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A meta-analysis of ecological functions and economic benefits of co-culture models in paddy fields

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ABSTRACT

The co-culture of rice and poultry/aquatic animals has become a popular strategy to ensure the critical ecological functions and economic benefits of this ecosystem in recent years. Yet, quantitative synthetic effects of co-culture models on ecological functions and economic benefits in paddy fields are poorly understood. This study conducted a meta-analysis of 4707 observations from 224 published papers on the outcomes of co-culture models in paddy fields. On aggregate, co-culture models significantly reduced CH_4 emissions by 14.8 % as compared with rice monoculture, but did not affect rice yields, N_2O emissions, and greenhouse gas intensity (GHGI). However, significant differences in rice yields, CH_4 emissions, GHGI, and economic benefits were observed among various co-culture models and rice-growing regions. Particularly, the co-culture models in East Asia significantly increased rice yields (+2.2 %), reduced CH_4 emissions (–22.1 %), and GHGI (–9.4 %). Importantly, co-culture models improved rice grain quality. Furthermore, co-culture models increased soil fertility (7.8–16.2 %), nutrients content in paddy water (26.2–87.0 %), and net ecological and economic benefits (31.7–71.1 %), while decreasing diseases, pests, and weeds (37.0–84.6 %) in paddy fields. Additionally, we suggest that the production of poultry or aquatic animals that alters input and output would increase net income, and it is necessary to develop co-culture models in paddy fields according to regional differences in the agricultural environment. Therefore, our study provides a reference for maximizing ecological and economic benefits of suitable co-culture models in rice-planted areas.

1. Introduction

Food security is becoming a global challenge due to the stagnation in net cultivated areas, the shortage of water resources, and the dramatic increase in population (Godfray et al., 2010; MacDonald, 2010). Rice production is a key component of global food security because paddy provides the staple food for more than half of the world's population, including almost all East and Southeast Asians (Alexandratos and Bruinsma, 2012; Khoshnevisan et al., 2021). In recent decades, rice yields with the monoculture model have substantially increased, mainly resulting from the use of nitrogen (N) fertilizers and pesticides, the breeding of new crop cultivars, and the advanced field management (Tilman et al., 2011; Jiang et al., 2017). However, this rice monoculture model with higher applications of fertilizers and pesticides negatively

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affects the environment of the agriculture system, such as non-point source pollution, soil fertility decline, and rice quality reduction (Xia et al., 2016; Zheng et al., 2017). Moreover, with the increasing demand for poultry or aquatic animals, the co-culture models integrated by rice monoculture and freshwater aquaculture are prosperous in recent decades, which is another key component of global food security by providing rich protein (Datta et al., 2009; Mohanty et al., 2009; Xie et al., 2011).

These co-culture models in rice fields are ancient agricultural production patterns and have been practiced from time immemorial (Zheng et al., 2017), such as rice-fish, rice-duck, rice-crayfish, rice-crab, and rice-turtle (Fig. 1a). For example, in China's mainland, co-culture models covered an area of more than 2.53 million hm^2 in 2020, accounting for 8.4 % of the total paddy field area, and this concept continues to be a rapidly increasing trend (Zeng, 2020). Importantly, this integrated production optimizes resource utilization through the complementary use of land and water, but also provides various socioeconomic and environmental benefits. As a consequence, such a co-culture model should be widely practiced in paddy fields with their abundant water sources. Based on our knowledge on the response of ecological functions and economic benefits to co-culture models in rice fields, we developed a conceptual scheme that presents the effects of co-culture models on soil parameters, water qualities, production status, and pests control (Fig. 1b). Indeed, co-culture models in paddy fields have been considered as an efficient way to produce poultry/aquatic animals and rice as well as to significantly improve soil qualities and reduce N fertilization (Hu et al., 2013; Yuan et al., 2020). Rice-crab, for instance, can produce higher crab yield and achieve low N fertilizer input and low N effluent (Hu et al., 2020). Therefore, the aims of developing co-culture models in paddy fields are to enhance production efficiency, reduce resource use, and improve environmental quality through increased recycling of nutrients and matter (Berg, 2002; Xu et al., 2022).

Although co-culture models in paddy fields have been demonstrated successfully and a considerable number of farmers have been trained through various projects, this integration still leads to environmental pollution risks due to the increased nutrient content of paddy water and a large amount of feed and animal manure input (Frei and Becker, 2005; Datta et al., 2009; Berg and Nguyen Thanh, 2018; Yi, 2019; Gao et al., 2020; Jin et al., 2020; Xu et al., 2021). Furthermore, former studies on co-culture models in paddy fields mostly involved unilateral studies on ecological functions and economic benefits with little relevant literature to comprehensively analyze the effects of integrated farming of rice and fish on all aspects above (Sun et al., 2021). Ecological rice-cropping models reduced CH_4 emissions but increased N_2O emissions, which were significantly correlated with increasing water dissolved oxygen (WDO) concentration in the flood water, as well as increasing soil redox

