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Nature-based solutions to increase rice yield in West Africa: an experimental assessment of the role of birds and bats as agricultural pest suppressors

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Abstract

Rice is widely consumed as a staple food being cultivated worldwide. However, in West Africa, it is not produced in sufficient amounts. Rice is thought to suffer from intensive damage by arthropods reducing the quality and quantity of the grain. Birds and bats are believed to control arthropod pests, potentially enhancing rice productivity and food security. Hence, there is a need to find nature-based solutions for mitigating pest-induced rice losses. The present study aimed to examine whether birds and bats, by suppressing arthropod abundance, alleviate plant damage and then boost rice yield. As such, we hypothesised that the exclusion of these vertebrate predators would lead to an increase in leaf and grain damage and a decrease in rice yield. A total of 14 sets of paired experimental exclosures and control parcels were established in a rural area in Northern Guinea-Bissau. Arthropod assemblages and plant damage were surveyed throughout the rice cycle; when rice matured, rice yield was assessed by comparing the dry weight between exclosures and controls. We used Structural Equation Models to indirectly relate the exclosure effect on rice yield. Results showed an increase in the abundance of arthropods within exclosures, positively associated with leaf yellowing and negatively with yield. However, yellowing showed no direct effect on yield. Our findings suggest that birds and bats are potential suppressors of rice pests and that they are likely contributing to reduce yield gaps in West Africa. Enhancing the abundance of these aerial predators could increase predatory pressure on pests, likely boosting rice productivity without intensification, landscape changes, or reliance on pesticides, thus contributing to increased food security and maximising biodiversity.

Keywords: Ecosystem services, exclosure experiments, Guinea-Bissau, productivity, predation

Resumo

À escala mundial, o arroz é cultivado e amplamente consumido como alimento base da dieta humana. Contudo, na África Ocidental o arroz não é produzido em quantidade suficiente de modo a satisfazer a procura. Acredita-se que a produtividade do arroz seja afetada por fatores abióticos como a composição do solo, disponibilidade de água ou variações da temperatura que conduzem a uma redução da quantidade e qualidade do arroz produzido. No entanto, fatores bióticos afetam igualmente a produção, por exemplo, através de vertebrados que predam o grão e, especialmente pelo impacto das pragas de insetos. Diversas ordens de artrópodes podem danificar várias partes da planta – folha, caule, panículos e raiz – especialmente hemípteros e coleópteros podem ser responsáveis em grande parte por danos nas folhas e panículos. Danos nas folhas podem reduzir em grande percentagem a produtividade do arroz devido ao impacto na fisiologia da planta; já um panículo danificado pode conduzir a um enfraquecimento dos grãos com perda de quantidade e qualidade para consumo.

Face à necessidade de aumentar a produtividade do arroz, a intensificação da agricultura e uso de pesticidas aumentam também. Tendencialmente, isto pode culminar num aumento do cultivo e na introdução de químicos na agricultura. O uso excessivo de pesticidas para além de não ser favorável ao bem-estar humano, pode ser igualmente prejudicial para os predadores das pragas. Assim, surge uma necessidade de encontrar soluções à base da natureza de modo a mitigar as perdas de arroz induzidas pelas pragas.

O presente estudo procurou examinar os efeitos de predadores vertebrados voadores no dano das plantas e produtividade do arroz, através da atividade dos artrópodes. O estudo focou-se em três questões principais: 1) será que as populações de artrópodes variam dentro e fora das exclusões? 2) se existirem diferenças nas populações de artrópodes, estas resultam em diferentes taxas de dano nas plantas? e 3) se a taxa de dano nas plantas afeta diferentemente a produtividade do arroz dentro e fora das exclusões? Hipotetizamos que os predadores aéreos insetívoros suprimem os artrópodes herbívoros, o que resulta na diminuição do dano nas folhas e num aumento da produtividade do arroz. Previmos também que a abundância de artrópodes e dano nas plantas iria diminuir e a produtividade do arroz aumentar em áreas expostas a aves e morcegos. O inverso seria observado em áreas onde estes predadores voadores serão excluídos.

