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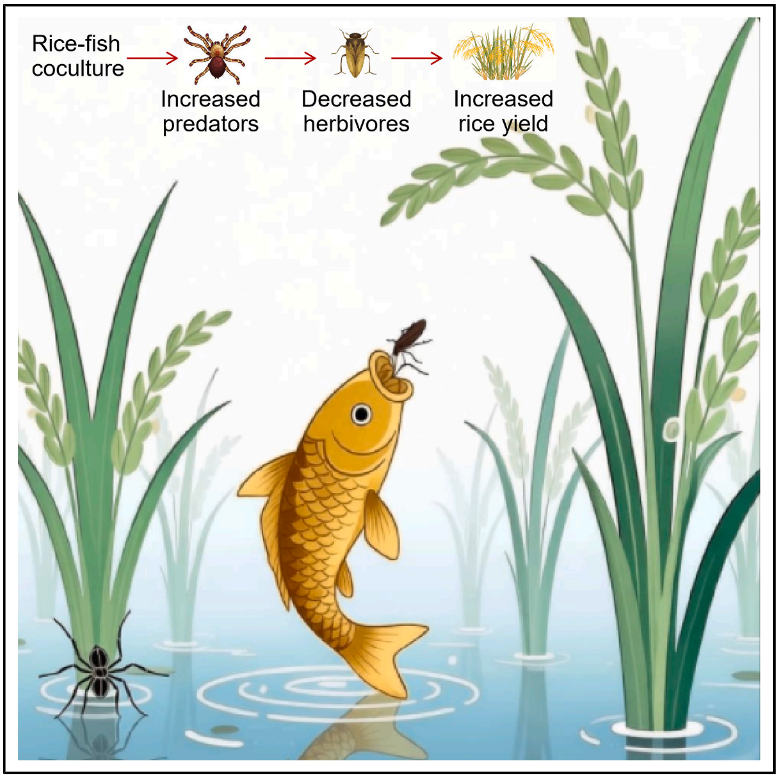
Trophic cascades drive sustainability in the agricultural heritage rice-fish coculture system

Graphical abstract



Highlights

- Rice-fish coculture benefits natural enemies and crop yields but decreases pests
- An enemy-driven top-down effect suppresses herbivore populations
- Fish preferentially target herbivores while sparing predatory spiders
- Rice-fish coculture offers viable solutions to pressing food security challenges

Authors

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In brief

Wan et al. reveal that rice-fish coculture enhances invertebrate natural enemies (i.e., predators and parasitoids), suppresses pests (i.e., invertebrate herbivores, diseases, and weeds), and boosts rice yields, validating its role as a sustainable agricultural system that harnesses biodiversity for ecological intensification and natural pest regulation.

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Trophic cascades drive sustainability in the agricultural heritage rice-fish coculture system

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SUMMARY

Biodiversity-mediated trophic cascades are well established for plant diversity, but the role of biodiversity in the millennia-old Asian rice-fish agroecosystems has not been synthesized. We show in a meta-analysis of 113 studies worldwide that rice-fish coculture increases yields by 12.5%, while enhancing the abundance of invertebrate natural enemies (predators/parasitoids) by 99.3% and suppressing pest invertebrate herbivores (24.1%), disease (38.8%), and weeds (45.7%), compared with rice monoculture. These effects persist across organic and non-organic systems, as well as temperate and tropical zones. Biological pest control played a dominant role in enhancing crop production, with enemy-driven top-down effects suppressing herbivore populations. Four-year field experiments confirmed these patterns, demonstrating biological control and top-down effects. Behavioral assays further show fish preferentially target herbivores (e.g., planthoppers) while sparing predatory spiders, reinforcing trophic cascades. Our findings validate rice-fish coculture as a highly productive, sustainable agricultural system that enhances biodiversity, crop yields, and provides significant fish harvests for animal protein and additional farmer income. This approach aligns with the Food and Agriculture Organization (FAO) goals by harnessing biodiversity for ecological intensification and natural pest regulation, offering viable solutions for global food security and nutritional challenges.

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INTRODUCTION

Biodiversity-ecosystem functioning relationships (BEFs) have been a recent focus of ecological research,[1–9] with extensive evidence demonstrating that biodiversity enhances ecosystem functioning, such as plant productivity[1–6] and biological control.[7,8,10] While terrestrial ecosystems, including grasslands, forests, and agroecosystems, have dominated BEF studies,[11–17] the focus on plant diversity as a basis for promoting productivity ignores the potential role of domesticated animals in multi-trophic systems, in which the diversity of domesticated animals and cultivated plants varies greatly.[18] This gap is particularly striking in the millennia-old integrated crop-animal systems, such as rice-fish cocultures in Asia[19–22] and silvopastoral systems in Europe.[23] Owing to their documented ecological benefits, such systems are increasingly considered as models of sustainable practice, with some even designated as Globally Important Agricultural Heritage Systems (GIAHSs) by the Food and Agriculture Organization (FAO). They offer untapped potential for offsetting the impacts of conventional intensive agricultural practices by reducing chemical inputs, increasing carbon sequestration, and providing ecosystem services to surrounding areas.[24]

Biodiversity has been shown to enhance plant productivity and crop yield through a variety of mechanisms.[1–6] The *resource-use complementarity hypothesis* (CE) posits that niche partitioning and facilitation among species reduce competitive overlap, while the *selection effect* (SE) emphasizes the dominant contribution of high-yield species in more diverse communities, where the *net biodiversity effect* (NE) equals the sum of CE and SE.[1] Beyond these well-studied bottom-up processes, promoting biodiversity has been shown to support natural enemy populations that, in turn, strengthen top-down predation, leading to improved control of herbivorous pests—a phenomenon encapsulated in the *enemies hypothesis*.[25] Plant diversity provides critical resources (e.g., habitat structure) that sustain predators and parasitoids, reducing herbivore pressure and indirectly boosting plant productivity.[7,8,26] This tri-trophic perspective underscores biodiversity's multifaceted role in ecosystem regulation, extending beyond simple resource competition to include complex biotic interactions.[27,28]

Across Asian agricultural landscapes, traditional practices demonstrate the strategic integration of animals for ecological pest management. For example, Asian pasture systems have long employed the conservation of rosy starlings as a biological control strategy to suppress grasshopper and locust populations, highlighting the region's deep-rooted agroecological wisdom.[14,18] In rice-based agroecosystems, diverse rice-aquatic animal systems have been developed across Asia, integrating species such as crabs, turtles, crayfish, shrimps, ducks, and frogs.[22] Notably, rice-fish and rice-duck systems are widely practiced in Asia and have comparable societal and ecological importance.[18] While rice-aquatic animal systems exist, we focus specifically on rice-fish coculture due to its wider geographic adoption, more extensive research documentation, and recognition as a GIAHS by the FAO.[19,20] This rice-fish integrated system has ecological benefits, including enhanced invertebrate predator populations,[29,30] reduced pest herbivore abundance and damage,[19,30] decreased weed biomass,[31] and lower incidence of diseases such as sheath blight.[19] This has led to reduced pesticide use in these systems while increasing rice yields.[32] There have also been contrasting findings. For example, red tilapia (*Oreochromis niloticus*) coculture reportedly exacerbates stink bug damage to rice.[33] Nevertheless, the potential for improved pest suppression under reduced insecticide use highlights the promise of rice-fish coculture for sustainable agriculture.[34] Here, we present a comprehensive literature synthesis to identify the generalizability of these effects.[35] This study, while policy-relevant, critically addresses the scalability of rice-fish coculture across diverse socioeconomic and agroecological contexts, providing a foundation for its promotion under varied policy mechanisms.

Previous meta-analyses have indicated that rice-fish coculture can enhance rice yield,[22,36–39] improve soil fertility,[22] reduce greenhouse gas emissions,[40] decrease nitrogen losses,[37] and mitigate insect pest infestations[41] and weeds.[22] However, these meta-analyses have focused only on a small subset of specific pest species, overlooking broader groups of invertebrate natural enemies critical to the provision of natural pest control. Nor have earlier studies accounted for variation across rice field types, climatic zones, and different experimental designs. In addition, a critical gap remains in understanding the indirect effects mediated by pests and the cascading impacts of natural enemies on the relationship between rice-fish coculture in comparison with rice monoculture systems.

To address these knowledge gaps, we conducted a meta-analysis of 113 paired studies of rice-fish coculture vs. rice monoculture, with 791 observations on the effects of rice-fish coculture on trophic groups in rice farming systems (i.e., rice, pests, and invertebrate natural enemies composed of predators and parasitoids) around the world (Figure 1A). We assessed the effects of rice-fish coculture on a wide range of pest groups: herbivores (pest snails and insect pests), major rice diseases (blight disease and blast disease), and weeds. We hypothesized that, compared with monoculture, rice-fish coculture (1) enhances rice production directly through improved fertilization via fish-derived nutrients (e.g., nitrogen from excretions) and soil aeration, and (2) increases rice production indirectly by decreasing pest pressure on rice through the predation of fish on pests, strengthening top-down effects of diverse natural enemies on insect pests in line with the *enemies hypothesis*. We also hypothesized that these direct and indirect effects were similar across environmental contexts, climatic zones, and experimental settings. To test these hypotheses, we first quantified the effects of rice-fish coculture on rice yields, as an increase in rice yields is important for its widespread adoption by farmers.[42] We calculated the percentage change in rice yields using data from the 77 studies that had paired observations of rice yield in rice-fish coculture vs. rice monoculture. Next, we compiled data from all 113 studies and used meta-regression models to calculate log response ratios (lnRRs) as effect sizes to examine the response of rice, pests (herbivores, disease, and weeds), and invertebrate natural enemies (predators and parasitoids) to rice-fish coculture. We further applied structural equation models to test for direct and indirect rice-fish coculture-mediated effects on rice performance (i.e., growth, reproduction, and quality), pest performance (herbivore reproduction and damage, rice disease damage, and weed growth and reproduction), and natural enemy performance (i.e., predator and parasitoid abundance).[8]

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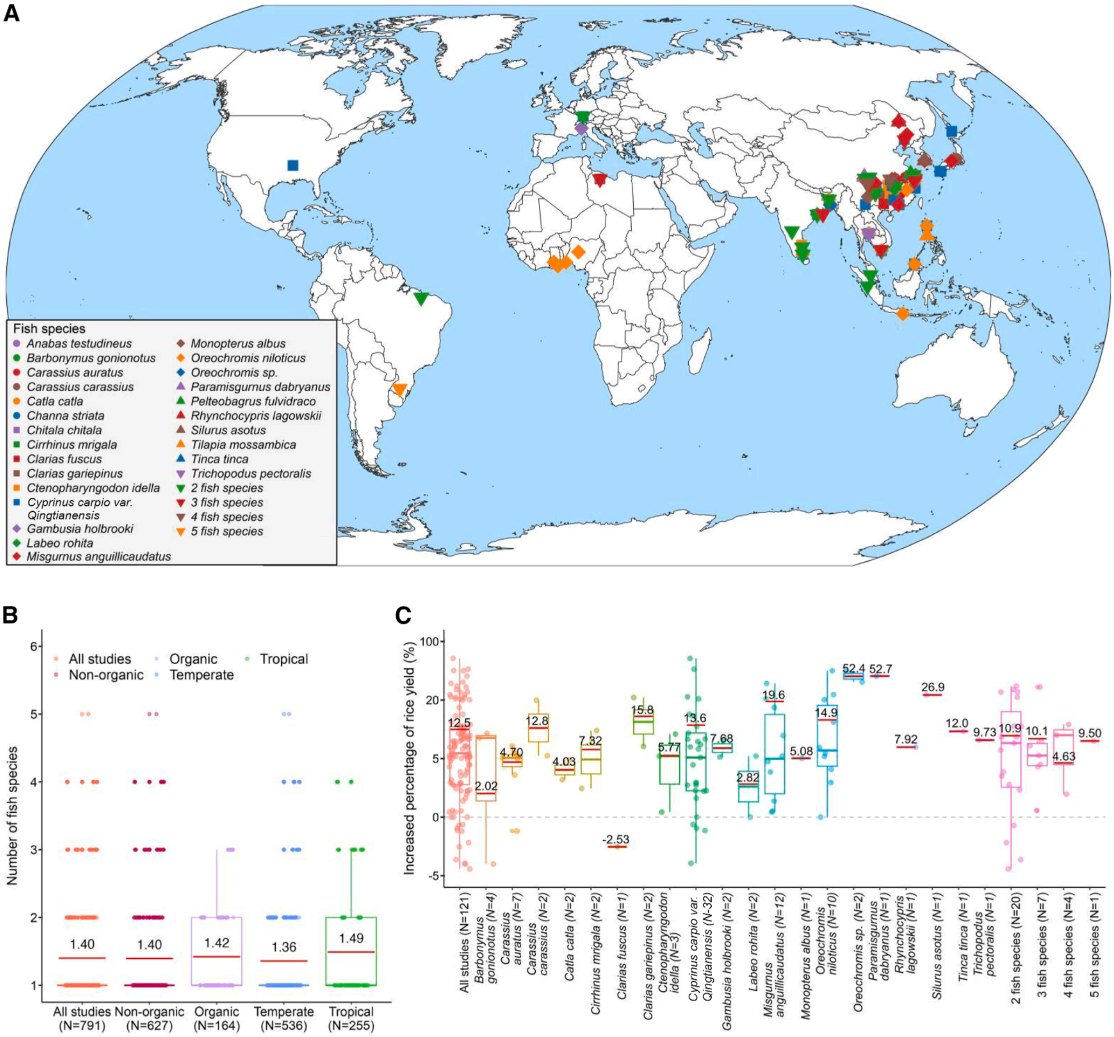

Figure 1. Global distribution of the 113 matched studies comparing rice monoculture and rice-fish coculture

(A) Study locations across 18 countries in 4 continents. The circle size corresponds to the number of fish species in coculture (Map package in R).