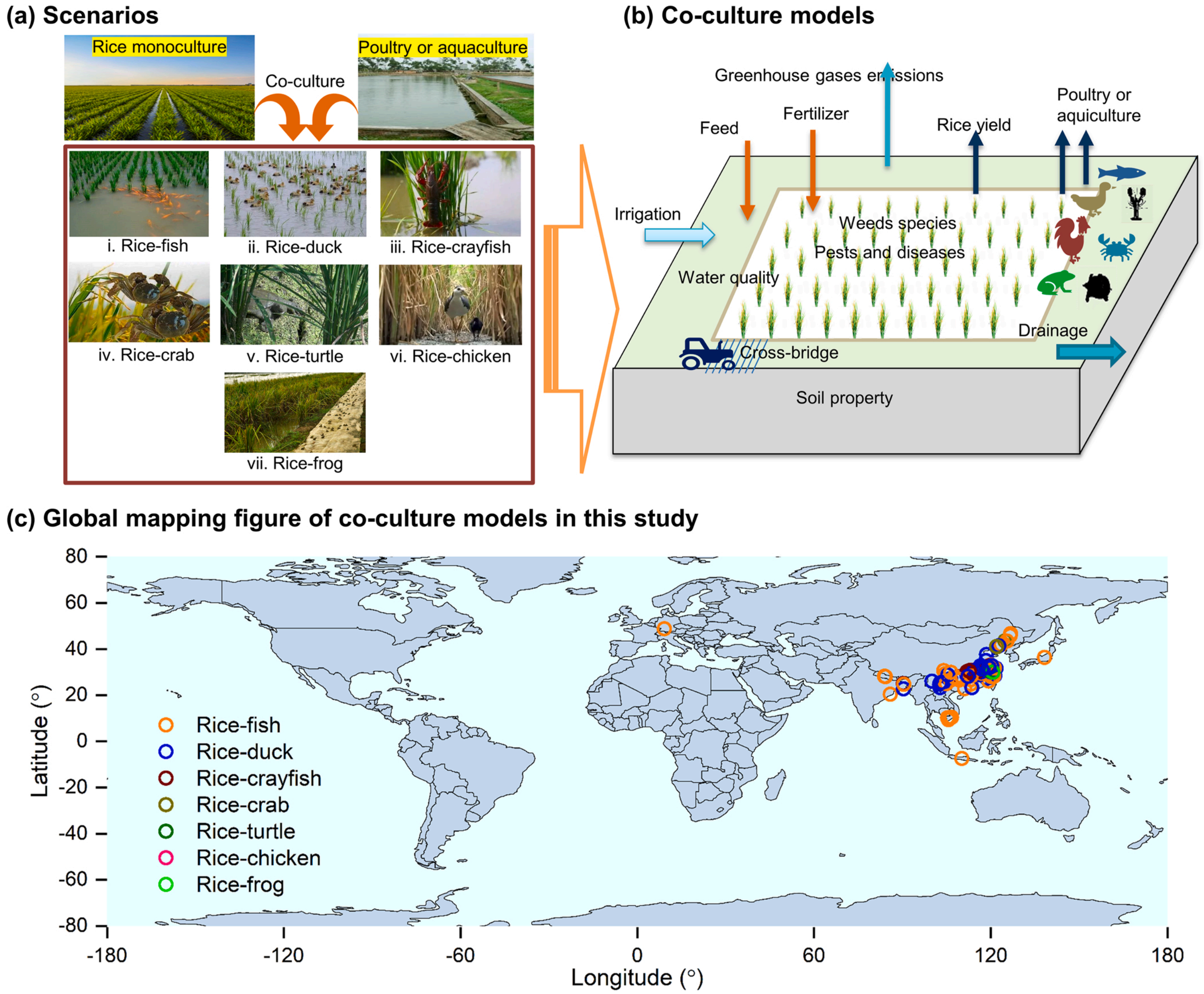

Fig. 1. Main scenarios (a), conceptual scheme (b), and global distributions (c) of co-culture models in this study.

potential (Eh), dissolved organic carbon (DOC) content, and available N (AN) content (Chen et al., 2021; Sun et al., 2021). However, the percentage change of soil properties, rice grain qualities, and biodiversity in co-culture models have not been quantitatively assessed. Moreover, the relationship between ecological functions and economic benefits of co-culture models with their controlling factors (e.g., plant parameters, soil properties, pests control rates) are generally neglected (Oehme et al., 2007). Therefore, it is of great significance to comprehensively analyze the ecological and environmental benefits of co-culture models in paddy fields for sustainable agriculture production and development.

Here, we conduct a meta-analysis to determine the effect of co-culture models on 1) soil properties, 2) water qualities, 3) diseases, pests, and weeds, and 4) ecological and economic benefits from 224 published papers (up to October 31, 2021, see Dataset), to provide a measure for quantitative estimation of ecological functions and economic benefits of co-culture models in paddy fields. Our objective was to address two important questions: 1) how do the various co-culture models influence ecological functions and economic benefits in different geographic regions compared to the rice monoculture system? and 2) what are the potential factors driving these effects of co-culture models on ecological functions and economic benefits?

2. Materials and methods

2.1. Data collection

Information about soil properties, water qualities, plant parameters, diseases, pests, weed species, and economic position associated with co-culture models in paddy fields was retrieved from the Web of Science (http://apps.webofknowledge.com/) and China National Knowledge Infrastructure databases (http://www.cnki.net/).

The following keywords were used for the preparation of the database: the co-culture model (rice-fish, rice-duck, rice-crayfish, rice-crab, rice-turtle, rice-chicken, and rice-frog), soil property (soil fertility, soil physical, chemical, and biological properties), greenhouse gas emissions (CH_4 emissions, N_2O emissions, global warming potential (GWP), and greenhouse gas emission intensity (GHGI)), water quality, plant parameter (grain yield, yield components, and grain quality), diseases, pests and weeds species, economic position (input, output, income, the ratio of output and input, and the economic and ecological benefits), and rice paddy (rice, paddy, rice field, and paddy field). The following criteria were systematically used to narrow down appropriate studies: 1) the experimental design must include a rice monoculture model as a control; 2) when considering the multiple effects of co-culture models in paddy fields, at least one of the target variables (soil property, greenhouse gas emissions, water quality, plant parameter, diseases, pests, and weeds species, and economic position) were reported; 3) *details on the experimental design, geographic distribution, and climatic conditions must be provided to enable the comprehensive analysis of published data;* 4) when different publications included the same data from one study, we recorded the data only once; 5) when a study included two or more co-culture models, we considered them distinct observations. The suitable data and related experimental information were extracted directly from tables and text, or indirectly from figures using GetData Graph Digitizer 2.22. Finally, 4707 observations were obtained from an overall of 224 studies (Text S1). The geographic distribution of the experimental sites is shown in Fig. 1c.

2.2. Meta-analysis

The meta-analysis was conducted as described by Hedges et al. (1999). *The effects of co-culture models on each variable (X) were quantified according to the natural log-transformed response ratio (Ln R) using the following equation* (Xia et al., 2021):

$$Ln\ \mathrm{R} = Ln\ (\mathrm{X}_{CS} / \mathrm{X}_{RM}) \tag{1}$$

where X_{CS} *and* X_{RM} *represent the mean of the co-culture model and the rice monoculture model for the variable* X*, respectively. The results are presented as the percentage of changes ((*R*–1)* × *100) in the variables in co-culture models. Positive percentage changes denote an increase due to co-culture whereas negative values indicate a decrease in the respective variables.*

In this meta-analysis, we adopted a function of the sample size of Xia et al. (2017) and Yu et al. (2022) to weight effects sizes. The equation was as follows, where N_{CS} and N_{RM} denoted the number of replicates of the co-culture model and the rice monoculture model, respectively:

$$Weight = (N_{\mathrm{CS}} \times N_{\mathrm{RM}}) / \ (N_{\mathrm{CS}} + N_{\mathrm{RM}}) \tag{2}$$

Mean effect sizes and 95 % confidence intervals (*CIs*) were generated by a bootstrapping procedure with 4999 iterations, using MetaWin 2.0 (Rosenberg et al., 2000). The means of the categorical variables were significantly different from each other if their 95 % *CIs* did not overlap.