Um total de 14 conjuntos de pares de parcelas de exclusões e controlos foram estabelecidas numa zona rural no norte da Guiné-Bissau. As exclusões consistem em áreas onde as aves e morcegos estão ausentes, enquanto nas zonas controlo estes vertebrados não foram excluídos, estando o arroz sobre as mesmas condições de gestão. As exclusões mantiveram-se fechadas durante todo o ciclo do arroz. Efetivamente, as três fases de desenvolvimento do ciclo baseiam-se em: (1) fase vegetativa, onde ocorre a germinação e o panículo inicia a formação; (2) reprodução, durante a qual o panículo emerge; (3) preenchimento dos grãos e maturação. As populações de artrópodes e a proporção de dano nas plantas – folha, caule e grão – foram amostrados mensalmente de setembro a novembro de 2022. Quando maduro a produtividade de 500 grãos de arroz foi estimada comparando o peso seco entre exclusões e controlos. Estatisticamente, utilizámos Modelos Lineares Generalizados (GLMs) e Modelos Lineares Mistos Generalizados (GLMMs) para determinar, separadamente, o efeito da exclusão e do mês na abundância dos artrópodes e no dano das plantas – amarelecimento das folhas, desfoliação e outras marcas. A análise foi repetida para as ordens de artrópodes mais observadas. Relativamente ao dano no grão e produtividade, GLMs foram igualmente utilizados, contudo sem avaliar a variação com o mês, uma vez que os dados são apenas representativos do último mês. Ajustámos também *Structural Equations Models* (SEM) para relacionar indiretamente o efeito da exclusão na produtividade do arroz, através de um conjunto de equações de GLMMs. Estes modelos consistem numa análise de caminhos, baseada num conjunto de variáveis diretamente interrelacionadas. Considerámos separadamente os dois tipos de dano nas folhas – amarelecimento e desfoliação. As relações avaliadas foram: (1) o efeito da exclusão na abundância dos artrópodes, (2) o efeito da abundância de artrópodes no dano das folhas, (3) efeito da abundância de artrópodes na produtividade do arroz, (4) efeito do dano das plantas na produtividade do arroz. Uma análise semelhante foi realizada analisando separadamente o dano no grão – *whiteheads* e mancha.

Os resultados revelaram um aumento dos artrópodes dentro da exclusão, como esperado. Este aumento ocorreu principalmente na ordem Araneae, provavelmente devido a uma libertação do mesopredador e a um possível favorecimento, por parte da estrutura da exclusão, da construção de teias e proteção. Para averiguar o impacto apenas dos insetos, a abundância das aranhas, como artrópodes predadores, foi excluída e testada a relação com as restantes variáveis respostas num SEM – exclusão, dano nas folhas e produtividade. Os resultados não evidenciaram influência dos insetos nas restantes variáveis, sugerindo uma possível desvantagem na utilização do método de exclusão devido à estrutura poder, de facto, favorecer a proliferação das aranhas. Considerando o dano nas plantas, a exclusão não produziu efeito nos danos na planta nem na produtividade, contrariamente ao previsto. Ocorreu, no entanto, uma variação sazonal positiva na abundância geral dos artrópodes. No caso do dano nas folhas, a desfoliação diminuiu ao longo dos meses, enquanto as outras marcas aumentaram a sua incidência da estação húmida para a seca. Estas oscilações podem ser explicadas pela abundância e dieta de aves e morcegos poderem variar de acordo com a estação. A ação de variadas pragas de artrópodes em alturas diferentes do ciclo do arroz pode culminar também numa alteração da incidência do dano produzido.

Através da análise dos SEMs, os resultados indicam uma relação positiva entre a exclusão e abundância dos artrópodes. Esta última demonstrou-se positivamente associada ao amarelecimento das folhas e negativamente à produtividade. Contudo, nenhuma outra variável resposta – desfoliação, whiteheads e mancha no grão – evidenciaram uma relação com a produtividade do arroz. Acredita-se que os artrópodes podem afetar a produtividade tanto direta como indiretamente através de vetores virais. Assim, é possível que apesar de o amarelecimento das folhas não tenha afetado significativamente a produtividade, este, aliado a um dano direto dos artrópodes revelou afetar a produtividade.