(B) Number of fish species in rice-fish coculture systems across all studies, non-organic and organic studies, and temperate and tropical zones.

(C) Effects of fish species in rice-fish coculture systems on rice yields. The lines within each box denote the median, the outer borders of the boxes show the upper and lower quartiles, the lines outside of the boxes depict the maximum and minimum number of individuals, and the red lines in each box represent the average value of the number of fish species. Change of rice yield = (rice yield in rice-fish coculture − rice yield in rice monoculture) ÷ rice yield in rice monoculture × 100%. The units of rice yield include ton·ha^{-1}, kg·ha^{-1}, Mg·ha^{-1}, kg·plot^{-1}, kg·666.7 m^{-2}, kg·m^{-2}, kg·5 dot^{-1}, g·m^{-2}, kg·25 m^{-2}, and q·ha^{-1}.

See also Data S3.

Finally, we used a 4-year field experiment in eastern China to better understand the underlying causality of these direct and indirect links between rice-fish coculture and rice production. To evaluate the context dependency and applied implications of these links, we analyzed variations across environmental contexts ("rice field types," organic vs. non-organic, where organic is defined as without agrochemical inputs in both rice monoculture and coculture fields and non-organic as with the same agrochemical inputs in both rice monoculture and coculture fields), climatic zones (temperate vs. tropical), and experimental settings ("experimental types," plot vs. pot). Our findings indicate that top-down effects provide the mechanism by which rice-fish coculture enhances ecosystem services by simultaneously increasing biological pest control and rice production.

RESULTS AND DISCUSSION

Direct effect of rice-fish coculture on different trophic groups

The data from all 113 studies with 791 observations showed that an average of 1.40 fish species were introduced in the rice fields (Figure 1B). We assessed the direct and indirect effects of rice-fish coculture on overall measures of (1) rice performance, composed of rice growth, reproduction, and quality (e.g., taste, milled rice rate, and protein content)[43]; (2) herbivore performance, composed of herbivore abundance and herbivory damage; (3) weed performance, composed of weed growth and reproduction; (4) disease performance as disease damage; (5) natural enemy performance, composed of invertebrate predator

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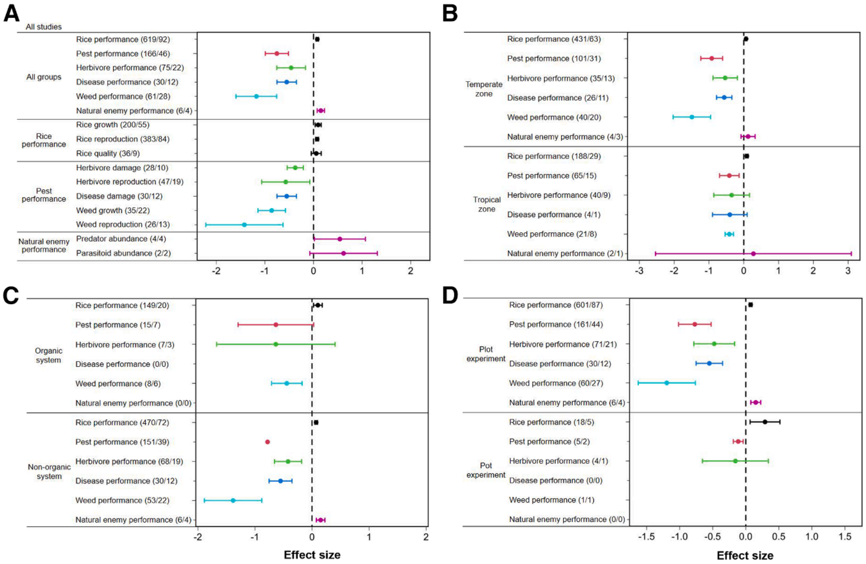

Figure 2. Mean effect sizes (lnRRs) of response categories of different trophic groups to rice-fish coculture

(A) Across all studies.

(B) In temperate and tropical zones.

(C) In organic and non-organic systems.

(D) In plot and pot experiments.

The horizontal lines indicate the 95% confidence intervals around the means. The numbers in brackets indicate the number of observations and articles, respectively.

See also Data S1A–S1F.

abundance and parasitoid abundance; and (6) aggregated pest performance, composed of herbivore reproduction and damage, rice disease damage, and weed growth and reproduction.[8]

Our results, based on 791 observations, concluded that the presence of fish (a binary variable that only considers fish presence but not the number of fish species in a rice field) enhanced rice performance across all studies (effect size [ES] = 0.0781, confidence interval [CI] = 0.0531 to 0.103, degree(s) of freedom [df] = 618, and $p < 0.001$) (Figure 2A). When we split the aggregate indicator of rice performance into rice growth, reproduction, and quality, we also found that each showed positive responses to the presence of fish (rice growth, ES = 0.0962, CI = 0.0347 to 0.158, df = 199, and $p = 0.002$; reproduction, ES = 0.0747, CI = 0.0451 to 0.104, df = 382, and $p < 0.001$; quality, ES = 0.0564, CI = −0.0455 to 0.158, df = 35, and $p = 0.278$) (Data S1A–S1C). All responses of rice performance to the presence of fish were positive for temperate and tropical zones (temperate, ES = 0.0736, CI = 0.0419 to 0.105, df = 430, and $p < 0.001$; tropical, ES = 0.0879, CI = 0.0494 to 0.126, df = 187, and $p < 0.001$) (Figure 2B; Data S1D). The subdivision of rice performance into growth, reproduction, and quality revealed consistent positive effects across field types, climatic zones, and experimental types (Figures 2A–2D; Data S1A–S1F).

Rice-fish coculture consistently improved rice performance, with mean enhancements of 9.25% across all studies, 17.2% in organic systems vs. 6.74% in non-organic systems, 9.16% in temperate zones vs. 9.44% in tropical zones, and 7.86% in plot experiments vs. 55.4% in pot experiments (Data S2). While the predation of pests by fish is a key driver of these outcomes, complementary processes also contribute to system productivity. These processes include nutrient cycling via fish excreta, modified water dynamics that suppress weed growth, and enhanced habitat complexity supporting natural enemies (see below for detailed mechanistic analyses). The lower yield gain in non-organic systems may reflect a partial suppression of the system's natural biological control by chemical inputs. This suggests a significant opportunity to further enhance productivity in conventional settings: strategically replacing broad-spectrum chemical pesticides with augmentation biological control (e.g., inoculative releases of natural enemies) or selective biopesticides could amplify the top-down pest suppression already inherent to rice-fish coculture. Such an integrated management shift would strengthen the trophic cascades documented here, potentially raising yields in non-organic systems closer to the levels observed in organic systems, thereby accelerating the agroecological transition at scale. Rice-fish coculture enhanced rice productivity through three tested mechanisms. First, fish excrement elevates soil organic matter and microbial activity, particularly nitrogen-fixing bacteria, thereby improving nutrient cycling and soil fertility.[19] Second, predation by fish suppresses pathogens, insect pests, and weeds,[19,30] while deeper water levels restrict herbivore access to the bases of plant shoots.[29] Third, the system's structural complexity fosters predator populations, creating cascading ecological benefits. For example, higher water levels and adjacent ditches can improve the habitat for predators (e.g., predatory spiders), as evidenced by increased movement, predation, and the probability of mating. Additionally, water-rich habitats can increase the abundance of alternative prey (e.g., non-pest chironomids in rice fields), supporting predators in rice-fish coculture systems.[18,44,45]

Across the 113 studies, 77 had paired observations of rice yield in rice-fish coculture vs. rice monoculture providing 121 comparisons. Using these, we found that the presence of fish increased rice yield (mean = 12.5% increase, IQR [interquartile range] = 2.33–13.2), with gains varying with fish species, underscoring the potential to enhance agricultural sustainability (Figure 1C).

Across all studies, rice-fish coculture significantly decreased the overall performance of pests (ES = −0.754, CI = −0.992 to −0.516, df = 165, and $p < 0.001$). When considered as composite groups, the presence of fish affected herbivores (ES = −0.460, CI = −0.755 to −0.165, df = 74, and $p = 0.003$), rice diseases (ES = −0.552, CI = −0.752 to −0.351, df = 29, and $p < 0.001$), and weeds (ES = −1.18, CI = −1.60 to −0.757, df = 60, and $p < 0.001$) (Figure 2A). Moreover, the pest-suppression effect was consistently observed across temperate and tropical zones (Figure 2B), organic and non-organic systems (Figure 2C), as well as plot and pot experiments (Figure 2D). The presence of fish reduced pest pressure by an average of 34.7% when all pest groups (i.e., herbivores, disease, and weeds) are combined, with a greater efficacy in temperate zones (40.8%) than in tropical zones (25.2%). Fish-rice coculture also had more pronounced impacts, reducing pest pressure in non-organic systems (35.3%) than in organic (28.1%) systems and in plots (35.1%) than in pots (19.4%) (Data S2). These significant responses largely held when these aggregate performance indicators for each pest group (i.e., herbivores, disease, or weeds) were partitioned into individual components, i.e., when weed performance was considered in terms of its component metrics of weed growth and reproduction (Data S1C).

On average, rice-fish coculture decreased herbivore pressure (herbivore abundance and damage) by 24.1% across all studies (Data S2). Rice-fish coculture significantly reduced herbivore performance (i.e., herbivore damage and reproduction) in temperate zones (ES = −0.535, CI = −0.886 to −0.184, df = 34, and p = 0.004), non-organic systems (ES = −0.420, CI = −0.658 to −0.182, df = 67, and $p < 0.001$), and in plot experiments (ES = −0.478, CI = −0.786 to −0.169, df = 70, and p = 0.003) (Data S1D–S1F). These findings support two key hypotheses. First, the predation hypothesis posits that fish directly prey on rice insect pests.[22] Second, the *environmental regulation hypothesis* (ERH) proposes that higher water levels in rice-fish systems reduce herbivore feeding areas (e.g., rice planthoppers can no longer feed at the base of plants), while adjacent ditches provide additional habitats for key predators (e.g., predatory mirids, spiders, ladybirds, and parasitoids), increasing their movement, predation, and mating success, thereby promoting biological pest control.[10,18,44,46] These effects were context-dependent, with neither tropical zones (ES = −0.348, CI = −0.863 to 0.164, df = 39, and p = 0.179) nor organic systems (ES = −0.634, CI = −1.67 to 0.404, df = 6, and p = 0.186) showing significant herbivore pest suppression. The non-significant effects in tropical zones and organic systems may reflect greater variability in pest pressures or local management conditions. In particular, intensive pesticide use in some tropical rice systems can disrupt natural enemy communities and contribute to herbivore resurgence, potentially masking the pest-suppression benefits of rice-fish coculture under certain conditions.

On average, rice-fish coculture decreased weed and disease pressure by 45.7% and 38.8% across all studies (Data S2). Rice-fish coculture demonstrated consistent weed suppression across all studies (ES = −1.18, CI = −1.60 to −0.757, df = 60, and $p < 0.001$), with significant effects observed in both temperate (ES = −1.49, CI = −2.03 to −0.953, df = 39, and $p < 0.001$) and tropical zones (ES = −0.416, CI = −0.536 to −0.296, df = 20, and $p < 0.001$). The practice also effectively controlled weeds in organic (ES = −0.443, CI = −0.710 to −0.175, df = 7, and p = 0.006) and non-organic systems (ES = −1.38, CI = −1.89 to −0.880, df = 52, and $p < 0.001$), as well as in plot experiments (ES = −1.19, CI = −1.63 to −0.762, df = 59, and $p < 0.001$). Similarly, rice-fish coculture significantly suppressed rice diseases overall (ES = −0.552, CI = −0.752 to −0.351, df = 29, and $p < 0.001$), particularly in temperate zones (ES = −0.563, CI = −0.784 to −0.342, df = 25, and $p < 0.001$), non-organic systems (ES = −0.552, CI = −0.752 to −0.351, df = 29, and $p < 0.001$) and plot experiments (ES = −0.552, CI = −0.752 to −0.351, df = 29, and $p < 0.001$). In tropical zones, however, the CI of the effect size overlapped zero, suggesting no significant effect (ES = −0.401, CI = −0.899 to 0.0980, df = 3, and p = 0.083) (Data S1D–S1F). The mechanical disturbance generated by fish in the water may have contributed to suppressing some diseases. For example, fish activity dislodges morning dew from rice leaves, reducing opportunities for spore germination of some fungal diseases.[19] Fish may also actively consume and disrupt fungal disease mycelia, effectively suppressing sheath blight development. Furthermore, fish contribute to near-complete weed control in rice paddies through direct herbivory and uprooting.[19]

We next assessed whether invertebrate natural enemy (predators and parasitoids) responses to rice-fish coculture varied across climatic zones, field types, and experimental types. Meta-analysis revealed a significant overall positive effect on natural enemies (ES = 0.151, CI = 0.0760 to 0.226, df = 5, and p = 0.004), with consistent results in non-organic systems (ES = 0.151, CI = 0.0760 to 0.226, df = 5, and p = 0.004) (Figure 2A). On average, rice-fish coculture increased natural enemy abundance by 99.3% across all studies (Data S2). No significant effects were observed between organic and non-organic systems, temperate and tropical zones, or plot and pot experiments (Figures 2B–2D; Data S1D–S1F), potentially due to limited sample sizes. Rice-fish coculture enhanced invertebrate predator abundance through three mechanisms. Elevated water levels and adjacent ditches create favorable microhabitats that increase spider movement, predation rates, and mating success.[47] Concurrently, water-rich environments support higher populations of non-pest chironomids, providing supplemental prey for predatory spiders.[46] Farmers adopting rice-fish coculture often deliberately reduce, suspend, or eliminate prophylactic pesticide applications (such as insecticidal seed coatings) to protect the fish, which thereby enhances the survival and efficacy of natural enemies. The effects of each fish species on trophic groups varied (Data S3). We found that having more than 1 fish species generally resulted in a better biological control (Data S4). Rice-fish coculture systems also support vertebrate predators (e.g., frogs), which contribute to pest suppression through direct predation of herbivores like brown planthoppers.[48] The stable aquatic environment and reduced pesticide use in these systems create favorable conditions for frog populations to thrive and enhance their biological control function.

