaike's information criterion; *wi*, Akaike weights that represent the relative likelihood of the models for each model, divided by the sum of these values across all other models.

4 DISCUSSION

This study analyzed avian control of pests in agricultural and forest systems. The global scope of this meta-analysis provides insights into birds as pest regulators for different ecosystems, climates, and pest types. The results of our meta-analyses support the hypothesis of a pervasive positive effect of birds on pest control despite our vote-counting analysis pointing to a considerable number of neutral effects. Further, avian regulation showed positive effects on both ecological and economic indicators. Our results suggest that birds are of pivotal importance for the implementation of environmentally friendly techniques to avoid or reduce the use of pesticides in productive ecosystems.

4.1 Birds regulate crop and forest pests

Our analysis demonstrated that a high proportion of observations showed avian regulation of pests (positive values of indicators of interest) in all ecosystem types except herbaceous crops and agroforestry ecosystems, which exhibited more observations with neutral (47% and 52%, respectively) than with positive effects (25% in both cases). Most of these observations were conducted in woody crops (for example, vineyards, olive groves, and fruit orchards) and based on a comparison of control (bird presence) and bird exclusion treatments. For example, Garcia et al.[24] excluded insectivorous birds from apple tree branches infested with aphids, which resulted in increased shoot damage and aphid outbreaks. Similarly, Peisley et al.[52] conducted a bird exclusion experiment and found that damage to apple trees was higher in the absence of birds. Other studies used nest-boxes for insectivorous birds and conducted experiments with sentinel prey showing high occupation of nest-boxes and higher predation rates near them.[16,53] Following the introduction of raptors in New Zealand vineyards, Kross et al.[54] reported a significant decrease in the abundance of frugivorous passerines and a 95% reduction in grape removal. However, Martínez-Núñez et al.[55] reported a lack of regulation of olive-tree pests by birds and suggested habitat management to allow the accessibility of bird species that could provide biological control.

In agroforestry systems, most studies were conducted in coffee plantations and used enclosures to exclude birds. Results showed that insect abundance was greater in the absence of insectivorous birds in coffee[23,56–59] and cacao plantations.[60] Similarly, arthropod abundance and leaf damage in plants were reduced in the presence of birds in coffee farms.[61] Other studies reported that vertebrate exclusion, including birds, led to a reduction in fruit production.[62]

Studies in herbaceous crops and pastures (for example, golf courses, airports, corn and kale crops, alfalfa yields, grasslands) also showed avian regulation of pests. These studies included different methodologies such as falconry and bird exclusion (Figure 1). Falconry reduced the abundance of undesirable birds by 73%.[63] In airports, trained raptors changed the behavior of other birds that disrupted aviation operation.[64] Bird exclusion in kale crops (*Brassica oleracea acephala*) increased the number of leaves infested with aphids by 130%.[65] Birds reduced the abundance of insect pests in alfalfa (*Medicago sativa*) by 33%.[22] In addition, Tremblay et al.[66] found that cutworm (*Agrotis* spp.) and weevil (*Sphenophorus* spp.) densities were higher in corn plots from which insectivorous birds were excluded. Birds also limited grasshoppers (Orthoptera: Acrididae) in grasslands.[67,68] Labuschagne et al.[69] showed that carnivorous birds reduced rodent abundance, which resulted in lower crop damage in agricultural systems.

Studies in forest plantations and natural forests also showed avian regulation of pests (Figure 1). Most studies evaluated bird predation rates on arthropods or leaf damage after bird exclusion or after installing nest-boxes for insectivorous birds.[26,29,70–73] These studies reported a positive correlation between the predation rate of pests and the abundance of insectivorous birds, suggesting a positive role of birds for forest pest control. The low number of studies showing negative effects might be due to publication bias, because negative findings have lower priority for publication;[74] however, we did not find such publication bias in our study.

4.2 Effects of moderators

Our meta-analysis revealed that avian control of pests is modulated by ecosystem. We found a greater effect size (greater pest regulation) on natural ecosystems (forests and grasslands) than on agroecosystems (agroforestry, woody, and herbaceous crops). Authors found that birds significantly reduced pest density (in forests[26,29,70,71] and in grasslands[67,68]), but did not relate their findings to the effect of local context on avian control. Instead, most referred to a top-down effect limited to two trophic levels and focused on predator–prey dynamics.[75] Similar to our results, a previous study on biological control across different crop types (coffee crop, apple crop, vineyards) and agriculture types (traditional, organic, mixed) showed variation among pest abundance, crop damage, and yield, but the effect of avian regulation was positive in most cases despite higher disaggregation of moderator levels.[76]