Devido à falta de conhecimento na área, estudos futuros podiam priorizar esforços na identificação das pragas do arroz e perceber se, de facto, são presas das aves e morcegos nestas plantações. A análise dos fatores bióticos como fungos e de abióticos como a composição do solo podem permitir uma melhor compreensão do real impacto na produtividade. Em suma, os nossos resultados sugerem que as aves e morcegos podem controlar as populações de artrópodes e potencialmente suprimir as pragas do arroz. A criação de áreas de nidificação e abrigos, aliadas a um diálogo com os produtores versando a importância destes vertebrados, podem surgir como futuras medidas e políticas de conservação, com vista a aumentar a abundância e diversidade destes predadores. Tais ações podem conduzir a um aumento da pressão predatória sobre as pragas. Isto possivelmente levará a um incremento na produtividade do arroz sem intensificação agrícola, alteração da paisagem ou dependência de pesticidas, contribuindo para o aumento da segurança alimentar e maximização da biodiversidade, na área rural da África Ocidental.

Palavras chave: Serviços de ecossistemas, exclusões, Guiné-Bissau, produtividade, predação

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Abbreviations

AM – Before midday

PM – After midday

GLM – Generalized Linear Model

GLMM – Generalized Linear Mixed Model

QQ plot – Quantile - quantile plot

SEM – Structural Equation Model

1 | Introduction

Nature-based solutions involving various ecosystem services offer an alternative approach to pest management in rice fields, reducing the reliance on chemical pesticides. Rice pests endanger food security, diminishing rice quality and yield (Wanger et al., 2014). Biological pest control, such as that undertaken by birds and bats, might help control pest populations, decreasing yield loss and preventing the use of chemicals in rice fields (Bhalla et al., 2023; Borkhataria et al., 2012).

Rice is extensively consumed worldwide as a staple food, being produced in nearly all continents (IRRI, 2020; Muthayya et al., 2014). In Africa, rice demand for consumption is rapidly growing, challenging rice production and prompting the necessity to import about 50% of the rice supply in West African countries (Tondel et al., 2020). This region serves as the primary rice producer in Africa and rice stands out as the most nutritious and available grain consumed in West Africa (Adjah et al., 2022). Despite its importance throughout West Africa, rice is not cultivated in sufficient quantity and quality to feed the whole population. Therefore, there is a heavy reliance on imports from other countries to fulfil the demand (Medagbe et al., 2020). Depending on the water source, three types of rice cultivation are mainly practiced in the region: irrigated lowland, rainfed lowland, and upland (Niang et al., 2017). Notably, rice productivity has shown no improvement in this region and stagnation has been occurring, primarily attributed to some limiting growth environmental factors or biological productivity reducers (Diagne et al., 2013; Saito et al., 2013).

In small-scale plantations, the amount of nutrients in the soil, water availability and temperature variations may lead to yield fluctuations (Haefele et al., 2013; Nhamo et al., 2014; Senthilkumar et al., 2020; Tanaka et al., 2017). Multiple vertebrate species inflict damage on rice by eating grains or leaves (e.g., rodents or granivorous birds) (Moinina et al., 2021). However, insects have been identified as great contributors to the destruction of vast amounts of rice and other crops across Africa (Dhaliwal et al., 2010) . Indeed, insect-associated rice loss is estimated at ca. 10-15% per year (IRRI, 2011). Hence, the fact that rice development occurs in warm and humid environments, ideal for insects to grow and prosper, favours the expansion of pests (Pathak & Khan, 1994; Tanwar et al., 2010).

Multiple arthropod orders include rice pests, which can directly impact various parts of the plant or transmit viral diseases (Edde, 2022; Heinrichs & Barrion, 2004). Specifically, Hemiptera, Coleoptera and Lepidoptera are responsible for several types of damage, mainly to leaves and panicles (ramification composed of the rice grains) (Heinrichs & Barrion, 2004). Damage that occurs at the leaf level has the potential to affect the physiology of the plant, reducing both the quantity and quality of rice (Nasiruddin & Roy, 2012). Concerning leaf yellowing, 10-100% of the yield could be lost, depending on the plant's developmental stage and environmental factors (Kouassi et al., 2005). At the panicle level, the impact may structurally weaken the grain, resulting in a decrease in overall productivity (Borkhataria et al., 2012; Mau et al., 2020; Reissig, 1986). Therefore, there is a need to perceive the extent of the impact that insect damage may have on rice productivity.