Mediation analysis of top-down effects in rice-fish coculture

We obtained 371 estimates of interactions between pairs of rice and pests derived from 24 articles to test the direct and indirect effects of rice-fish coculture on rice performance, pest performance, and their interactions, using multilevel structural equation models (Figures S1A and S1B; Data S1G–S1J). In these models, we aggregated different pests together, i.e., herbivores, rice diseases, and weeds. We found that the presence of fish directly suppressed pests (estimate = −1.13, $p < 0.001$) and directly enhanced rice performance (estimate = 0.245, p = 0.028) compared with rice monoculture. At the same time, fish increased rice performance indirectly via decreased pest performance (estimate = −0.014, p = 0.636) (Figure 3A). Similar patterns are observed across different climatic zones (temperate, estimate = −0.001, p = 0.978; tropical, estimate = −0.0785, p = 0.273), rice field types (organic, estimate = −0.00114, p = 0.989; non-organic, estimate = −0.0227, p = 0.470), and experimental types (plot, estimate = −0.0137, p = 0.640; pot, no data) (Figures 4A–4E; Data S1G–S1J). We also detected direct and indirect effects when we tested for the influence of herbivores, diseases, and weeds on rice performance separately (coculture vs.

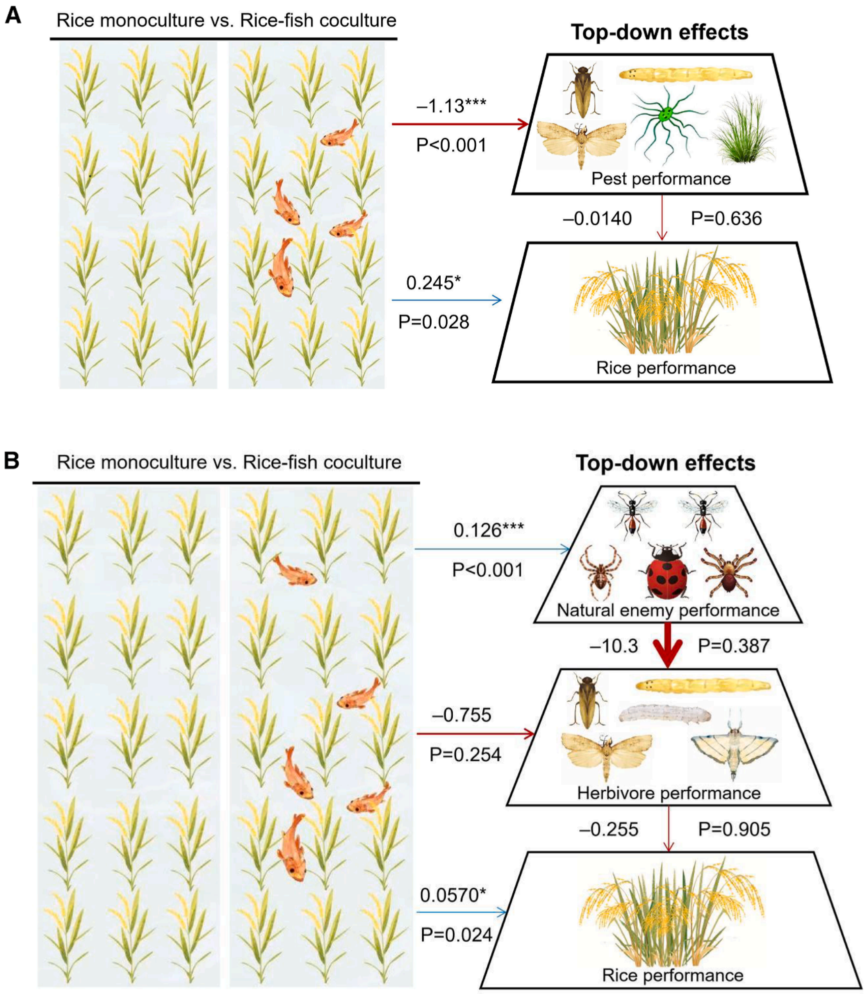

Figure 3. Path analyses showing top-down effects across all studies

(A) Interactions between pest and rice performances ($N = 371$).

(B) Interactions among natural enemy, herbivore, and rice performances ($N = 32$). Rice performance includes rice growth, reproduction, and quality. Pest performance includes (i) herbivore performance (i.e., herbivore damage and reproduction), (ii) rice disease performance (i.e., rice disease damage), and (iii) weed performance (i.e., weed growth and reproduction). Natural enemy performance includes invertebrate predators and parasitoid abundances. *$p < 0.05$, **$p < 0.01$, and ***$p < 0.001$. The blue and red arrows denote positive and negative relationships, respectively. The numbers next to each arrow are the estimated coefficients from structural equation models, and line width is proportional to the magnitude of the coefficients.

Image credits, N.-F.W.

See also Data S1G and S1H.

herbivores, estimate = −0.732, $p = 0.0239$; herbivores vs. rice, estimate = −0.0194, $p = 0.863$; coculture vs. diseases, estimate = −0.577, $p < 0.001$; diseases vs. rice, estimate = −0.0144, $p = 0.883$; coculture vs. weeds, estimate = −1.416, $p < 0.001$; weeds vs. rice, estimate = −0.0214, $p = 0.605$) (Data S1G–S1J).

For a subset of studies ($n = 32$) that examined rice-fish coculture across all three trophic levels (rice-herbivore-natural enemy interactions), we tested its effects on tri-trophic interactions. Structural equation modeling indicated a positive, direct effect of rice-fish coculture on the performance of natural enemies (estimate = 0.126, $p < 0.001$) and rice (estimate = 0.0570, $p = 0.024$), a negative, direct effect on herbivores (estimate = −0.755, $p = 0.254$), and negative, indirect effects mediated through trophic cascades (natural enemies vs. herbivores, estimate = −10.3, $p = 0.387$; herbivores vs. rice, estimate = −0.255, $p = 0.905$). These results suggest that rice-fish coculture promotes a top-down cascade that suppresses herbivore pests (Figure 3B). This system's structure creates cascading ecological benefits, reducing or eliminating the need for chemical pesticides. Furthermore, the economic value of the fish itself acts as a powerful incentive for farmers to minimize or forgo pesticide applications, as these chemicals can harm the aquatic stock. This reduction in pesticide input not only lowers production costs but also crucially protects the populations of invertebrate predators (e.g., spiders), whose sustained abundance is essential for the top-down pest suppression in paddy ecosystems.

Field experiment on rice-fish coculture effects on trophic groups and interactions

A 4-year field experiment indicated that the abundances of herbivores (planthoppers, stemborers, and leafrollers) were all lower (Figures 5A–5F), while the predatory spider abundance was higher (Figures 5G and 5H), in rice-fish coculture than in rice monoculture plots, even though herbivore populations varied both interannually and intra-seasonally during the survey periods (Data S5A). In addition, we found that both rice yield and thousand-grain weight were higher in rice-fish coculture than in rice monoculture (Figures 6A and 6B). The abundances of planthoppers, stemborers, and leafrollers were 15.7%–24.0%, 22.2%–35.3%, and 15.9%–31.3% lower, respectively, while predator abundance, rice yield, and thousand-grain weight were 11.0%–31.1%, 1.51%–6.20%, and 2.18%–6.07% higher in coculture than in monoculture within the 4 years (2021–2024), respectively. In short, our 4-year field experiment confirmed the conclusions of the meta-analysis, supporting the hypothesis that rice-fish coculture promotes agricultural sustainability by decreasing pests, benefiting predators, and enhancing rice production. The additional production of fish also boosts farmers' incomes, a benefit that is particularly valuable in regions experiencing rapid growth in demand for animal protein.

Based on data from the 4-year field experiment with 48 paired observations of predatory spider abundance vs. average herbivore community abundance vs. rice production (rice yield and thousand-grain weight) (Data S5B), we used structural equation models to test the direct and indirect effects of rice-fish coculture vs. rice monoculture on trophic groups and on top-down effects.

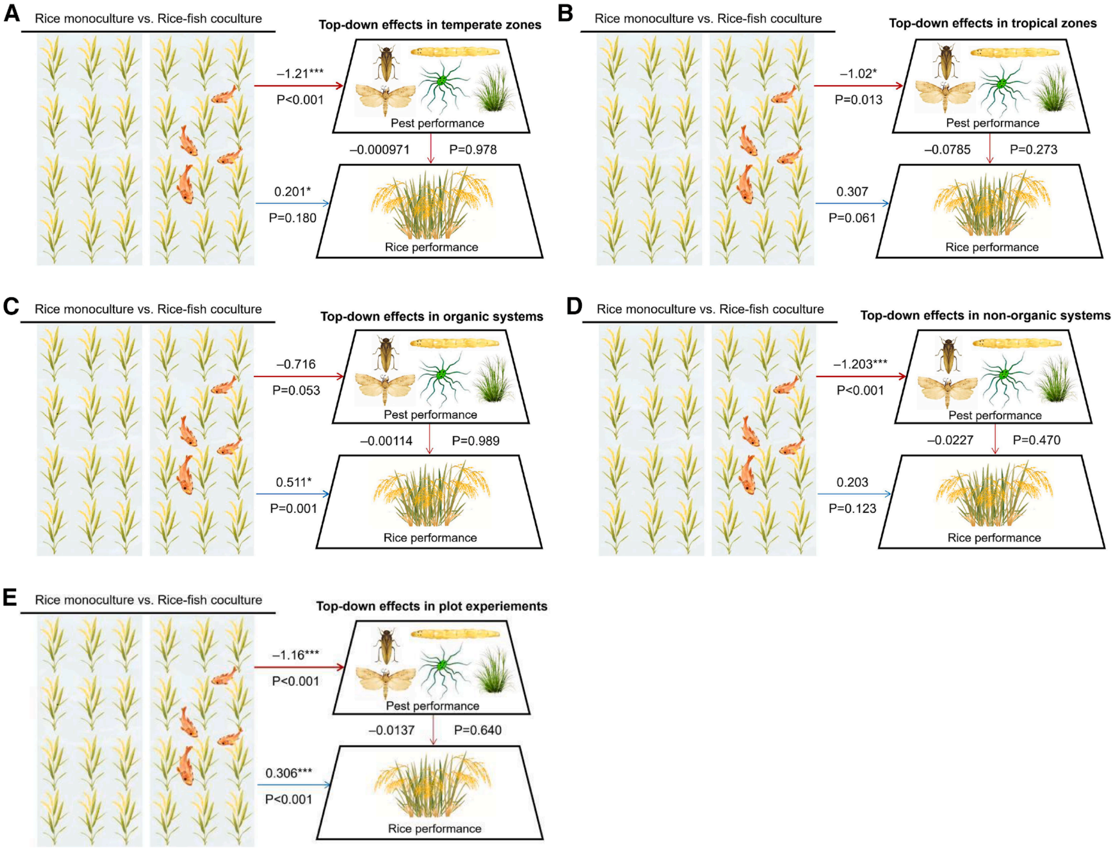

Figure 4. Path analyses showing top-down effects across different climatic zones, rice field types, and experimental studies

(A) Temperate zones (*N* = 236).
(B) Tropical zones (*N* = 135).
(C) Organic systems (*N* = 58).
(D) Non-organic systems (*N* = 313).
(E) Plot experiments (*N* = 369).
Mediation effects cannot be analyzed for pot experiments (*N* = 2). Rice performance is composed of the growth, reproduction, and quality of rice. Pest performance includes (i) herbivore performance, composed of damage and reproduction of invertebrate herbivores; (ii) rice disease performance, composed of damage of rice diseases; and (iii) weed performance, composed of growth and reproduction of weeds. *$p < 0.05$, **$p < 0.01$, and ***$p < 0.001$. The blue and red arrows denote positive and negative relationships, respectively. The numbers next to each arrow are the estimated coefficients from piecewise structural equation models, and line width is proportional to the magnitude of the coefficients.
Image credits, N.-F.W.
See also Data S1I and S1J.