3. Results

3.1. Rice yields and greenhouse gas emissions as affected by co-culture models

The average value of all observations showed that when compared with the rice monoculture model, co-culture models had no effect on rice yields, N_2O emissions, and GHGI ($P > 0.05$), but decreased CH_4 emissions by 14.8 % ($P < 0.05$; Fig. 2). However, rice-duck and rice-chicken increased rice yields by 4.4 % ($P < 0.05$) and 16.8 % ($P < 0.05$), respectively (Fig. 2a). For geographic distribution, rice yields increased by 2.2 % and 4.3 % in East Aasia and South Asia ($P < 0.05$), respectively, while decreased by 6.7 % in Southeast Asia ($P > 0.05$), and showed no obvious change in Europe (Fig. 2a). Rice yields increased with an increasing effective panicle ($P < 0.0001$; Fig. S1a), grain number per panicle ($P < 0.0001$; Fig. S1b), and seed rate ($P < 0.0001$; Fig. S1d). These yield components differed by different co-culture models and geographic distributions (Table S1). The relationships between rice yields and environmental factors revealed that rice yields as affected by co-culture models were positively correlated with aboveground biomass, soil total potassium (TK), soil bulk density (BD), and water total N (WTN), but were negatively correlated with soil Eh and rice planthopper ($P < 0.05$; Table 1). Overall, the effect of co-culture models on rice yields had a time-dependent effect, and rice yields increased with the increasing duration of co-culture models ($P < 0.05$, $N = 128$; Fig. S2). In addition, co-culture models significantly improved the grain quality, including the processing quality (brown rice percentage +1.2 %, milled rice percentage +3.2 %, and head rice percentage +6.6 %), appearance quality (chalkiness degree –43.6 %, and chalky grain percentage –23.3 %), and eating/cooking quality (gel consistency +4.2 % and amylose content –6.6 %) ($P < 0.05$; Fig. 3).

Except for rice-fish, all other co-culture models reduced CH_4 emissions ($P < 0.05$; Fig. 2b). Among them, rice-duck, rice-crayfish, rice-crab, and rice-turtle decreased CH_4 emissions by 19.0 %, 31.0 %, 41.2 %, and 18.4 %, respectively. Furthermore, there were significant regional differences in CH_4 emissions after changing the rice monoculture model to the co-culture model. For instance, co-culture models decreased CH_4 emissions by 22.1 % in East Aasia, while increased CH_4 emissions by 49.5 % and 19.9 % in South Asia and Europe, respectively ($P < 0.05$; Fig. 2b). The linear regression analysis showed that CH_4 emissions as affected by co-culture models were positively correlated with mean annual temperature (MAT), mean annual precipitation (MAP), DOC content, microbial biomass carbon (MBC), and dehydrogenase activity, but were negatively correlated with aboveground biomass, soil Eh, soil nitrate N (NO_3^--N)(SNO3) content, soil ammonium N (NH_4^+-N)(SNH4) content, soil urease activity, and water pH (WpH) (Table 1).

Regarding N_2O emissions, there are significant differences in N_2O emissions among co-culture models and regions ($P < 0.05$; Fig. 2c).

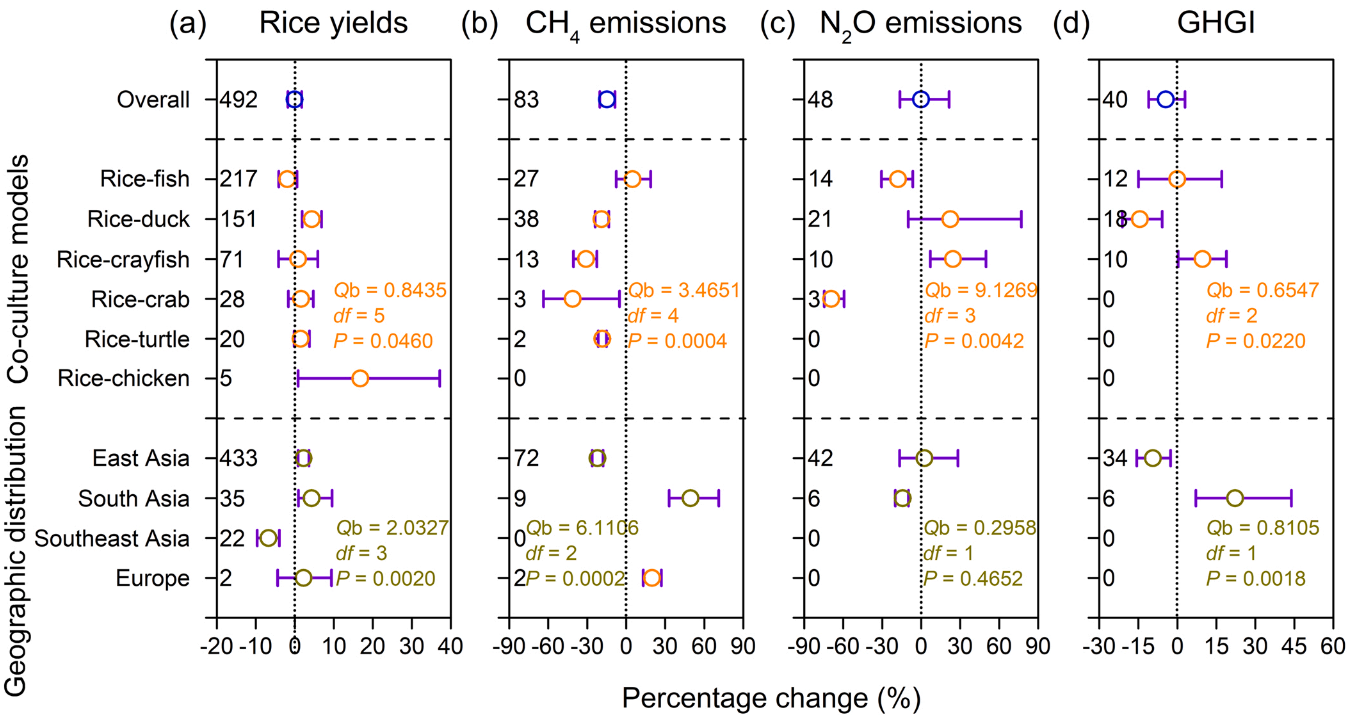

Fig. 2. Effects of co-culture models on rice yields (a), CH_4 emissions (b), N_2O emissions (c), and GHGI (d) and its percentage change for the specific co-culture model and geographic distribution. Error bars represent 95 %*CIs*. If a bar falls on the positive side and does not intersect with zero, we interpret that the specific co-culture model or the geographic distribution provides a significant effect on each variable, and the opposite if it falls on the negative side of the forest plot. The numbers in each graph represent the sample size. Between-group heterogeneity (*Q*b) was calculated to determine the effects of categorical variables. A significant *Q*b value ($P < 0.05$) suggests that the effect of the categorical variable was significant. GHGI, greenhouse gas emission intensity.