While there is a propensity for intensive use of chemical pesticides to control insect pests, their cost-effectiveness remains low (Wilson & Tisdell, 2001). Moreover, excessive use of pesticides causes risks to human health and to pest predators (Way & Heong, 1994). Inappropriate application and prolonged exposure to pesticides may also lead pests to develop resistance, proving their inefficient use (Bhalla et al., 2023). Contrarily, nature-based solutions for suppressing pests, such as biological control, are a cheap and sustainable alternative to the use of chemical pesticides (Bommarco et al., 2013; Naranjo et al., 2015). Ecosystem services provided by insectivorous bats and birds are a nature-friendly way of regulating pest populations as revealed by numerous studies conducted on different regions and crops (Bhalla et al., 2023; Karp et al., 2013; Maas et al., 2013). However, their role in increasing yield is not always detected (Borkhataria et al., 2012).

One way to understand the role of bats and birds on arthropod communities and overall crop yield is to perform exclusion experiments (Ferreira et al., 2023; Maas et al., 2019). These consist of pairing experimental exclosures with controls (under the same conditions, without an excluding structure) and evaluating the impacts that the exclosure has on arthropod abundance and diversity, and crop productivity (Maas et al., 2019). These studies have been successfully applied to survey various plantations, such as cacao (Ferreira et al., 2023), coffee, cotton (Maas et al., 2019) and rice (Bhalla et al., 2023).

We conducted an exclosure experiment on rainfed lowland rice fields in Guinea-Bissau, to examine the top-down effects of insectivorous aerial vertebrate predators on plant damage, due to arthropod activity, and rice productivity. The main questions of this study were: 1) do arthropod assemblages differ between inside *versus* outside exclosures? 2) do differences in the arthropod assemblages result in different rice plant damage rates? and 3) does the plant damage rate affect rice yield differently inside and outside the exclosures? We hypothesized that insectivorous aerial vertebrate predators suppress herbivorous arthropods, which in turn reduces leaf damage and increases rice yield. We thus predicted that arthropod abundance and plant damage will be lower, and rice yield will be higher, in control areas compared to areas where these predators are excluded.

2 | Methods

2.1 | Study area

The study was conducted between the cities of Farim and Mansaba (Oio region), in northern Guinea-Bissau, West Africa. The six targeted rice fields were within the area surrounding the villages of Bereco, Djalicunda, Bironqui, Demba So, Mambonco and Mansaba (Figure 2.1). Guinea-Bissau has a tropical semi-humid climate, with a seasonal rainy season starting in early June until October/November. This period of rainfall contributes to a regional annual rainfall fluctuation ranging from 1200 to 1400 mm (Catarino et al., 2001).

Our study was conducted in areas of rainfed lowland rice, in fields surrounded by woodland patches and cashew plantations. The rice cycle has three different development stages: (1) a vegetative phase, in which plant germination takes place and the panicle starts its growth; (2) reproduction begins, leading the panicle to heading – i.e., panicles exit from the rice stem; and (3) grain filling and maturation occur. Following this last stage, the rice is ready to be harvested for peeling and consumption. Each rice field consisted of a mosaic of parcels. Within the same field, parcels differed in rice development stages and management options. However, each parcel was managed by a single rice producer and subjected to uniform management practices and conditions, without the use of pesticides.

This study is part of a wider project - EcoPestSupression - aiming to investigate the role of birds and bats as pest suppressors in rice fields, in Guinea-Bissau.

2.2 | Experimental exclosures

During the second half of June 2022, before rice seeding, a total of 14 exclosures were deployed (Figure 2.1). Experimental exclosures were built using a bamboo frame (3 × 3 × 2 m) secured with stainless steel cables. A commercial anti-bird black net with 2 cm mesh made with braided nylon was used to prevent foraging birds and bats from accessing rice while allowing access to arthropods. Exclosures were left open, with the nets fully retracted, until all the rice was sown. Afterward, exclosures were closed, only being opened to allow human access during sampling, weeding, and harvesting. The exclosures remained in the fields for six months, until the rice from all parcels was harvested (December 2022).