We found that rice-fish coculture had positive effects on predator abundance (estimate = 25.4, $p < 0.001$) and rice production (estimate = 0.539, $p = 0.798$), while its direct effect on herbivore abundance was negative (estimate = −7.81, $p < 0.001$). We also detected indirect effects mediated by top-down trophic cascades (i.e., predators vs. herbivores, estimate = −0.257, $p < 0.001$; herbivores vs. rice, estimate = −0.00820, $p = 0.908$) (Figure 6C; Data S5B).

Behavioral experiment on mechanisms of rice-fish coculture effects on herbivores and predators

We conducted a pot-based behavioral experiment in rice-fish coculture systems to investigate the predatory effects of fish on spiders and rice planthoppers. We tested two local fish species individually in separate pot setups. The first species is the Oujiang color common carp (*Cyprinus carpio* var. *Qingtianensis*), a red, soft-scaled carp native to the region. It is a representative species of a GIAHS,[19] with a long history of integration into local rice farming and strong adaptability to paddy field ecosystems. The second species is the crucian carp (*Carassius auratus*), which is also native to local aquatic environments and widely incorporated into regional rice cultivation practices for its role in maintaining paddy ecological balance. To ensure the accuracy of our findings, we strictly controlled all environmental variables across pot setups. These included consistent rice varieties, planting densities, water levels, and soil fertility, minimizing any external interference to focus on the predatory differences between the two fish species. We found that common carp had a greater predation rate on brown planthoppers (*Nilaparvata lugens*) compared with that of crucian carp, and that the predation rate was higher when the ushered planthopper was 20 or

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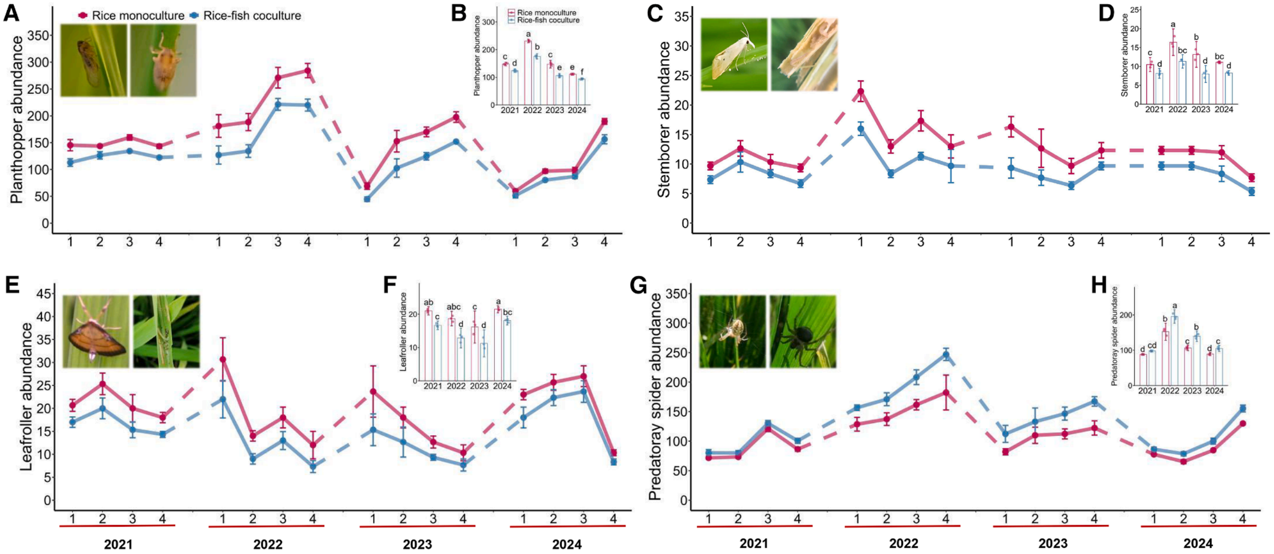

Figure 5. Field experiment to test the abundances of invertebrate herbivores and their predatory spiders

(A) Dynamics of rice planthopper (*Nilaparvata lugens*, *Sogatella furcifera*, and *Laodelphax striatellus*) abundance.
(B) Average abundance of rice planthoppers.
(C) Dynamics of rice stemborer (*Chilo suppressalis*) abundance.
(D) Average abundance of rice stemborers.
(E) Dynamics of rice leafroller (*Cnaphalocrocis medinalis*) abundance.
(F) Average abundance of rice leafrollers.
(G) Dynamics of predatory spider abundance.
(H) Average abundance of predatory spiders.
The abundance units are individuals per 100 rice clusters. Data are shown as means with error bars for standard errors (*N* = 3 independent plots per treatment). The dashed lines indicate periods without observation between 2 years, due to the rice harvest or when the crop following after rice is planted with horsebeans (*Vicia faba*) in each plot. The numbers on the *x* axes indicate the four samplings of arthropods from early to mid-July to early to mid-September (i.e., from the seedling to maturity stages) at 2–4 week-intervals from 2021 to 2024. Bars that do not share a letter differ significantly from one another based on Tukey's honestly significant difference (HSD) multiple comparisons following a one-way ANOVA.
Image credits, Y.C. (nymphs and adults of planthoppers) and N.-F.W. (larval and adult stemborers, larval and adult leafrollers, and predatory spiders).
See also Data S5A.

30 individuals per pot compared with the lowest density (10 individuals per pot) (Figure 6D; Data S5C). We observed no predation by the fish on the wolf spider (*Pardosa pseudoannulata*) (Videos S1–S4). This beneficial effect may not apply to all key predators in rice systems. Some species, such as dragonfly nymphs, can fall prey to fish in these coculture setups.

Our meta-analysis (Figure 7) and 4-year field experiments demonstrate that rice-fish coculture systems enhance rice yield and production while increasing natural enemy abundance and suppressing herbivorous insects, pathogens, and weeds through three mechanisms: direct pest control (e.g., fish physically consume insect herbivores and weeds), indirect predator-mediated cascades (e.g., fish-derived habitat improvements that elevated spider populations), and reduced pesticide application driven by the need to protect fish stocks, thereby suppressing insect pests via density-dependent predation. While the rush toward intensified rice production has become widespread, the high potential of these GIAHSs to support sustainable agriculture needs to be acknowledged. In addition to the benefits for the production of rice, fish can be harvested and sold as an additional product, increasing the profitability of the system to the farmer. For example, in the Yangtze River Delta region in China, for crucian carp cultivation in rice fields, the fish yield per hectare ranges from 178 to 201 kg in one rice cropping cycle.[30] Often, fish are the main economic driver of these coculture systems. What may appear to be a simple, yet practical diversification of crop and animal species delivers substantial benefits by strengthening beneficial multitrophic interactions and enhancing biological control. By increasing ecosystem services, these practices represent sustainable intensification, facilitating a reduction or even elimination of chemical inputs, thereby providing policymakers with a proven model to integrate agroecological practices with global food security objectives, which are aligned with the UN Sustainable Development Goals.

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to, and will be fulfilled by, the lead contact, Nian-Feng Wan (nfwan@ecust.edu.cn).

Materials availability

All data generated or analyzed during this study are included in this study and its supplemental information files. The experimental protocols used in this research are available from the corresponding author upon reasonable request.

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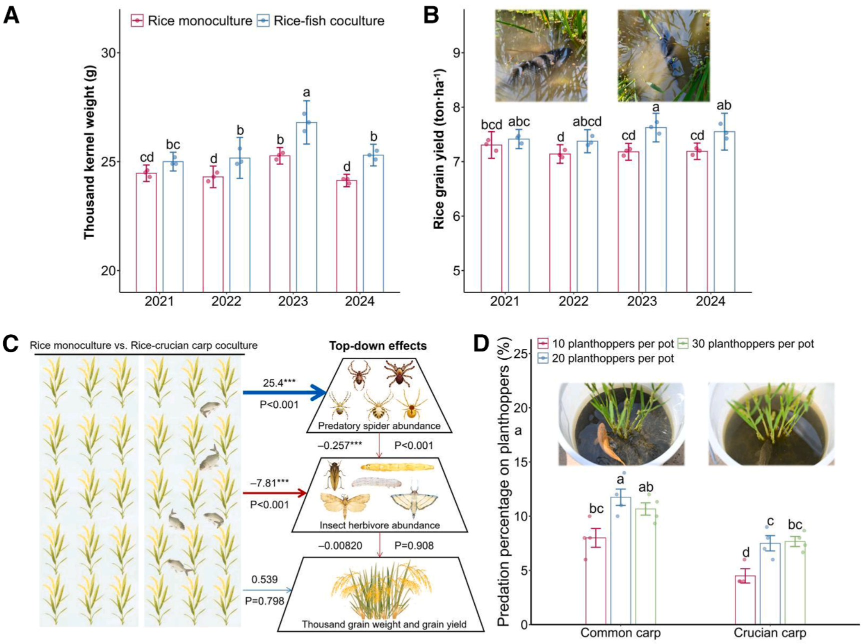

Figure 6. Field and pot experiments to test the effects of rice-fish coculture on rice production

(A) Average thousand-kernel weight (g) in each year ($N = 3$).

(B) Average rice grain yield (ton·ha^{-1}) in each year ($N = 3$).

(C) Interactions among predatory spiders, herbivores, and rice ($N = 48$).

(D) Predation percentage of common carp (*Cyprinus carpio* var. *qingtianensis*) or crucian carp (*Carassius auratus*) on brown planthoppers (*Nilaparvata lugens*) in a behavioral experiment ($N = 4$). Common carp and crucian carp have no predation on wolf spiders (*Pardosa pseudoannulata*) ($N = 4$). In the behavioral experiments on fish preying on brown planthoppers and wolf spiders, the video recording lasts for 20 min for each observation (five individual observations were considered as one biological replicate, and four biological replicates were performed). In each behavioral experiment in each pot, we introduced 10, 20, or 30 third-instar brown planthoppers; or three female wolf spiders; or three male wolf spiders, respectively, to test the effects of common carp or crucian carp on preying brown planthoppers or wolf spiders. Data are shown as means with error bars for standard errors. In Figures 6A, 6B, and 6D, bars that do not share a letter differ significantly from one another based on Tukey's HSD multiple comparisons following a one-way ANOVA (predation percentage data underwent arcsine-square root transformation to meet parametric assumptions).
Image credits, N.-F.W.
See also Data S5B, S5C, and Videos S1–S4.

Data and code availability

- All data used in this analysis have been deposited at the Figshare repository https://doi.org/10.6084/m9.figshare.31742416.
- All original code has been deposited at the Figshare repository and is available at https://doi.org/10.6084/m9.figshare.31742416.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

N.-F.W. conceived the idea and drafted the article. N.-F.W., S. Shen, M. Li, Y.C., F.-Y.P., and Q.L. collected, checked, and/or analyzed the data. N.-F.W., Y.C., F.-Y.P., and J.L. performed the field experiments. Y.C. and F.-Y.P. conducted the behavioral experiment on fish. N.-F.W., S. Shen, M. Li, Y.C., F.-Y.P., X.C., B.A.W., Y.-Q.H., A.H., M. Loreau, B.S., N.E., D.W.C., J.W., C.M.-N., T.T., Q.L., S.Q., S. Sun, Y.Y., Q.S., J.-X.Z., Y.-T.Z., T.-L.J., J.L., and J.-J.T. wrote the manuscript. All authors edited and approved the final draft.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS
  - ○ Definition of rice-fish coculture and the number of added fish species
  - ○ Study selection
- METHOD DETAILS
  - ○ Predictor variables
  - ○ Meta-analysis for rice yield
  - ○ Definition of effect size and its measures
  - ○ Meta-regression
  - ○ Meta-regression models for model comparison and parameter evaluation
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  - ○ Meta-analytic path analysis via residual regressions
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  - ○ Field experiment design
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- QUANTIFICATION AND STATISTICAL ANALYSIS
  - ○ Meta-regression and path analysis
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  - ○ Data analysis for behaviour experiment

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2026.03.046.