Rice-fish and rice-crab decreased N_2O emissions by 17.7 % and 69.2 % ($P < 0.05$), respectively, while N_2O emissions in rice-crayfish increased by 24.5 % ($P < 0.05$). In addition, N_2O emissions decreased by 14.2 % in South Asia ($P < 0.05$), while it had no obvious changes in East Asia. The linear regression analysis illustrated that N_2O emissions as affected by co-culture models were significantly positively correlated with soil organic carbon (SOC), soil Eh, MBC, SNH4 content, soil urease activity, soil dehydrogenase activity, and WDO (Table 1).

Concerning GHGI, rice-crayfish increased GHGI by 9.7 %, while rice-duck decreased GHGI by 14.4 % ($P < 0.05$; Fig. 2d). Also, there are significant differences in GHGI among different regions ($P < 0.05$). As affected by co-culture models, GHGI increased by 22.2 % in South Asia, whereas it reduced by 9.4 % in East Asia ($P < 0.05$).

3.2. *Soil fertility and other soil parameters as affected by co-culture models*

Overall, co-culture models increased the contents of main soil fertility indexes (P < 0.05), wherein the contents of soil total N (TN), AN, total phosphorus (TP), TK, available potassium (AK), and soil organic matter (SOM) increased by 16.2 %, 8.0 %, 10.1 %, 7.8 %, 7.8 %, and 12.8 %, respectively, except for available phosphorus (AP) content (Fig. 4a). All co-culture models increased the contents of TN and SOM (P < 0.05), and the increase of TN and SOM contents in rice-crayfish was the largest, reaching 32.4 % and 32.0 %, respectively (Table S2). Except for rice-turtle, all co-culture models increased the contents of AN, TP, and TK content (P < 0.05), and it also was rice-crayfish that had the largest increase, reaching 23.3 %, 15.4 %, and 14.7 %, respectively (Table S2). Correlation analysis showed that TN was positively correlated with other soil fertility indexes (TP, AP, TK, AK, and SOM, P < 0.01; Fig. S3a), and negatively correlated with soil bulk density (P < 0.01), while SOM content was positively correlated with aboveground and underground biomass as affected by co-culture models (P < 0.01; Fig. S3b).

In terms of soil physical properties, co-culture models resulted in much higher increases in non-capillary porosity (21.6 %, *N* = 35), soil porosity (5.3 %, *N* = 43), and content of > 0.25 mm aggregate (10.4 %, *N* = 9) compared to the rice monoculture model, while decreasing bulk density and soil compaction by 9.6 % and 13.0 %, respectively (P < 0.05; Fig. S4). As to soil chemical properties, co-culture models increased the contents of Fe^{2+}, Mn^{2+}, TC, and SOC by 132.3 % (*N* = 14), 72.2 % (*N* = 10), 26.2 % (*N* = 57), and 12.1 % (*N* = 28), respectively, and decreased SNO3 content by 20.5 % (*N* = 35) (P < 0.05; Fig. S4). With regard to soil biological properties, co-culture models increased the total microbial quantity, soil bacteria, and actinomycetes by 60.3 % (*N* = 5), 37.3 % (*N* = 24), and 20.1 % (*N* = 6), respectively (P < 0.05; Fig. S4). In addition, in terms of activity of soil enzymes, co-culture models increased the activities of cellulase, dehydrogenase, protease and catalase by 21.8 % (*N* = 6), 17.6 % (*N* = 10), 7.6 % (*N* = 5), and 6.3 % (*N* = 15), respectively (*P* < 0.05; Fig. S5).

3.3. *Water quality as affected by co-culture models*

On average, WDO and the water temperature (WT) had no significant response to the change from the rice monoculture model to the co-culture model (Fig. 4b). However, co-culture models increased the contents of water TN (WTN), NO_3^--N (WNO3), NH_4^+-N (WNH4), TP (WTP), and chemical oxygen demand (COD) in flooded water of rice paddy by 48.8 %, 28.4 %, 60.0 %, 87.0 %, and 26.2 %, respectively, while it reduced WpH by 2.5 % ($P < 0.05$; Fig. 4b). In co-culture models, WDO was negatively correlated with WpH, and COD content positively correlated with the contents of WTN and WTP ($P < 0.05$; Table S3). Additionally, the effects of co-culture models on WDO, COD, and WpH were different ($P < 0.01$; Table S4). For example, rice-fish and rice-crayfish decreased the content of WDO by 13.7 % and 21.7 % (*P* < 0.05), respectively, but rice-duck increased WDO content by 53.2 % (*P* <

Table 1

Single-factor regression equations for relationships of rice yields, CH_4 emissions, and N_2O emissions with environmental factors.