Tscharntke et al.[31] argued that the relationship between pest control and natural habitats is not clear and that natural ecosystems can have positive or negative effects on pest control. Following their argument, natural habitats could be sufficient in amount, proximity, composition, or configuration to provide large enough enemy populations for pest control. The heterogeneity provided by natural ecosystems could be related to a higher abundance of both pests and natural enemies,[77] influencing biotic interactions within natural habitats and adjacent crops.[31,78] Moreover, biological control of pests depends on factors that operate at multiple spatial and temporal scales.[10,31] In this regard, Boesing et al.[28] showed that pest suppression was greater in landscapes with a higher cover of native habitats and in adjacent agroecosystems. Other studies showed that the net effect of birds depends on the location of the farmed field and the amount of seminatural habitat that surrounds it. Thus, we can expect higher pest regulation in farms surrounded by a low proportion of seminatural habitats, whereas if the proportion of seminatural habitat is high, an intraguild predation effect can disrupt avian pest control. In our study, both natural ecosystems and herbaceous crops showed lower sample sizes and higher effect size variability, suggesting that the reported effect could be also due to a higher heterogeneity within each category of this variable.[79]

Our results are in agreement with another study that showed that climate did not modulate pest regulation, effect sizes were consistent across climate types.[76] Nearly half of our analyzed studies were conducted in tropical climates (48%) followed by temperate (35%) and Mediterranean climates (17%). Temperate climates exhibited a higher but non-significant effect size (Figure 3), which could be due to the marked seasonality that contributes to higher fluctuation of pest populations.[33] Mediterranean regions showed a similar effect size and higher variability than tropical regions.

According to our results, avian control was effective only for invertebrate pests. Insectivorous birds are capable of regulating pest populations, which might result in a reduction in plant damage and a subsequent increase in economic profit.[33,80] However, based on our model selection procedure, there were no differences in the avian control of invertebrate and vertebrate pests. Research focused on raptors has received less attention and the number of studies is still low.[32] Most studies analyzed here found positive effects of raptors on pest regulation by both direct effects (for example, consumption of vertebrate pests) and indirect effects (for example, intimidation), which can vary under different environmental conditions.[30,54,69,81–83] However, some of these studies did not address long-term variation and thus the major drivers of pest regulation are difficult to determine.[69] Our result encourages further studies on pest regulation by raptors.

Our study shows that birds provide the service of pest regulation; however, bird species can also contribute to ecosystem disservices,[84] which can be direct damage (product damage such as fruit consumption) or indirect damage (intraguild predation on other natural enemies of pests).[85,86] We encourage research that focuses on the net effect of birds because the number of observations accounting for negative effects of birds in our meta-analysis was low. Studying and identifying the underlying mechanisms, which usually involve cascading effects by suppression of herbivore pest predators,[23,30,69,84,87,88] are complicated but elemental to understand interactions across all levels of the food chain (crops, pests, and birds).[84] Birds can suppress agricultural pest predators, and numerous articles highlight that this is a context-dependent phenomenon.[87,89] Moreover, we identified some structural factors conditioning pest control by birds that should be considered in further studies. At a landscape scale, factors such as landscape complexity,[22,28] land-use gradient,[62] and distance to natural habitats[90] may modulate pest regulation by birds. At a smaller scale, other modulating factors may include distance to edges,[73] forest heterogeneity,[72] the presence of hedgerows,[91] vegetation complexity,[57] shade levels,[62,90,92] canopy cover management,[59] the presence or absence of perches or artificial breeding sites,[28] and local farming practices.[88]

Sustainability implies a balance in both ecological and economic aspects, and determining the net outcomes (ecosystem services vs. ecosystem disservices) of avian control is important to design management policies for application at different scales.[15,84,88,93] We found that avian control was effective, as highlighted by both ecological and economic indicators of pest regulation; however, the number of studies contrasting monetary value in the presence or absence of regulatory birds is low. For example, in coffee plantations in Costa Rica there is evidence of the effectiveness of insectivorous birds in regulating herbivorous arthropod abundance and preventing damage valued at US$75–600 per ha per year.[21,23,94] By contrast, the number of articles evaluating the effect of birds on product damage or benefit is high.[19,24,60,62,90,95]

5 CONCLUSION

Our results provide insights into the role of birds as biological control agents and the ecological context that modulate this regulating service. Integrated pest management (IPM) should include birds as components of biological control in natural and agroecosystems. Furthermore, other components of IPM (for example, chemical and physical interventions) should be managed with caution to prevent interference with the avian regulator agent. Most importantly, there is an urgent need to develop conservation and restoration projects for agroforestry systems that consider avian pest control as a potential and achievable ecosystem service that can be a benefit not only for biodiversity, but also to farmers. The development of adequate IPM and policies that recognize environmental and economic aspects of production should consider the influence of landscape and local contexts. Farm management practice that incorporates IPM and policies considering birds as natural enemies are key to implementing environmentally friendly pest management that reduces pesticide use and increases crop sustainability.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available via Figshare[96].

SUPPORTING INFORMATION

Supporting information may be found in the online version of this article.

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