Two parcels were sampled in each rice field, except in Bironqui where four parcels were sampled. Both exclosure and control plots were set within the same parcel, at least 10 m apart, and subjected to the same farming procedures throughout the entire duration of the experiment (Fig. A1).

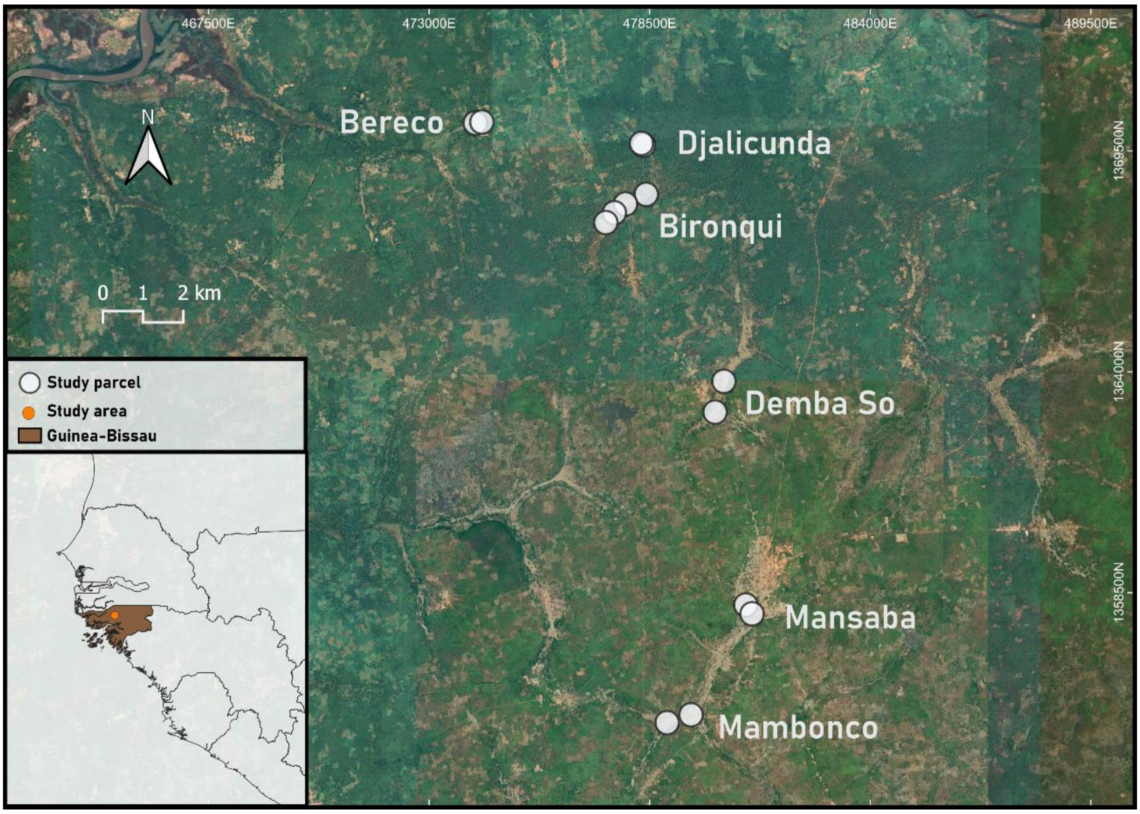

Figure 2.1. Location of the 14 sampled parcels in the study area as denoted by the white dots. Inset shows study area location in Guinea-Bissau and West Africa.

2.3 | Rice and arthropod sampling

Both rice growth and damage, and arthropod abundance were quantified monthly, from September to November. Rice and arthropods were sampled along 1 m in two rice rows in both exclosures and controls. To assess arthropod abundance, individuals were counted during the survey and photographed for later identification (Table 1). The survey was performed once per month, between 9 AM and 5 PM, to ensure similar insect activity (Ruttan et al., 2016). Rice growth was measured through rice plant height (averaging six random measurements) and plant density. Rice damage was considered at the leaf, stem and grain levels (Fig 2.2). At the leaf level, three categories were sampled: defoliation, yellowing and other marks. Pecky rice and whiteheads were examined representing grain damage. It was also observed whether the panicles (ramification composed of rice grains) lacked any grain. The plant was counted as damaged whenever one leaf or panicle was affected. Although the initial 14 parcels were sampled, two parcels were abandoned, resulting in missing data for the last monitorization and harvest. Additionally, one of the parcels was harvested before the last data collection. Consequently, rice yield was assessed from a total of 11 sampled parcels.