Variable	Equation	R^2	P	N
Rice yields (RY)				
Aboveground biomass (AB)	$Ln\ RY = 0.4404 \times Ln\ AB + 0.0332$	0.4010	< 0.001	64
Rice planthopper (RP)	$Ln\ RY = -0.1032 \times Ln\ RP - 0.0386$	0.3585	< 0.001	26
Soil total K (STK)	$Ln\ RY = 0.1618 \times Ln\ STK + 0.0154$	0.2118	< 0.05	23
Soil bulk density (SBD)	$Ln\ RY = 0.3106 \times Ln\ SBD - 0.0496$	0.3668	< 0.05	10
Soil Eh (SE)	$Ln\ RY = -2.0175 \times Ln\ SE + 0.0720$	0.6119	< 0.0001	20
Water total N (WTN)	$Ln\ RY = 0.7678 \times Ln\ WTN + 0.3455$	0.3919	< 0.05	11
CH_4 emissions (ME)				
Mean annual temperature (MAT)	$Ln\ ME = 0.0578 \times Ln\ MAT - 1.1774$	0.4172	< 0.0001	83
Mean annual precipitation (MAP)	$Ln\ ME = 0.0003 \times Ln\ MAP - 0.5950$	0.0819	< 0.01	83
Aboveground biomass (AB)	$Ln\ ME = -0.1129 \times Ln\ UB + 0.1586$	0.5735	< 0.05	7
Soil DOC	$Ln\ ME = 0.5752 \times Ln\ DOC + 0.1426$	0.8171	< 0.01	7
Soil MBC	$Ln\ ME = 0.9454 \times Ln\ MBC - 0.1519$	0.9985	< 0.001	4
Soil Eh (SE)	$Ln\ ME = -0.0720 \times Ln\ SE - 2.0175$	0.6119	< 0.001	20
Soil NO_3^--N (SNO3)	$Ln\ ME = -0.5556 \times Ln\ SNO3 - 0.0329$	0.6413	< 0.001	16
Soil NH_4^+-N (SNH4)	$Ln\ ME = -0.3201 \times Ln\ SNH4 - 0.0766$	0.5695	< 0.001	21
Soil urease activity (SUA)	$Ln\ ME = -0.6099 \times Ln\ SUA - 0.0244$	0.7663	< 0.001	12
Soil dehydrogenase activity (SDA)	$Ln\ ME = 1.2964 \times Ln\ SDA - 0.0741$	0.9892	< 0.01	4
Water pH (WpH)	$Ln\ ME = -0.0798 \times Ln\ WpH - 0.0064$	0.6712	< 0.05	7
N_2O emissions (NE)				
SOC	$Ln\ NE = 1.1243 \times Ln\ SOC + 0.2254$	0.9657	< 0.001	6
Soil MBC	$Ln\ NE = 2.8430 \times Ln\ MBC + 0.3697$	0.9070	< 0.05	4
Soil Eh (SE)	$Ln\ NE = 4.0497 \times Ln\ SE + 0.2633$	0.5613	< 0.01	12
Soil NH_4^+-N (SNH4)	$Ln\ NE = 1.0982 \times Ln\ SNH4 - 0.0307$	0.8217	< 0.0001	19
Soil urease activity (SUA)	$Ln\ NE = 1.2551 \times Ln\ SUA - 0.0421$	0.8729	< 0.0001	12
Soil dehydrogenase acitvity (SDA)	$Ln\ NE = 3.9525 \times Ln\ SDA + 0.6470$	0.9372	< 0.05	4
Water DO (WDO)	$Ln\ NE = 0.7266 \times Ln\ WDO + 0.0791$	0.7606	< 0.0001	18

0.05). Besides, there was no significant difference in the response of nutrients (including WTN, WNO3, WNH4, and WTP) and WT among different co-culture models ($P > 0.05$).

3.4. Diseases, pests, and weed species as affected by co-culture models

Overall, co-culture models decreased the incidence of rice sheath blight, leaf blight, leaf blast, and leaf roller infestation by 69.2 %, 65.1 %, 37.0 %, and 65.4 % ($P < 0.05$; Fig. 4c), respectively. For pests, the numbers of rice term borer, planthopper, and leafhopper as affected by co-culture models reduced by 69.2 %, 64.0 %, and 83.0 % ($P < 0.05$; Fig. 4c), respectively. Moreover, co-culture models decreased weed number, weed species richness, and weed biomass by 82.0 %, 73.3 %, and 84.6 % ($P < 0.05$; Fig. 4c), respectively. The comprehensive studies on diseases, pests, and weeds caused by co-culture models in paddy fields were mainly concentrated in East Asia (Fig. S6a), wherein the main models were rice-fish and rice-duck (Fig. S6b). In terms of different co-culture models, the average reduction rates of diseases, pests, and weeds in rice-duck were as high as 63.8 %, 76.1 %, and 85.2 %, respectively, which were higher than those of other models (32.5 %, 42.4 %, and 56.1 %, respectively) ($P < 0.05$; Fig. S6b). In addition, there were significant differences in the response of rice leaf roller infestation, rice term borer, and weed numbers among different co-culture models ($P < 0.05$; Fig. S6b).

3.5. Ecological and economic benefits as affected by co-culture models

Compared to the rice monoculture model, although co-culture models had higher costs for input by 19.4 %, their output and income increased by 26.5 % and 31.7 %, respectively ($P < 0.05$), and the ratio of output and input tended to increase by 6.3 % ($P > 0.05$; Fig. 4d). In addition, co-culture models resulted in much higher increases in ecological and economic benefits (EEB, $P < 0.05$; 71.1 %) and much lower decreases in GWP-cost ($P < 0.05$; 21.5 %). The correlation analysis showed that compared to the rice monoculture model, the higher input of co-culture models brought higher output ($P < 0.001$) and higher income ($P < 0.05$; Table S5). Meanwhile, income was positively correlated with ecological and economic benefits ($P < 0.05$; Table S5), indicating that co-culture models could realize higher ecological and economic benefits without affecting rice production (Figs. 2a and 4d). Regarding the economic benefit, the input, output, and income differed among all co-culture models, and these economic indexes were also significantly different among various geographic regions ($P < 0.05$; Table 2). For example, among co-culture models, rice-turtle had the highest input, output, and income, whereas rice-fish had the lowest (Table 2). In comparison to the rice monoculture model, rice-fish and rice-crayfish increased the ratio of output and input by 8.4 % and 36.4 % ($P < 0.05$), respectively, while rice-crab decreased it by 25.7 % ($P < 0.05$).

4. Discussion

4.1. Response of rice productivity to co-culture models in paddy fields

Specific co-culture models (i.e. rice-duck and rice-chicken) showed a significant increase in rice yields (Fig. 2a), despite the absence of an overall effect. This should be because of: 1) better biocontrol of harmful pests by foraging of poultry and suppressing weeds to improve N use efficiency, resulting in higher aboveground and belowground biomass and more positive effects on rice components (Table S1), then promoting rice growth (Gurung and Wagle, 2005; Berg and Nguyen Thanh, 2018; Li et al., 2019); and 2) more excreta of poultry in paddy fields than that of aquatic animals (Li et al., 2017; Ding et al., 2021), which led to a significant increase of total N content in surface water, and then improve the yield composition and rice yields (Table 1). The effect of co-culture models on rice yields seems to also depend on the geographic position (Fig. 2a). The relatively lower MAT and MAP in East Asia and South Asia compared to Southeast Asia (Fig. S7) might be one reason for the higher rice yields in these regions, but future researches are needed to uncover the specific reasons. In our study, lower MAT and MAP probably lead to higher aboveground biomass of rice (Fig. S8), whereas higher rice biomass is usually accompanied by higher yields (Jiang et al., 2017). Therefore, Our results suggested the need to carry out suitable co-culture models in paddy fields according to different geographic regions.