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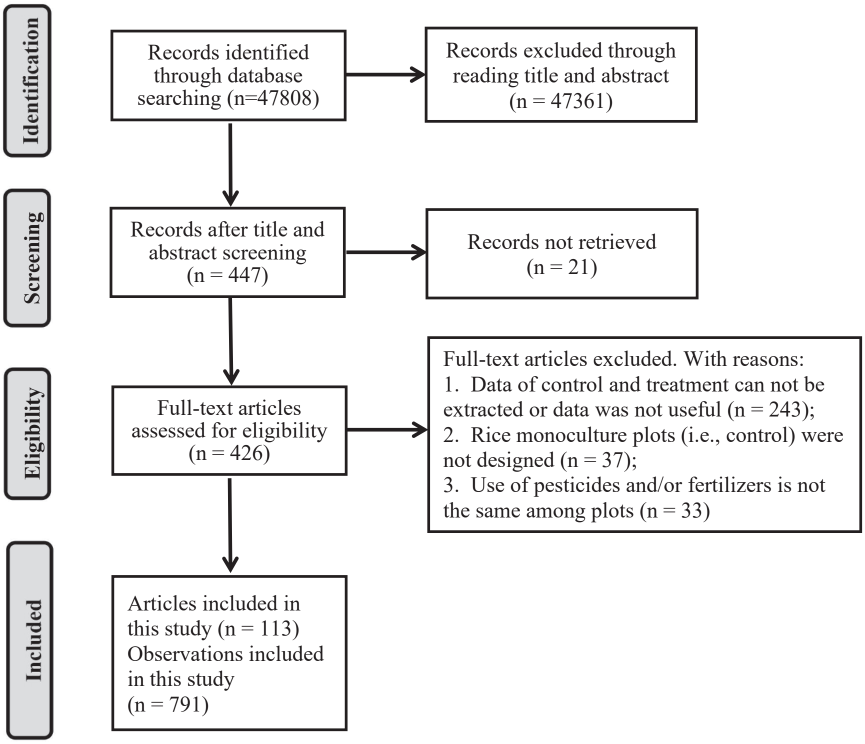

Figure 7. A PRISMA (preferred reporting items for systematic reviews and meta-analyses) describing the progress of data acquisition through the meta-analysis

Its records are identified in terms of the numbers and subsequently processed with respect to inclusions and exclusions to derive the final dataset, which is used to assess the effects of rice-fish coculture on the performance of rice, pests, and invertebrate natural enemies.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
All country distribution of the experiments of rice-fish coculture effects on tri-trophic groups-2025-0904.xlsx	Lists of included articles in this meta analysis in the Supplementary References; Figshare data	https://doi.org/10.6084/m9.figshare.31742197
Matched data of rice and disease in rice-fish co-culture vs. mono-rice-2025-0906.xlsx	Lists of included articles in this meta analysis in the Supplementary References; Figshare data	https://doi.org/10.6084/m9.figshare.31742197
Matched data of rice and herbivores in rice-fish co-culture vs. mono-rice-2025-0904.xlsx	Lists of included articles in this meta analysis in the Supplementary References; Figshare data	https://doi.org/10.6084/m9.figshare.31742197
Matched data of rice and pest in rice-fish co-culture vs. mono-rice-2025-0905.xlsx	Lists of included articles in this meta analysis in the Supplementary References; Figshare data	https://doi.org/10.6084/m9.figshare.31742197
Matched data of rice and weed in rice-fish co-culture vs. mono-rice-2025-0904.xlsx	Lists of included articles in this meta analysis in the Supplementary References; Figshare data	https://doi.org/10.6084/m9.figshare.31742197
Matched data of rice, herbivore and natural enemy in rice-fish co-culture vs. mono-rice-2025-0905.xlsx	Lists of included articles in this meta analysis in the Supplementary References; Figshare data	https://doi.org/10.6084/m9.figshare.31742197
Rice yield between rice-fish co-culture vs. mono-rice-2025-0904.xlsx	Lists of included articles in this meta analysis in the Supplementary References; Figshare data	https://doi.org/10.6084/m9.figshare.31742197
data of all trophic groups for rice-fish co-culture vs. mono-rice-2025-0904.xlsx	Lists of included articles in this meta analysis in the Supplementary References; Figshare data	https://doi.org/10.6084/m9.figshare.31742197
data of all trophic groups for rice-fish co-culture vs. mono-rice-2025-0904.xlsx	Lists of included articles in this meta analysis in the Supplementary References; Figshare data	https://doi.org/10.6084/m9.figshare.31742197
Field experiment data for path analysis in rice monoculture vs. rice-fish coculture-2025-0905.xlsx; Four-year experimental data of rice, herbivore and predator in Shanghai, China-2025-0905.xlsx	Field experiment was conducted at Situan Town, Fengxian District, Shanghai of 874 China (30.94°N, 121.71°E); Figshare data	https://doi.org/10.6084/m9.figshare.31742197
Tukey's HSD multiple comparisons following a one-way ANOVA in field experiment-2025-0906.xlsx	Field experiment was conducted at Situan Town, Fengxian District, Shanghai of 874 China (30.94°N, 121.71°E); Figshare data	https://doi.org/10.6084/m9.figshare.31742197
Percantage of two fish species prey on planthoppers or spiders in behaviour experiment-2025-0915.xlsx	Behaviour experiment of fish preying on brown planthoppers and their predatory spiders, was conducted in Fengxian campus of East China University of Science and Technology, China; Figshare data	https://doi.org/10.6084/m9.figshare.31742197
Software and algorithms		
All code of rice-fish coculture vs. rice monoculture-2026-0315-CB-final.zip	This paper; Figshare data	https://doi.org/10.6084/m9.figshare.31742416
R version 4.3.1	The R Project for Statistical Computing	R Core Team[49]
R package "metafor" 3.8-1 to perform meta-regression and publication bias assessment	The R Project for Statistical Computing	Viechtbauer[50]
R packages "nlme" to residual regression in path analyses	The R Project for Statistical Computing	Pinheiro et al.[51]

(Continued on next page)

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Continued

REAGENT or RESOURCE	SOURCE	IDENTIFIER
"piecewiseSEM" to residual regression in path analyses	The R Project for Statistical Computing	Lefcheck[52]
Biological samples		
Rice variety "Huruan 1212" in field experiment	This paper	N/A
Rice variety "Huxiangjing 106" in behaviour experiment	This paper	N/A
Fish (*Carassius auratus*) in field experiment	This paper	N/A
Fish (*Cyprinus carpio* var. *qingtianensis* and *Carassius auratus*) in behaviour experiment	This paper	N/A
Planthoppers, stemborers, and leafrollers in rice fields	This paper	N/A
Brown planthopper (*Nilaparvata lugens*) in behaviour experiment	This paper	N/A
Wolf spider (*Pardosa pseudoannulata*) in behaviour experiment	This paper; Wolf spiders are from Jinggangshan Agricultural Science and Technology Park, Xingqiao Town, Jizhou District, Ji'an City, Jiangxi Province, China (27.14°N, 114.88°E)	Research team of Professor Yonghong Xiao, Jinggangshan University, China

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Definition of rice-fish coculture and the number of added fish species

Here we considered "rice-fish coculture" as any increase in the number of fish species, relative to a rice monoculture (i.e., control group without fish). Namely, "rice-fish coculture" is a binary variable (zero or one), indicating whether fish species are present, irrespective of the number of fish species added. Here "number of added fish species" is a continuous variable describing the increase in fish species between the control (i.e., rice monocultures without fish species) and the rice-fish cocultures (i.e., rice-fish coculture with a number of fish species). When comparing rice monocultures with the treatment (i.e., rice-fish coculture, with≥1 fish species in rice fields), we ensured that comparisons were also made between the same trophic groups for rice, herbivores, rice diseases, and weeds. Results for "rice-fish coculture" are shown in Figures 2, 3, 4, and S1–S3; Data S1A–S1L and S2. Results for "number of added fish species" are shown in Data S1H, S1J, S1K, S1M, and S4).

Study selection

To identify relevant studies, we performed a systematic literature search on the Web of Science platform (i.e., Web of Science Core Collection, BIOSIS Previews, Derwent Innovations Index, KCI-Korean Journal Database, MEDLINE, Preprint Citation Index, ProQuestTM Dissertations & Theses Citation Index, and SciELO Citation Index), China Wangfangdata (https://wanfangdata.com.cn) and China National Knowledge Internet (https://www.cnki.net/) (up to late September 2025). The search employed the following Boolean string: ["rice-fish"] AND ["predat*" OR "parasit*" OR "wasp*" OR "natural enem*" OR "herbivor*" OR "pest" OR "biological control" OR "yield"]. This initial search returned 47808 articles (Figure 7 for a PRISMA diagram). We first screened titles and abstracts to determine whether articles measured relevant response variables relating to the effects of rice-fish coculture on i) the growth, reproduction and quality of rice; ii) the growth and reproduction of invertebrate herbivores; iii) the rice disease damage; iv) the growth and reproduction of weeds; and v) the abundances of invertebrate predators and parasitoids. This screening excluded 47,361 articles. From the remaining 447 full-text articles, we applied inclusion/exclusion criteria, and obtained our final selection of 113 articles based on the following criteria[19,21,30,31,33,53–160]: i) the means, standard deviations (or standard errors) and sample sizes of the selected variables could be extracted from the text, tables, figures, or supplemental information; ii) where pesticides and fertilizers were used, the amount and identity/type must be the same across all treatments (rice-fish coculture, ≥1 fish species) and control (rice monoculture). For articles lacking reported standard deviations, standard errors, or confidence intervals, we calculated standard deviations using the "All Cases" method, according to Nakagawa et al.[161] With the help of AI, we translated the articles with non-English or non-Chinese language. Articles were screened by N.F.W., S.S., M.L. and Y.C. Data were extracted from the articles by N.F.W., S.S., F.Y.P. and Q.L during which regular cross-checking was performed to ensure consistency in extracted effect sizes.

We used data giving the mean values of multiple sampling dates or years. If these mean values were not presented, we used the data of the latest sampling period.[8,28] For articles that covered more than one experimental location, we considered these experimental results separately (see locations in Figure 1A). When numeric values were not provided directly, we extracted them from

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figures using the ''GetData Graph Digitizer'' 2.26. Where data were not directly accessible from figures or text, we contacted the corresponding authors for clarification. To avoid pseudo-replication of data, we excluded multiple comparisons conducted within a single experiment (i.e., we selected just one comparison).[7] Observations in rice monoculture were considered as controls, while those in rice-fish coculture were considered as the treatments. When an article included different numbers of fish species, measurements for the control groups without fish were compared to all other treatments with different richness levels of fish species and treated as independent paired observations. When extracting the data on rice yield in rice-fish coculture systems, we removed the water ditch area without rice plants. For example, in an area of 500m^2 rice-fish coculture plots with 25m^2 water ditch area (i.e., 5% of non-planted area of the total field), rice yield was reported as 4.30 Mg·ha^{-1}, which we re-calculated to 4.53 Mg·ha^{-1} (i.e., 4.30÷0.95=4.53).

METHOD DETAILS

Predictor variables

Five categorical predictor variables and one continuous predictor variable were derived in association with each lnRR effect size.

Trophic group

A categorical variable indicates whether the organisms whose lnRR effect size responses were as primary producers or different classes of pests. Where lnRR effect sizes described pests, these were classified by an aggregate categorical variable (i.e., rice pests), including invertebrate herbivores, rice diseases, and weeds. A further classification distinguished between the sub-groups of invertebrate herbivores, rice diseases that infest rice and cause damage to rice, or weeds (i.e., pest plants in rice fields, competing for water, light, and nutrients with rice). Moreover, we considered an aggregate categorical variable (i.e., pests) including invertebrate herbivores, rice diseases, and weeds.

Response category

Response categories included i) growth, reproduction, and quality of rice (i.e., rice performance); ii) damage and reproduction of herbivores (i.e., herbivore performance); iii) abundances of invertebrate natural enemies predators and parasitoids (i.e., natural enemy performance); iv) rice disease damage (i.e., disease performance); and v) weed growth and reproduction (i.e., weed performance). We divided the lnRR effect size response variables into multiple categories nested within each trophic group. These were as follows—i) *Rice performance*: This represents the principal metric used in the assessment of the biodiversity–productivity relationship. This was the metric exposed to the negative effects resulting from the activity of the pests. Note that the effect of these pests on rice performance was directly assessed within the path analysis framework described below. Measures of rice performance included rice growth, reproduction, and quality. Rice growth was assessed as growth rate and size characteristics (e.g., plant weight, plant height, culm height, aboveground biomass, dry matter biomass of rice plants, leaf area, leaf biomass, root length, number of tillers per plant). Rice reproduction included the yield of grains, reproductive plant parts, seeds per unit, and reproductive traits measured on individual plants (e.g., grain yield, number of panicles, panicle weight, thousand kernel weight, number of spikelets, filled grain number per panicle, seed-setting rate, and rice kernel set percentage). Rice quality included rice appearance, taste value, brown rice rate, head rice rate, milled rice rate, and protein content percentage, referring to The Ministry of Agriculture of the People's Republic of China.[43] ii) *Pest herbivore performance*: This included snail and invertebrate herbivore reproduction (e.g., herbivore population abundance and survival rate), and herbivory damage (e.g., percentage or grade of herbivore damage to rice). iii) *Rice disease performance*: This included disease damage (e.g., disease index of rice sheath blight, incidence of rice blast, incidence of sheath blight disease, percentage of stripe blight in rice clusters, and severity of leaf blight disease). iv) *Weed performance*: This was composed of weed growth (e.g., weed biomass, dry matter weight, and fresh weight), and weed reproduction (e.g., weed population/community abundance or density). Studies on plant-feeding nematodes and plant-feeding rodents were not found in this meta-analysis. v) *Overall metric of pest performance*: This was an overall metric that integrated lnRR effect sizes for the performances of invertebrate herbivores, rice diseases, and weeds. This was done by binding the observations of herbivore, disease, and weed performances.