Table 1. Summary of the continuous variables measured according to each of four categories: rice growth, herbivory, grain damage/yield and arthropod assemblage.

Category	**Variable**	**Description**	**Range**	**$\bar{x}$ ± SD**
Arthropod assemblage	Arthropod abundance	Abundance of arthropods observed. Classified at the order level	1.0 - 54.0	7.9 ± 7.1
	Insect abundance	Abundance of insects observed. Classified at the order level	1.0 - 14.0	5.1 ± 2.8
Rice growth	Width	Width of the rice row (cm)	24.0 - 104.0	66.0 ± 15.2
	Plant density	Number of rice plants per m^2	7.2 - 227.0	102.6 ± 44.6
Leaf damage	Yellowing	% of plants affected by yellowing	1.0 - 82.2	22.1 ± 15.8
	Defoliation	% of plants damaged by herbivores	0.0 - 33.3	11.0 ± 9.4
	Other marks	% of plants with stained leaves	5.0 - 100.0	81.4 ± 27.5
Grain damage / yield	Pecky rice	Average number of plants with stained grains or fully brown	1.0 - 63.0	20.8 ± 18.7
	Whiteheads	Average number of plants with broken or empty	1.0 - 9.0	3.3 ± 1.7
	Rice yield	Dry weight of 500 pealed grains (g)	5.5 - 11.0	8.8 ± 1.5

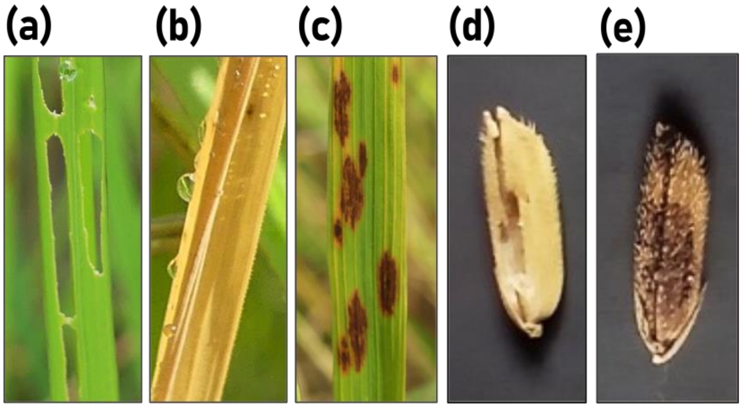

Figure 2.2. Photographic examples of each of the three types of leaf damage: (a) defoliation, (b) yellowing, (c) other marks, and grain damage: (d) whiteheads, (e) pecky rice.

2.4 | Rice yield estimation

A total of 20 panicles were collected per exclosure and control plots once the rice was mature. Rice panicles were weighed and exposed to the sun until dry (i.e., weight stable for at least five days) (Nwilene, 2018). In lab conditions, 500 rice grains were detached from each group of 20 panicles and dried for 24 h at 80ºC. Grains were peeled using a pestle and a mortar, similar to the locally traditional way, and then weighed to quantify yield.

2.5 | Data analysis

To assess the effect of the exclosure on arthropod abundance and plant damage, an exploratory graphical analysis of the data was performed. Subsequently, Generalized Linear and Mixed Models (GLMs and GLMMS, respectively) were used to examine separately the effect of the exclosure and month on arthropod abundance and leaf damage – yellowing, defoliation and other marks. The same analysis was conducted for the arthropod Orders that were most frequently observed. Pairs of exclosure and controls were linked by a parcel code and both the pairs and month were used as explanatory variables. Random effects were applied considering the pairs of exclosure-control, however, when the variance was nearly zero, this random effect was removed being replaced by GLMs following the same procedure. Leaf damage were the only variables analysed with GLMMs. Regarding analysis for 1) arthropod abundance: the Poisson distribution with a log link function was found to be best fitted despite evidencing overdispersion of the data and to account for different sampling efforts, an offset accounting for the number of rice plants was included; and 2) leaf damage: Gaussian distribution with identity function was used. Similarly, we conducted an analysis to estimate the effect of the exclosure on 3) grain damage and yield, applying a Gaussian distribution, with an identity link function. However, the effect of month was not included in this analysis. QQ plot was used to check for normality and the GLM residuals were used to check for homoscedasticity. Only data with a percentage of evidence higher than 5% was used, excluding stem damage and lack of grain variables (~ 1%) from the statistical analysis.