We also found that the milled and head rice percentage (processing qualities) and the gel consistency increased, while the chalkiness degree and chalky grain percentage (appearance qualities) and amylose content (cooking qualities) decreased (Fig. 3), which meant that co-culture models generally improved rice quality though the activities of poultry and aquatic animals and their excrement as a type of organic fertilizer (Quan et al., 2008; Zhao et al., 2021). In addition, it was noted that the contents of protein, essential amino acid, and non-essential amino acid tended to be decreased in the co-culture systems ($P > 0.05$; Fig. 3), suggesting that the effects of co-culture models on rice

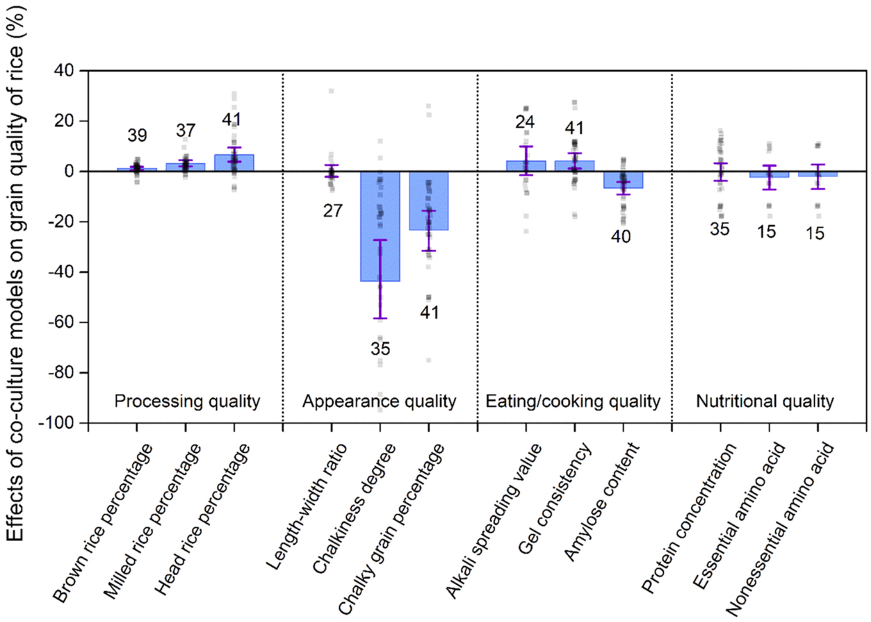

Fig. 3. Response of grain quality (processing quality, appearance quality, eating/cooking quality, and nutritional quality) to co-culture models. Error bars represent 95 %*CIs*. If a bar falls on the positive side and does not intersect with zero, we interpret that the co-culture systems provide a significant effect on each variance, and the opposite if it falls on the negative side of the forest plot. The numbers nearby each column represent the sample size, and the gray dots represent the percentage change of a single sample.

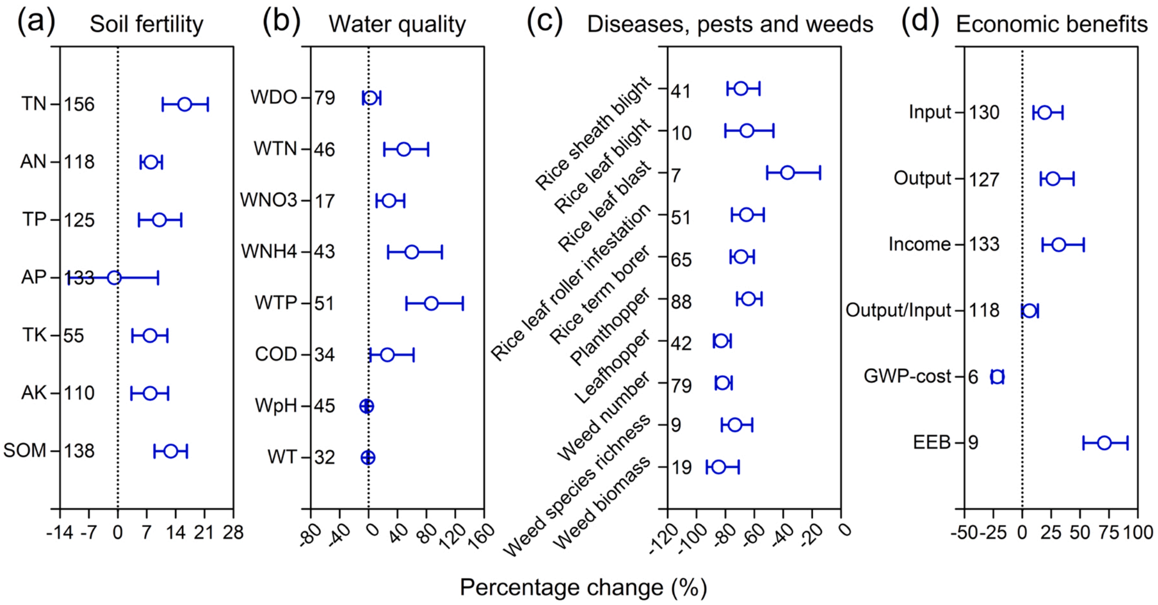

Fig. 4. Percentage change in main soil fertility parameters (a), water quality parameters (b), rice diseases, pests, and weeds (c), and the ecological and economic benefits (d) as affected by co-culture models. Error bars represent 95 %*CIs*. If a bar falls on the positive side and does not intersect with zero, we interpret that co-culture models provide a significant effect on each variance, and the opposite if it falls on the negative side of the forest plot. The numbers represent the sample size. TN, total N; AN, available N; TP, total phosphorus; AP, available phosphorus; TK, total potassium; AK, available potassium; SOM, soil organic matter; WDO, water dissolved oxygen, WTN, water total N; WNO3, water nitrate; WNH4, water ammonium; WTP, water total phosphorus; COD, chemical oxygen demand; WpH, water pH; WT, water temperature; GWP-cost, global warming potential cost; EEB, ecological and economic benefits.

quality might need to be verified by long-term experiments.