Climatic zone type

A categorical variable reflecting whether a certain study was performed in the temperate or tropical zones. Temperate zones ranged from 23.5°N to 66.5°N and from 23.5°S to 66.5°S, and the tropical zones ranged from 0−23.5°N and from 0−23.5°S. Data from greenhouse and indoor experiments were removed from models considering climatic predictors, as the climate in these indoor conditions is controlled artificially.[8]

Type of experimental study

This variable describes where the studies used plot-based experiments (rice was planted directly into ground soil; in field-based plots) or pot-based experiments (rice planted into soil in above-ground vessels). Common garden experiments with a few or several replicated plots and open field experiments in rice fields were considered as plot experiments. Pots, containers, bottles, trays, boxes, and tankers were considered as pot experiments. Greenhouse experiments were considered as plot or pot experiments. Indoor and laboratory experiments were considered as pot experiments.

Rice field types

A categorical variable indicating whether experiments employed rice-fish coculture or rice monoculture systems, categorized as organic or non-organic. Organic systems did not apply synthetic agrochemicals (including chemical pesticides and fertilizers), but synthetic agrochemicals were used in non-organic systems.

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Number of added fish species

A continuous variable describing the number of fish species added to the rice-fish coculture treatment. When we compared the fish species of the control (i.e., rice fields without fish) with that of the treatment (i.e., rice-fish coculture, ≥1 fish species), we confirmed that both the control and treatment were compared on the same trophic groups among the invertebrate herbivores, rice diseases, weeds and rice. In addition, we tested for fish species-identity effects by including fish species as a random effect in meta-analysis (Data S1A), and we conducted meta-analysis in different subgroups that categorized by fish species (Data S3).

Meta-analysis for rice yield

We derived a new Data including paired observations of rice yield in rice monoculture vs. rice-fish coculture in each experiment. In total, among all the 113 studies, we extracted the data of 77 studies with 121 paired observations. Firstly, we calculated the increased percentage of rice yields. Increased percentage of rice yield = (rice yield in rice-fish coculture–rice yield in rice monoculture) ÷rice yield in rice monoculture×100%. Units of rice yield include ton·ha^{-1}, kg·ha^{-1}, Mg·ha^{-1}, kg·plot^{-1}, kg·666.7m^{-2}, kg·m^{-2}, kg·5 dot^{-1}, g·m^{-2}, kg·25 m^{-2}, and q·ha^{-1}.

Definition of effect size and its measures

To test the effect of fish species on the various groups (growth, reproduction and quality of rice, damage and reproduction of herbivores, abundances of predators and parasitoids, rice disease damage, weed growth and reproduction; and moreover, an aggregate pest categorical variable including herbivores, rice diseases, weeds, predators and parasitoids), we calculated the effect size and lnRR of these groups. The first proposed formula by using Equations 1 and 2:

$$lnRR_1 = \ln\left(\frac{m_1}{m_2}\right), \qquad \text{(Equation 1)}$$

$$v(lnRR_1) = \frac{sd_1^2}{n_1 m_1^2} + \frac{sd_2^2}{n_2 m_2^2} = \frac{CV_1^2}{n_1} + \frac{CV_2^2}{n_2}, \qquad \text{(Equation 2)}$$

where m_1 and m_2 are the observed mean value in the treatment and control groups, sd_1 and sd_2 are the standard deviations (SDs) in the treatment and control groups, and n_1 and n_2 are the sample sizes in the treatment and control groups. m_1, m_2, sd_1, sd_2, n_1 and n_2 were extracted from original articles. Namely, mean value, SD and sample sizes of both treatment and control groups were included in our Data to conduct meta-regression. This was done in order to deal with missing standard deviations (SDs) in Data, using the approach of Nakagawa et al.,[161] which is suited to accounting for missing SDs. Nakagawa et al.[161] proposed this new method weighting average coefficients of variation estimated from studies that do report SDs in the Data. This is done by using Equations 1–6:

$$lnRR_2 = \ln\left(\frac{m_1}{m_2}\right) + \frac{1}{2}\left(\frac{CV_1^2}{n_2} - \frac{CV_2^2}{n_1}\right), \qquad \text{(Equation 3)}$$

$$v(lnRR_2) = \frac{CV_1^2}{n_1} + \frac{CV_2^2}{n_2} + \frac{CV_1^4}{2n_1^2} + \frac{CV_2^4}{2n_2^2}, \qquad \text{(Equation 4)}$$

$$lnRR_3 = \ln\left(\frac{m_1}{m_2}\right) + \frac{1}{2}\left(\frac{\left[\sum_{i=1}^{K}\frac{n_{1i}CV_{1i}}{\sum_{i=1}^{K}n_{1i}}\right]^2}{n_1} - \frac{\left[\sum_{i=1}^{K}\frac{n_{2i}CV_{2i}}{\sum_{i=1}^{K}n_{2i}}\right]^2}{n_2}\right), \qquad \text{(Equation 5)}$$

$$v(lnRR_3) = \frac{\left[\sum_{i=1}^{K}\frac{n_{1i}CV_{1i}}{\sum_{i=1}^{K}n_{1i}}\right]^2}{n_1} + \frac{\left[\sum_{i=1}^{K}\frac{n_{2i}CV_{2i}}{\sum_{i=1}^{K}n_{2i}}\right]^2}{n_2} + \frac{\left[\sum_{i=1}^{K}\frac{n_{1i}CV_{1i}}{\sum_{i=1}^{K}n_{1i}}\right]^4}{2n_1^2} + \frac{\left[\sum_{i=1}^{K}\frac{n_{2i}CV_{2i}}{\sum_{i=1}^{K}n_{2i}}\right]^4}{2n_2^2}, \qquad \text{(Equation 6)}$$

where $CV = s_d/m$ is the coefficient of variation; s_d and n are the corresponding SDs and sample size, respectively; CV_{1i} and CV_{2i} are the CVs from the ith study (study: i=1,2,…,K). The proposed Equations 3–5 can improve the accuracy and precision of the overall mean estimate. We can use Equations 5 and 6 to calculate the effect sizes and sample variances when SDs are missing, and use Equation 1 and 2 to calculate the effect size and sample variances when SDs are not missing. We use Equation 5 to calculate effect when the Data includes missing SDs, whereas use Equation 1 when the Data do not include missing SDs. We use lnRR as the response variable for different models except for path analyses described below.

Meta-regression

Meta-regression[162] was applied to test whether the effect sizes of different trophic groups could be explained by increasing fish species richness and the various predictor variables. Specifically, we fitted three-level mixed-effects meta-regression models, using the R package metafor (version 3.8-1). The effect size metric lnRR was calculated using the function "lnrr_laj()" in R.file implemented using the package "func.R" developed by Nakagawa et al.[161] This was used to calculate the effect size metric lnRR for each observation as well as the unbiased sample variance estimates as defined under Equation 6 (using the function "v_lnrr_laj()" in R.file "func.R"). Fish species richness, trophic groups, trophic group response categories, climatic zones, study types, and rice field types, were included as moderators whose effects were assumed to be fixed. We also constructed a null model without any predictors. In all models, we treated 'study identity' as a random effect (Data S1A and S1B). To handle non-independence in effect sizes of each study, we added a random effect as a unique identifier for each effect size in every study (EsID), which allows true effect sizes to vary within studies, and to account for the within-study effect and quantify within-study heterogeneity. To ensure robust estimates and account for differences in precision across studies and effect sizes, we weighted effect sizes by the inverse of the sum of the variance-covariance matrix components. This approach explicitly incorporates the non-zero covariances that arise from correlations in sampling variance within the same source articles, as well as from random-effect variance.[163] Phylogenetic correction for fishes was also undertaken to investigate the effects of fish species richness on trophic groups. To do this, fish species phylogenies were included as a random effect with phylogenetic relatedness as part of the correlation structure. Specifically, we matched the fish species included in our analysis with the available synthetic tree in the R package "rotl", then the relationships between each matched fish species were returned so that they could be used to draw phylogenetic trees. To adjust for repeated measurement of control values, we assigned the argument "V" in "rma.mv()" function with the sampling variance-covariance matrix estimated as follows in Equations 7–9[163]:

$$v_1 = \frac{\left[\sum_{i=1}^{K} \frac{n_{1i} CV_{1C,i}}{\sum_{i=1}^{K} n_{1C,i}}\right]^2}{n_{1C}} + \frac{\left[\sum_{i=1}^{K} \frac{n_{2i} CV_{1T,i}}{\sum_{i=1}^{K} n_{1T,i}}\right]^2}{n_{1T}} + \frac{\left[\sum_{i=1}^{K} \frac{n_{1i} CV_{1C,i}}{\sum_{i=1}^{K} n_{1C,i}}\right]^4}{2n_{1C}^2} + \frac{\left[\sum_{i=1}^{K} \frac{n_{2i} CV_{1T,i}}{\sum_{i=1}^{K} n_{1T,i}}\right]^4}{2n_{1T}^2}, \quad \text{(Equation 7)}$$

$$v_2 = \frac{\left[\sum_{i=1}^{K} \frac{n_{1i} CV_{1C,i}}{\sum_{i=1}^{K} n_{1C,i}}\right]^2}{n_{1C}} + \frac{\left[\sum_{i=1}^{K} \frac{n_{2i} CV_{2T,i}}{\sum_{i=1}^{K} n_{2T,i}}\right]^2}{n_{2T}} + \frac{\left[\sum_{i=1}^{K} \frac{n_{1i} CV_{1C,i,}}{\sum_{i=1}^{K} n_{1C,i}}\right]^4}{2n_{1C}^2} + \frac{\left[\sum_{i=1}^{K} \frac{n_{2i} CV_{2i}}{\sum_{i=1}^{K} n_{2T,i}}\right]^4}{2n_{2T}^2}, \quad \text{(Equation 8)}$$

$$v_{12} = \frac{\left[\sum_{i=1}^{K} \frac{n_{1i} CV_{1C,i}}{\sum_{i=1}^{K} n_{1C,i}}\right]^2}{n_{1C}} + \frac{\left[\sum_{i=1}^{K} \frac{n_{1i} CV_{1C,i}}{\sum_{i=1}^{K} n_{1C,i}}\right]^4}{2n_{1C}^2}, \quad \text{(Equation 9)}$$

where the subscripts $1T$ and $2T$ represent the different treatment group who share the control value in a same group; the subscript $1C$ represents the 1st control group; n represents the number of observations, CV represents the coefficients of variance of observed value. Taking this approach, 24 fish species defined the correlation structure based on the fish phylogeny (Data S1A and S1B).[164,165]

For each mixed-effects meta-regression model, we first fitted a base model by treating the number of added fish species and trophic group as the fixed effect terms. Second, the interactions between the trophic group and other predictor variables (climatic zones, study types, and rice field types) were also included in the model to assess whether model fit was improved, using a likelihood-ratio test (LRT). Third, the trophic group response category (nested within trophic group) and the interactive effects between the response category and predictors were also included in the model (using a LRT to allow model comparisons) (Data S1A). For example, the model with "trophic group + study type" was compared to the base model with just trophic group, and the model with "trophic group + trophic group × study type" would be compared to a model with "trophic group + study type" (Data S1A and S1B). To examine whether the mean effect sizes of (added) fish species, response category and other predictors differed significantly from zero, we acquired estimations with their 95% confidence intervals, which were derived from the fitted meta-regression models. To assess the between-study heterogeneity in these models, I^2 statistics were calculated[163,166,167] (Data S1A–S1F) and orchard plots[168] are presented in Figure S3.

Meta-regression models for model comparison and parameter evaluation

We performed meta-regression analysis using the R package metafor (version 3.8-1), in which we took log ratio response (lnRR) as the effect size measure (in the function "lnrr_laj()" in R.file "func.R" developed by Nakagawa et al.[161] Unbiased sample variance estimates were constructed to evaluate the variances of lnRRs (in the function "v_lnrr_laj()" in R.file "func.R"). To avoid the potential bias induced by repeated control values, we set the sampling covariance matrix according to Equations 7–9. We employed a likelihood ratio test to compare full model with null models to investigate the significance of the interactive effects between trophic groups or integrated trophic groups and various moderators. This refers to trophic groups (invertebrate herbivores, rice diseases, weeds, predators, parasitoid and rice), response categories (growth, reproduction and damage of herbivores; damage of rice diseases;

weed growth, reproduction; abundance of predators and parasitoid; and growth, reproduction and quality of rice) and different moderators (i.e. types of study, climatic zones, rice field types, and number of added fish species). The null model corresponded to the equation:

$$\beta_{ij} = \text{trophic groups} + r_i + w_{ij} + \varepsilon_{ij}.$$

The full model corresponded to the equation:

$$\beta_{ij} = \text{trophic groups} + \text{moderators} + r_i + w_{ij} + \varepsilon_{ij},$$

$$\beta_{ij} = \text{trophic groups} + \text{moderators} + \text{trophic groups} \times \text{moderators} + r_i + w_{ij} + \varepsilon_{ij},$$

where β_{ij} is the jth effect size of study i, r_i is the random effect that represents the heterogeneity between studies or the phylogenetic relatedness of the fish species within the ith study, and w_{ij} is the random effect that indicates the heterogeneity of the jth effect size within the ith study. In addition, ε_{ij} represents the random error term with variance equal to the lnRR's sample variance estimate.

In all cases, trophic group response categories were nested within trophic groups. For example, invertebrate herbivore response categories (i.e., herbivore growth, herbivore reproduction, and herbivore damage) were nested in the invertebrate herbivore group. See above for a description of these for each of the antagonists. Additionally, response categories of herbivore growth, herbivore reproduction, herbivore damage, rice disease, weed growth, weed reproduction, predator abundance, and parasitoid abundance were nested into the overall pest grouping. Using this approach, relevant response category effects could have an impact on the corresponding trophic group effect.