4.2. Response of greenhouse gas emissions to co-culture models in paddy fields

Overall, co-culture models decreased CH_4 emissions by 14.8 % ($P < 0.05$, Fig. 2b). CH_4 is mainly produced by methanogens via the biological decomposition of organic matter in an anaerobic environment (Luo et al., 2022). In co-culture models, although the higher DOC and MBC contents in paddy soils are caused by a greater stimulation of the excrement of poultry or aquatic organisms (Frei et al., 2007a; Bhattacharyya et al., 2013), bioturbation from these animals, such as paddling, trampling, foraging, and digging burrows for refuge, sped up the occurrence of oxygen-rich environment, which is beneficial to CH_4 oxidation and so, reducing CH_4 emissions. Interestingly, we found that CH_4 emissions as affected by co-culture models in paddy fields diverged in different geographical regions, reducing in East Asia and increasing in South Asia ($P < 0.05$; Fig. 2b). Indeed, most previous studies in East Asia have been shown that CH_4 emissions from paddy fields notably reduced under any co-culture model (Fu et al., 2008; Zhan et al., 2011; Zhang et al., 2011; Xu et al., 2017; Sun et al., 2019; Khoshnevisan et al., 2021). Meanwhile, studies in South Asia suggested that CH_4 emissions from

Table 2

Percentage change (%) of ecological and economic benefits in different co-culture models and geographic regions with a 95%CIs.

Co-culture models	Input			Output			Income			Output/Input			GWP-cost			EEB		
	N	Mean	95 %CIs	N	Mean	95 %CIs	N	Mean	95 %CIs	N	Mean	95 %CIs	N	Mean	95 %CIs	N	Mean	95 %CIs
Specific model	Qb = 21.1621, $df = 5$, $P < 0.001$			Qb = 14.4989, $df = 5$, $P < 0.01$			Qb = 21.8982, $df = 5$, $P < 0.01$			Qb = 2.2262, $df = 5$, $P = 0.2226$			Qb = 0.0105, $df = 1$, $P = 0.3990$			Qb = 0.1977, $df = 2$, $P = 0.0574$		
Rice-fish	73	8.2	0.6–20.6	69	16.9	8.3–32.1	71	20.1	7.4–40.0	63	8.4	0.8–17.4	2	− 17.66	− 23.1 to − 11.8	4	92.1	66.9–106.4
Rice-duck	41	74.7	50.5–102.9	42	72.7	56.1–91.3	46	94.4	72.5–121.4	44	− 1.8	− 13.3–9.0	4	− 23.41	− 28.1 to − 18.5	4	46.8	40.2–56.0
Rice-crayfish	4	91.3	60.3–118.1	4	167.9	141.2–208.9	4	278.4	190.7–445.3	3	36.4	8.1–83.5	0	-[a]	–	0	–	–
Rice-crab	8	122.6	75.5–174.5	8	57.3	43.4–70.5	8	34.8	2.9–66.9	7	− 25.7	− 44.4 to − 4.1	0	–	–	0	–	–
Rice-turtle	3	219.4	32.7–368.8	3	227.4	107.0–463.3	3	294.2	105.2–772.9	2	− 4.4	− 24.0–20.2	0	–	–	1	114.8	–
Rice-chicken	1	11.5	–	1	21.9	–	1	29.6	–	1	− 57.8	–	0	–	–	0	–	–
Geographic distribution	Qb = 36.2457, $df = 2$, $P < 0.001$			Qb = 45.9193, $df = 2$, $P < 0.001$			Qb = 55.1665, $df = 2$, $P < 0.001$			Qb = 1.2548, $df = 2$, $P = 0.2382$								
East Asia	99	75.8	59.1–94.8	96	104.7	88.2–122.9	102	121.6	97.5–149.9	91	14.3	3.1–26.5	6	− 21.54	− 26.1 to − 16.7	9	71.1	51.5–92.2
South Asia	13	92.0	61.0–127.9	13	71.1	61.1–81.7	13	67.8	53.4–86.1	11	− 9.8	− 23.2–7.3	0	–	–	0	–	–
Southeast Asia	18	− 2.9	− 9.0–4.6	18	0.6	− 4.9–6.3	18	2.2	− 8.6–14.4	18	3.6	− 5.0–12.1	0	–	–	0	–	–

Qb represents the between-group heterogeneity, and the effects of different co-culture systems or geographic regions on responsive variables are considered as significant when P values are lower than 0.05. aNo data are available.

paddy fields significantly increased by 26 %− 112 % under rice-fish model (Frei and Becker, 2005; Datta et al., 2009; Bhattacharyya et al., 2013). This difference occurred might be attributed to the various MAT and MAP with geographical regions (Fig. S9 and Table 1). Rice paddy with higher MAT often stimulates the growth of methanogens, thereby releasing more CH_4 (Qian et al., 2022). Thus, co-culture models induced increases in soil DOC and MBC contents likely spur CH_4 production in coordination with the increase in MAT. Besides, higher MAP and its consequent effects on the increased soil water content limits the availability of oxygen and provides more favorable conditions for CH_4 production as soils tend to be over extended periods to be predominantly anaerobic, thus improving CH_4 fluxes.

Overall, N_2O emissions from paddy fields were not significantly affected by co-culture models, but they differed among co-culture models (Fig. 2c). Specifically, N_2O emissions increased in rice-crayfish, while they decreased in rice-fish and rice-crab ($P < 0.05$; Fig. 2c). N_2O emissions are often affected by soil and waterlogging properties, and co-culture models play important roles by altering soil SOC, AN, soil Eh, and WDO (Sun et al., 2021). N_2O emissions increased in rice-crayfish as a result of the increase of excrement from aquatic organisms leading to more reaction substrates for denitrification (Xu et al., 2017; Sheng et al., 2018). The decrease in N_2O emissions in the latter two co-culture models might be explained by the reduction of WDO content (Table 1) as affected by the disturbance of fish and crabs (Ma et al., 2018) and the consumption by decomposition of SOM (Yi et al., 2019). Meanwhile, N_2O emissions were significantly reduced by 14.2 % in South Asia (Fig. 2c). These results were possibly attributable to deeper layers of flooded water in paddy fields reducing soil Eh and SNH4 content that directly regulated N_2O emissions (Li et al., 2008; Bhattacharyya et al., 2013).