We applied the likelihood ratio tests (LRT) to test the null model with the full model to explore the interactions between the trophic group response categories (herbivore growth, herbivore reproduction, herbivore damage, rice disease, weed growth, weed reproduction, predator abundance, parasitoid abundance, rice growth, rice reproduction, rice quality, pest) and the different moderators. The null model was as follows:

$$\beta_{ij} = \text{trophic group response categories} + r_i + w_{ij} + \varepsilon_{ij}.$$

The full model followed the equation:

$$\beta_{ij} = \text{trophic group response categories} + \text{moderators} + r_i + w_{ij} + \varepsilon_{ij},$$

$$\beta_{ij} = \text{trophic group response categories} + \text{moderators} + \text{trophic group response category} \times \text{moderators} + r_i + w_{ij} + \varepsilon_{ij}.$$

Subsequently, to estimate the effects and their corresponding confidence intervals of each trophic group, trophic group response category and their associations with the moderators, the following models were used:

$$\beta_{ij} = \text{trophic groups} + r_i + w_{ij} + \varepsilon_{ij},$$

$$\beta_{ij} = \text{trophic groups} + \text{moderators} + r_i + w_{ij} + \varepsilon_{ij},$$

$$\beta_{ij} = \text{trophic groups} + \text{moderators} + \text{trophic groups} \times \text{moderators} + r_i + w_{ij} + \varepsilon_{ij},$$

$$\beta_{ij} = \text{trophic group response categories} + r_i + w_{ij} + \varepsilon_{ij},$$

$$\beta_{ij} = \text{trophic group response categories} + \text{moderators} + r_i + w_{ij} + \varepsilon_{ij},$$

$$\beta_{ij} = \text{trophic group response categories} + \text{moderators} + \text{trophic group response category} \times \text{moderators} + r_i + w_{ij} + \varepsilon_{ij}.$$

Phylogenetic covariance structures for fish

Phylogenetic relationships between the species have the potential to bias the meta-analysis, as closely related species show greater commonality in their responses to increasing fish species, affecting assumptions of independence. However, accounting for this within the current modelling framework required us to focus on only those lnRR effect sizes that were based on a comparison of single species monoculture controls compared to a higher species treatment. For this sub-set of the data, it would be possible to identify where phylogenetic similarities between species in monocultures affected the overall community response to further increases in fish species, either for rice or pest performance. From the 113 articles, we obtained 791 observations from 466 articles that had a single species control from which the lnRR effect size was derived. Within this Data, the control groups included 24 fish species. We generated a phylogeny for these fish species based on a mega-tree of 74,531 species of extant vascular plants representing the largest phylogeny for vascular plants as implemented in rotl.[169] All 24 fish species were represented in this overall phylogeny. Following this, the potential effect of fish species was accounted for in all models by i) adding random intercepts for fish species identity, and ii) including the phylogenetic relatedness between fish species as part of the correlation structure.[170] Furthermore, each effect size was nested within the corresponding study to incorporate the hierarchical error structure of multiple effects coming from the same study.

Regression analysis of the number of added fish species

To examine whether the number of added fish species had additional explanatory variance for each trophic group, we ran further analyses using the logarithm of the number of fish species added between the control and the treatments from which the lnRR effect size was derived, e.g., $\log_2(1, 2, 3, \ldots)$. Next, we analyzed the relationships between the number of added fish species and the different effect sizes along with fitted meta-regression lines (Data S1M). In these meta-regression analyses, we considered the number of added fish species as a predictor and lnRR as the response to display the trend of lnRR with the number of added fish species. The "lme()" function in the "nlme" (version 3.1-162) library in the R statistical environment will be used to fit a linear model using generalized least squares.[51] Between-study heterogeneity will be explained in models using the function setting "random = list(~1|Code)" in the call to lme(). The R function "rsq.lmm()" in the "rsq" (version 2.5) library[171] to calculate R-square from the model object. Subsequently, we used the R function "Effect()" in the "effects" library[172] to calculate predicted values from the model object and a 95% confidence interval of the predicted values.

Meta-analytic path analysis via residual regressions

In this study, we focused specifically on comparing the ecological impacts of rice-fish coculture versus rice monoculture systems, examining how the presence or absence of fish influences trophic groups and their interactions within paddy fields. We did not explicitly investigate the interactive effects of crop diversification (e.g., rice varietal mixtures) and rice-fish coculture on trophic groups and their interactions. To explore the trophic interactions between plants and various groups of pests, we established a new data subset: i) comprising paired trophic observations (i.e., rice performance vs. herbivore performance, rice performance vs. rice disease performance, rice performance vs. weed performance, and rice performance vs. pest performance); ii) encompassing the paired observations of rice performance vs. pest performance in different climate zones, rice field types and study types (Data S1J); and iii) and comprising the paired observations of rice performance vs. herbivore performance vs. natural enemy performance (Data S1H). The lnRR effect sizes were derived from these pairwise data sets.

To analyze the direct effect of pests on rice performance in path analysis, residual regression was applied. In this analysis, we used the lnRR as the response variable. Specifically, the direct effects of increasing fish species on pests were estimated using a linear mixed-effects model:

$$\text{pest performance lnRR}_{ij} = \beta + r_i + \varepsilon_{ij}.$$

Following Emmenegger & Bühlmann.[173] The direct effect of fish species on rice performance was estimated by regressing the Pearson residuals of the linear mixed-effects model:

$$\text{rice performance lnRR}_{\text{ij}} = \beta \times \text{pest performance lnRR}_{ij} + r_i + \varepsilon_{ij}$$

on fish species. The direct effects of pests on rice were estimated by regressing the Pearson residuals extracted from the linear mixed-effects model:

$$\text{rice performance lnRR}_{ij} = \beta + r_i + \varepsilon_{ij}$$

on the Pearson residuals extracted from the linear mixed-effects model:

$$\text{pest performance lnRR}_{ij} = \beta + r_i + \varepsilon_{ij},$$

where β is the effect size, r_i is the random effect representing the heterogeneity between studies or the phylogenetic relatedness of the fish species within the ith study, and ε_{ij} is the random error term with variance equal to the lnRR's sample variance estimate.

We did the above path analysis to understand the relative effect of i) increasing fish species on the performance of the overall animal community, ii) the performance of the pest, and iii) the indirect effect on rice performance resulting from the response by the pest to increasing fish species. Specifically, the following models were constructed as input to residual regressions, and the β_0 and β_1 below were the effect of fish species and the effect of added fish species, respectively:

*Fish species/number of added fish richness–pest performance– rice performance (*Figure 3A*)*

a1. rice performance lnRR =

$$\beta_0 + \beta_1 \times \log_2(\text{the number of added fish species}) + r_i + w_{ij} + \varepsilon_{ij}.$$

a2. pest performance lnRR =

$$\beta_0 + \beta_1 \times \log_2(\text{the number of added fish species}) + r_i + w_{ij} + \varepsilon_{ij}.$$

Fish species / number of added fish species– invertebrate herbivore performance– rice performance

b1. rice performance lnRR =

$$\beta_0 + \beta_1 \times \log_2(\text{the number of added fish species}) + r_i + w_{ij} + \varepsilon_{ij}.$$

b2. invertebrate herbivore lnRR $= \beta_0 + \beta_1 \times \log_2(\text{the number of added fish species}) + r_i + w_{ij} + \varepsilon_{ij}.$

Fish species / number of added fish species – rice disease performance– rice performance

c1. rice performance lnRR =

$$\beta_0 + \beta_1 \times \log_2(\text{the number of added fish species}) + r_i + w_{ij} + \varepsilon_{ij}.$$

c3. rice disease performance lnRR =

$$\beta_0 + \beta_1 \times \log_2(\text{the number of added fish species}) + r_i + w_{ij} + \varepsilon_{ij}.$$

Fish species / number of added fish species– weeds performance– rice performance

d1. rice performance lnRR =

$$\beta_0 + \beta_1 \times \log_2(\text{the number of added fish species}) + r_i + w_{ij} + \varepsilon_{ij}.$$

d2. weeds performance lnRR =

$$\beta_0 + \beta_1 \times \log_2(\text{the number of added fish species}) + r_i + w_{ij} + \varepsilon_{ij}.$$

Fish species / number of added fish species– natural enemy performance– rice performance

e1. rice performance lnRR =

$$\beta_0 + \beta_1 \times \log_2(\text{the number of added fish species}) + r_i + w_{ij} + \varepsilon_{ij}.$$

e2. natural enemy lnRR =

$$\beta_0 + \beta_1 \times \log_2(\text{the number of added fish species}) + r_i + w_{ij} + \varepsilon_{ij}.$$

Fish species / number of added fish species– pest performance– rice performance in plot experiments, pot experiments, organic rice field, non-organic rice field, temperate climatic zones, tropical climatic zones respectively

f1. rice performance lnRR in different subgroups =

$$\beta_0 + \beta_1 \times \log_2(\text{the number of added fish species}) + r_i + w_{ij} + \varepsilon_{ij}.$$

f2. pest performance lnRR in different subgroups =

$$\beta_0 + \beta_1 \times \log_2(\text{the number of added fish species}) + r_i + w_{ij} + \varepsilon_{ij}.$$

In summary, for our path analyses, linear mixed-effects models were conducted with the R function “lme” of the package “nlme”, with random intercepts for study IDs. Heteroscedasticity was accounted for by providing fixed variances based on lnRRs and setting sigma to 1 in the lme call.

We applied Student’s t-tests to assess statistical significance within the path analysis for each of the above equations. A significant positive intercept shows that increasing the number of fish species increases the mean value of the pest performance or rice performance for a trophic group, and a negative intercept shows the reverse (Data S1H). We extracted the z-values of corresponding coefficients to test the effects of fish species on rice and different groups of pests (i.e., herbivores vs. rice, rice disease vs. rice, weeds vs. rice, and natural enemies vs. plants) (Data S1H). Likewise, we extracted the *z*-values of corresponding coefficients to test the effects of fish species on the interactions between performance values of rice and the aggregate indicator (i.e., pests) in different climatic zones (temperate and tropical zones - excluding greenhouse or indoor observations), study types (plot and pot experiments), and rice field type (organic and non-organic rice field), respectively. We explored the effects of number of added plant species relative to the control by constructing various models to explore the direct and indirect effects of added fish species on interactions (Data S1H). Likewise, we conducted the direct and indirect effects of the number of added fish species on rice and pests distinguishing between climatic zones, rice field type and in study type (Data S1J). The estimations and test statistics were extracted using the R function “coef()” (Data S1H and S1J). The relative goodness-of-fit analyses for path analyses of predictor variables (fish species), were conducted by extracting AIC (Akaike information criterion), AICc (corrected Akaike information criterion), BIC (Bayesian information criterion) and log-likelihood from the fitted models, using R functions “AIC()”, “AICc()”, “BIC()” and “logLik()” from the rsq package (version 2.5)[174] (Data S1K).

In the above path analysis for top-down effects in bi-trophic, we used mediation analysis to test whether the effect of an independent variable RF (i.e., rice-fish coculture vs. rice monoculture) on a dependent variable Y’ (i.e., herbivore performance, including herbivore damage and reproduction) (RF→Y’) is at least partly explained via the inclusion of a mediator variable X’ (i.e., pest performance, including herbivore damage, herbivore reproduction, disease damage, predator and parasitoid abundance) (RF→X’→Y’). In our top-down analysis, the 3 causal paths E1, E2 and E3 correspond to the effect of rice-fish coculture on pest performance, the effect of pest performance on rice performance, and the effect of rice-fish coculture on rice performance accounting for pest performance, respectively. The three causal paths correspond to parameters from two regression models, one in which pest performance is the outcome and rice-fish coculture is the predictor, one in which rice performance is the outcome and rice-fish coculture and pest performance are the simultaneous predictors, and one in which rice performance is the outcome and rice-fish coculture is the predictor. From these parameters, we can calculate the mediation effect (the product E1×E2) and total effect (E1×E2+E3) of rice-fish coculture on rice performance. In tri-trophic, we test whether the effect of an independent variable RF (i.e., rice-fish coculture vs. rice monoculture) on a dependent variable Y (i.e., herbivore performance, including herbivore damage and reproduction) (RF→Y) is at

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least partly explained via the inclusion of a mediator variable X (i.e., natural enemy performance, including predator and parasitoid abundance) (RF→X→Y). The effect of an independent variable RF on a dependent variable Z (i.e., rice performance, including rice growth, reproduction, and quality) is at least partly explained via the inclusion of a mediator variable Y (RF→Y→Z). In our top-down analysis, the five causal paths e1, e2, e3, e4, and e5 correspond to the effect of rice-fish coculture on natural enemy performance, the effect of natural enemy performance on herbivore performance, the effect of rice-fish coculture on herbivore performance accounting for natural enemy performance, the effect of herbivore performance on rice performance and the effect of rice-fish coculture on rice performance accounting for herbivore performance, respectively. The five causal paths correspond to parameters from three regression models, one in which natural enemy performance is the outcome and rice-fish coculture is the predictor, on in which herbivore performance is the outcome and rice-fish coculture and natural enemy performance are the simultaneous predictors, one in which rice performance is the outcome and herbivore performance is the predictors and one in which rice performance is the outcome and rice-fish coculture and herbivore performance are the simultaneous predictors. From these parameters, we can calculate the mediation effect (the product e2×e3 and e3×e4) and total effect (e2×e3+ e1) of rice-fish coculture on herbivore performance and total effect (e3×e4+ e5) of rice-fish coculture on rice performance (Figure S1).

Publication bias test

We assessed publication bias using regression tests[175,176] (Data S1B), which employ a partial slope test of association between effect size and the sample size. Here, a significant relationship ($p<0.05$) suggests publication bias. The trim-and-fill method was not employed as this is inappropriate for models with moderators.[177,178] Instead, we adopted the method suggested by Nakagawa et al.,[177] which uses a multilevel version of Egger regression to assess publication bias in mixed-effects meta-regression analysis. Following this approach, we fitted the following model to assess publication bias:

$$\text{lnRR}_{ij} = \beta_0 \times \text{trophic groups} + \beta_1 \times \text{sampling size}_{ij} + r_i + w_{ij} + \varepsilon_{ij}.$$

Here, we considered lnRR as a response variable. Different categories of trophic groups, climatic zones, study type, and rice field types were considered as predictors, respectively, and sampling sizes were considered as an additional moderator in the mixed-effect model, and the test statistics for the coefficients of sampling sizes were used to test for publication bias. As a result, publication bias was assessed for all models by testing H_0: $\beta_1 = 0$ (Data S1B). The Egger's regression test showed that there was publication bias for the 791 observations of the 113 cited articles in this paper (value of regression test=-0.967, P=0.334). We also derived the fail-safe N test to calculate the number of null-result studies that would have to be added to reduce the combined significance level (p-value) to a 0.05 alpha level. This fail-safe number can then be compared to a rule-of-thumb threshold, defined for this study to be 3965 (based on $5n + 10$, where n is the number of observations in the analyses considered to be 791). This derived the fail-safe number of 17139 for the whole Data of 113 cited articles. This means that at least 17139 studies with negative effects would be needed to be incorporated in our Data to result in a non-significant overall effect. This provides strong evidence that the results in this paper are stable for publication bias.

Field experiment design

Field experiment was performed at Situan Town, Fengxian District, Shanghai of China (30.94°N, 121.71°E). This site belongs to alluvial plains of the Yangtze River Delta in the east Asian monsoon zone with four distinctive seasons. The whole area of rice fields was about 46.7 ha. The field experiment followed a randomized complete block design with three replicates. Each block consisted of one treatment plot (rice-fish *Carassius auratus* coculture; 90m×150m) surrounded on three sides by three ditches (0.7-0.9m in depth and 0.9m in width), and a control plot (rice monoculture; 90m×150m) without ditches or fish. Blocks were spaced >50m apart to prevent spill-over effects among blocks. Two plots within each block were separated by >50m of buffer zone. Plots were established in late May 2020 when ditches of coculture plots were filled with irrigation water. A field experiment was performed from 2021 to 2024.

In each year in late May, a late maturing variety of rice (Huruan 1212) was mechanically dibbled (cluster spacing was 16 cm × 25 cm) and seeded at 60 $\text{kg}\cdot\text{ha}^{-1}$. Each year plots received 15.0 $\text{ton}\cdot\text{ha}^{-1}$ of organic fertilizers as the base fertilizer in middle-to-late May, 225 $\text{kg}\cdot\text{ha}^{-1}$ of compound fertilizer (N: P_2O_5: K_2O=15: 15: 15) at the seedling stage (early-to-middle June), 225 $\text{kg}\cdot\text{ha}^{-1}$ of compound fertilizer (N: P_2O_5: K_2O=15: 15: 15) at the tillering stage (late June), and 180 $\text{kg}\cdot\text{ha}^{-1}$ of compound fertilizer (N: P_2O_5: K_2O=15: 15: 15) at the booting stage (middle August).

During this experiment period from 2021 to 2024, to control rice disease and insect pests, each plot in each year received the same amount of the 24% Validamycin A Water Suspension (0.600$\text{kg}\cdot\text{ha}^{-1}$), 25% clothianidin water dispersible granules (0.300$\text{kg}\cdot\text{ha}^{-1}$), and 16% methiocarb-indoxacarb suspension concentrate (0.225 $\text{kg}\cdot\text{ha}^{-1}$). Weeds were removed by hand. Note that the application of these products was implemented to achieve consistency between treatments, but normal threshold-based practices for pesticide application were in operation in this system under non-experimental conditions (See Wan et al.[30]).

For each rice-fish coculture plot in late May 2020, when coculture plots were established, 1000 *Carassius auratus* (0.10 to 0.15 kg each) were released into the three surrounding ditches. Fish were not fed supplemental food to promote fish feeding on insect pests. To create ideal conditions for rice and fish growth, irrigation depth was maintained at 10–15 cm above the base of rice plants in coculture plots during the rice seedling stage; this avoided negative effects of flooding during the rice seedling stage and allowed small fish to move freely in rice fields. At the beginning of the tillering stage, as the abundance of insect pests and damage increased, irrigation depth was increased to 15–20 cm above the base of rice plants in coculture plots, to provide a more suitable environment (i.e., sufficient water, enough activity space, reduced water temperature) for fish to prey on insect pests. In rice monoculture plots, the depth

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of irrigation water was maintained at 3–5 cm. Irrigation was stopped 1 week before harvest for both plot types. Harvest operations were conducted in mid-to-late October in each year from 2021 to 2024. In each rice plot, we collected the rice ears using a ‘‘Z-style’’ sampling method with 10 dots (20 rice ears in each dot were randomly selected). Ears were dried in the sun for 5 days, threshed to separate the ears into individual grains, and 1,000 grains were weighed to determine thousand kernel weight. Then a harvester was used to obtain the grain yield in each plot.

Insect pests and invertebrate predators were collected from 100 randomly selected rice clusters in each plot. Only three groups of rice insect pests (i.e., planthoppers, stemborers and leafrollers), which represented the main insect pests on rice in eastern China,[179] were sampled as target insect pests. As predatory spiders accounted for more than 90% of natural enemies and played an important role in pest control in rice fields,[180] we sampled only spiders as target predators to test our hypothesis.

Insect pests and invertebrate predators were sampled at 2–4 week intervals from the seedling to maturity stages (i.e., from early-to-mid July to early-to-mid September each year), for a total of four sampling times per year. To sample, a white stainless-steel plate was placed at the base of rice plants[179] then rice plants were shaken so that insect pests and invertebrate predators fell onto the plate and were counted. To further investigate the abundance of stemborers and leafrollers, we checked for infested rice stems and foliage for each sampled plant and counted the stemborers and leafrollers. Thus, the abundance of rice stemborers or leafrollers at each sampling was the sum from the plate and from the infested stems or leaves.[179]

Behaviour experiment

To further explain above mechanisms, we conducted a behaviour experiment to test the predatory effect of fish on spiders and rice planthoppers, by using records of a video camera in 2025. We used two fish species: one is an indigenous, red, soft-scaled, common species of carp (Oujiang color common carp, *Cyprinus carpio* var. *Qingtianensis*) from Qingtian which is a ‘‘globally important agricultural heritage system’’ (GIAHS) as designated by the United Nations Development Program and the Global Environment Facility in 2005,[19] and the other is a native species (crucian carp, *Carassius auratus*) from Situan, Shanghai, China (see above field experiment). We used the wolf spider (*Pardosa pseudoannulata*), collected from Jinggangshan Agricultural Science and Technology Park, Xingqiao Town, Jizhou District, Ji’an City, Jiangxi Province, China (27.14°N, 114.88°E) (provided by the research team of Professor Yonghong Xiao, Jinggangshan University, China) as this species was the most important dominant spider species in China’s rice fields.[181] High-quality fragrant japonica rice variety ‘‘Huxiangjing 106’’ was used, as this variety has relatively weak resistance to brown planthopper (*Nilaparvata lugens*), provided by Professor Jinglan Liu at Yangzhou University of China. Oujiang color common carps and crucian carps (body weight: 250–300g) were acclimated in an indoor recirculating aquaculture system for 7 days prior to the experiment and subjected to a 5-day fasting period to standardize their hunger levels and stimulate natural foraging motivation.

Rice seedlings were planted in pots. The potting container was a cylindrical plastic pot with a top diameter of 44 cm, a bottom diameter of 37 cm, and a height of 52 cm. Each pot was filled with 25 kg of paddy field soil that has been air-dried, crushed and sieved. The base fertilizer was compound fertilizer (N: P_2O_5: K_2O=15: 15: 15) at 8.33g·kg^{-1} of soil. When seedlings were at the three-leaf and one-heart stages, we transplant them into above pots. We planted 1 hill of rice seedlings (2 seedlings per hill) in the center of each pot. During the growth period of rice, regular water management should be carried out and the use of any pesticides should be avoided. We selected potted rice plants at the heading stage that were vigorous and have uniform growth. To ensure the water was clear and facilitate subsequent observation and video recording, evenly cover the surface of each pot of soil with a 2 cm thick layer of aquatic plant mud (Nitley, particle size 1-4mm). This material could effectively adsorb suspended particles, prevent fish activities from muddying the water body, and was non-toxic and harmless to aquatic organisms. We slowly filled the basin with water until the water depth remained at 10 cm, and then installed the video camera properly. In each experimental pot, we ushered 10, 20, or 30 third-instar brown planthoppers, or 3 female spiders, or 3 male spiders, respectively. Namely, 10, 20, or 30 third-instar brown planthoppers in each pot together with a fish, and 3 female spiders or 3 male spiders in each pot together with a fish.[182]

After the prey (planthoppers and spiders) were evenly distributed in the pots, we carefully placed one Oujiang color common carp or one crucian carp that had been starved for continuous five days in one pot. Then the camera was immediately activated to start recording the behavior of fish preying on rice planthoppers and spiders. If rice plants were planted in clusters within the pots, the spiders and rice planthoppers introduced will affect the camera’s view due to their presence on the rice stems. Therefore, the leaves of the rice plants in the pots should be removed and only the main stems should be retained to record the fish predation activity. The video recording lasts for 20 minutes, and each processing was repeated 5 times. No one needed to be present during the recording to avoid interference to fish activity (Videos S1–S4). After the finish of recording, we carefully collected and counted the number of all surviving brown planthoppers and spiders, and then calculated the predation percentage of fish on planthoppers or spiders. Predation percentage was the number of planthoppers or spiders eaten by fish in a pot divided by the ushered number of planthoppers or spiders in a pot × 100% (Data S5C).

QUANTIFICATION AND STATISTICAL ANALYSIS

Meta-regression and path analysis

We used R version 4.3.1[49] to conduct all statistical analyses, and used R package ‘‘metafor’’ 3.8-1 to perform meta-regression and publication bias assessment.[50] In addition, we used R packages ‘‘nlme’’[51]] and ‘‘piecewiseSEM’’[52] to residual regression in path analyses. A significance level of 0.05 was used for all tests.

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Sensitivity analysis

We applied the trim and fill method to test the sensitivity. The trim and fill method is a nonparametric (rank-based) data augmentation technique proposed by Duval & Tweedie.[177] The method can be used to evaluate the number of studies missing from a meta-analysis based on the suppression of the most extreme results seen on one side of the funnel plot (Figure S2). The method then augments the observed data so that the funnel plot is symmetric and recomputes the summary estimate based on this derived data. Statistical values for this sensitivity analysis are presented for the different taxonomic groups of pest performance, invertebrate herbivore performance, rice disease performance, weed performance, natural enemy performance and rice performance from the overall 113 studies (Data S1L).

Data analysis for field experiment

Normality and homoscedasticity of all data were assessed by Kolmogorov–Smirnov and Levene's tests. ANOVAs were used to test fixed effects of rice field type (rice-fish coculture and rice monoculture), experimental year (2021, 2022, 2023 and 2024), and their interaction, sampling period (1 to 4 within a year) and the interaction of treatment × year × period, and random effect plot (treatment) on: abundance of herbivores (i.e., planthoppers, stemborers and leafrollers) and predatory spiders. Experimental year (2021, 2022, 2023, and 2024) and experiment sample period (1 to 4 within a year) were considered independent factors. Models without terms related to sampling period were used for rice thousand kernel weight and rice yield. Adjusted means contrasts were used to compare the differences among means for predictors with more than two combinations or levels. If the values of herbivore or spider abundance were significantly affected by the years, we considered the four years' data separately to compare the differences among means of rice monoculture and rice-fish coculture with Tukey's Honestly Significant Difference (HSD) test at the 0.05 leve (Data S5A and S5B). We use "aov()" function to conduct a two-way ANOVA analysis, with term "abundance $\sim$ year * treatment" in R. In terms of path analysis, we used structural equation model to do this.

Data analysis for behaviour experiment

We employed a two-way ANOVA under a general linear model framework to assess predation rates, examining the interactive effects of fish species (common carp vs. crucian carp) and planthopper density (10, 20, or 30 third-instar brown planthoppers) (Data S5C). We used "aov()" function to conduct two-way ANOVA analyse, with term "predation rate $\sim$ year * treatment" in R. Post hoc comparisons of means were performed using Tukey's HSD test (α=0.05), with Bonferroni correction for multiple testing. Prior to ANOVA, predation percentage data underwent arcsine-square root transformation to meet parametric assumptions.