4.3. *Response of soil property and water quality to co-culture models in paddy fields*

Soil nutrient contents of co-culture models were significantly higher than that of the rice monoculture model (Fig. 4a and Table S2), which indicated that co-culture models improved soil fertility in paddy fields (Yuan et al., 2020). In addition, the increases in non-capillary porosity, > 0.25 mm aggregate, and soil porosity, as well as the decreases in bulk density and soil compaction, indicated significant improvements in soil physical properties ($P < 0.05$; Fig. S4) which might be related to the input of rice straw, residual feed, and animal waste in co-culture models (Li et al., 2018; Wan et al., 2019; Yuan et al., 2020; Paramesh et al., 2021; Wu et al., 2021). However, Ali (2006) reported that prolonged rice-crayfish in paddy fields significantly degraded soil quality, drastically reduced rice production, and destroyed the aquatic and non-aquatic habitat inherent in the rice ecosystem. These results might be explained by a decrease in soil microbial diversity caused by the over-utilization of co-culture models. For instance, long-term rice--crayfish with increased co-culture density and harvest frequency reduced soil microbial richness and diversity compared with the rice monoculture model (Zhang et al., 2021). Thus, although this meta-analysis showed that co-culture models increased soil fertility and some soil quality parameters (Fig. 4a and Table S2), an unsuitable performance of co-culture models might lead to ecosystem unsustainability.

Compared with the rice monocultural model, the contents of WTN, WTP, WNH4, and WNO3 as affected by co-culture models increased during the growth period of rice ($P < 0.05$; Fig. 4b and Table S4). This phenomenon happens because of nutrient loss and non-point source pollution when the forage input or N fertilizer is applied to meet the target rice yields and also the animals yields in co-culture models (Oehme et al., 2007; Nayak et al., 2018; Sun et al., 2021). Chen et al. (2021) reported that a 20 % decrease in forage could not only make the environmental consequence of rice-crayfish equivalent to the rice-wheat rotation’s baseline but also with higher profit (decreased forage cost), which could resolve the contradiction between economic profit and environmental pressure, realizing a win-win during the rice-based rotation systems' shifting. However, in our study, co-culture models increased WTN, WNH4, and WTP ($P < 0.05$; Fig. 4b), and they were positively correlated ($P < 0.01$; Table S3), which was inconsistent with the results reported in previous studies showing little or no impact of co-culture models on the field water environment (Ding et al., 2013). Therefore, the continuous movement, feeding activities, and excretions of poultry or aquiculture, directly or indirectly influence the water quality parameters in paddy fields (Frei et al., 2007b; Li et al., 2018), and more attention should be paid to the eutrophication of co-culture systems and downstream rivers.

4.4. *Response of diseases, pests, and weeds to co-culture models in paddy fields*

Diseases, pests, and weeds are the major constraints on rice production (Li et al., 2019). In this study, without affecting rice production, co-culture models significantly decreased major pests and diseases of rice, but also reduced both the density and biodiversity of weeds (Fig. 4c and Fig. S6). Indeed, co-culture systems themselves formed a relatively perfect farmland ecosystem, in which weeds and pests became food sources for poultry or aquatic animals, and the excrements of these animals acted as fertilizer for rice growth. This ecosystem could effectively prevent and control diseases and pests and thus reduce the application amount of chemical fertilizers and pesticides (Zhen et al., 2006; Zheng et al., 2012; Zhao et al., 2014; Teng et al., 2016).

4.5. *Response of ecological and economic benefits to co-culture models in paddy fields*

Taking a long-term perspective, co-culture models provide a sustainable alternative to intensive rice mono-cropping, both from an economic as well as an ecological point of view (Berg, 2001). For example, rice yield increased with the increase of the duration of co-culture models (Fig. S2). In our study, there was no general correlation between income and rice yields in co-culture models (Table S5), indicating that income from poultry or aquatic animals was also an important component of economic benefits (Fig. 4d). Moreover, in the absence of a general effect, paddy soils in Esat Asia showed a significant decrease in GHGI (Fig. 2d), compared to the fields in South Asia, with also a significant decrease in GWP-costs and EEB (Fig. 4d) following establishing co-culture models. Therefore, the ecological and environmental benefits and the net ecosystem service values of co-culture models in paddy fields should be evaluated according to regional differences (Berg, 2002; Xie et al., 2011; Nguyen et al., 2014; Xu et al., 2021).

Co-culture models significantly increased the input, the output, and the net income, but they had no significant effect on the ratio of output and input (Fig. 4d and Table 2). These results indicated that co-culture models could achieve higher output through increasing labor input (Zheng et al., 2012), thus compensating for the increased input cost and achieving higher net economic income compared with the rice monoculture model (Bhattacharyya et al., 2013). Moreover, co-culture models reduced the input of pesticides and fertilizers to a certain extent, but also increased the labor cost of capturing or managing poultry or aquatic animals (Berg, 2002; Li et al., 2007). This may be a constraint on co-culture models. Therefore, it is imperative to establish a set of information-based management systems and incorporate precision agriculture to adapt production inputs site-specifically and achieve maximum benefits for co-culture models (Gebbers and Adamchuk, 2010). In addition, there were significant differences in economic income among different co-culture models and regions (Table 2). For example, rice-crayfish and rice-turtle were two of the most cost-effective co-culture models, and East Asia was the most promising region for developing a co-culture model (Table 2). This indicates that it is necessary to develop co-culture systems in paddy fields according to local conditions. At the same time, it is also necessary to strengthen the research of other regions (e.g., Europe, South America and Africa) suitable for the co-culture models to obtain higher EEB. Nevertheless, our study provides recommendations for suitable co-culture systems in these research areas.

5. Conclusions

Our dataset revealed that co-culture models in paddy fields guaranteed rice yields and grain quality, reduced CH_4 emissions, improved soil fertility, controlled diseases, pests, and weeds, and generated economic benefits, though reduced water quality. We identified significant differences in rice yields, CH_4, and N_2O emissions among different co-culture models and regions, which were related to various effects of each co-culture model on rice biomass, pests control, soil fertility, and water quality index, and difference in climatic variables among the regions. Moreover, our assessment of economic and environmental benefits suggests that the production of poultry or aquatic animals that alter input and output increases the net income. Finally, this study provides a reference for the maximization of the ecological and economic benefits from rice fields by employing regionally suitable co-culture models.

CRediT authorship contribution statement

G. B. Zhang provided the idea for this manuscript. H. Y. Yu conceived the research, collected the data, and performed analyses with substantial help from W. Y. Shen, X. T. Meng, and Jieyi Zeng. H. Y. Yu drafted the manuscript, and X. C. Zhang, G. B. Zhang, H. Y. Yao, and Kazem Zamanien contributed to further revising the text. All authors participated in the evaluation of the results, and read and approved the manuscript.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2022.108195.

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