To examine the indirect relationship between the effect of the exclosure on the rice yield, piecewise Structural Equation Models (SEMs) were performed with a set of GLMMs, using the data from the last month of sampling. These models consist of path analysis based on a set of directly interrelated variables (Lefcheck, 2016). Non-saturated models were used, and the model's goodness-of-fit was assessed using the Fisher's C as the test statistic, combining the *P* values of the set of GLMMs (Shipley, 2000). Firstly, SEMs were made considering separately the leaf damages – yellowing and defoliation. The set of GLMMs used as the basis set consisted of: (1) the effect of the exclosure on arthropod abundance; (2) the effect of arthropod abundance on the leaf damage; (3) the effect of arthropod abundance on rice yield; (4) effect of leaf damage on the rice yield. Each GLMM equation was fitted using a random effect regarding the pairs of exclosure-control. The variable "other marks" was excluded from this analysis due to the consistency of the data between exclosure and control. Secondly, a similar analysis was performed using grain damage – whiteheads and pecky rice. Additionally, to perceive the extent of the insects' impact on this experiment, the SEM considering leaf damage was repeated relating only to the abundance of insects, thereby excluding spiders as the predatory arthropod.

All the results were taken as significant when p value was less than 0.05. The GLMs and GLMMs were adjusted using the package *lme4* (Bates et al., 2014) and SEM required the use of the *piecewiseSEM* package (Lefcheck, 2016). All the statistical analyses were conducted using R version 4.2.2 (R Core Team, 2022).

3 | Results

3.1 | Arthropod abundance

A total of 635 arthropods from 10 orders were identified, with an average (± SD) of 7.9 ± 7.1 individuals per parcel. From these, 405 individuals were observed in the exclosures (10.1 ± 9.1 ind./per exclosure) and 230 in the controls (5.8 ± 3.0 ind./per control). The most abundant order was Araneae (28.7%), followed by Hemiptera (19.5%), Hymenoptera (12.0%), Orthoptera (11.3%), Diptera (10.7%) and Coleoptera (6.9%). Total arthropod abundance was higher inside the exclosures (Table 2, Fig. 3.1a). An increase in arthropod abundance was also recorded during the rice cycle (Table 2). In most instances, the exclosures and month had no effect on the abundance of individual arthropod orders (Table 2). Exceptions to this pattern were observed in Araneae. In this order, abundance was higher in the exclosures and increased with month (Table 2, Fig. 3.1b). Additionally, Diptera showed an increase in abundance through months, while Coleoptera displayed the opposite trend (Table 2).

Table 2. Summary results of Generalized Linear Models investigating effects of treatment and month on the total abundance of arthropods and for each order in separate. The exclosure effect was used as a binary variable, with Control as reference. The significance of the results is presented as: ***p < 0.001, *p < 0.05.

Response variable	Predictors	Estimate	Std. error	z-value	P-value
Total abundance	Intercept	-3.460	0.124	-27.886	<0.001***
	Exclosure	0.532	0.083	6.437	<0.001***
	Month	0.517	0.049	10.561	<0.001***
Orthoptera	Intercept	-4.781	0.331	-14.466	<0.001***
	Exclosure	0.242	0.238	1.018	0.309
	Month	0.182	0.144	1.258	0.209
Diptera	Intercept	-4.961	0.344	-14.425	<0.001***
	Exclosure	0.023	0.243	0.093	0.926
	Month	0.305	0.148	2.063	<0.05*
Hemiptera	Intercept	-3.995	0.244	-16.350	<0.001***
	Exclosure	-0.005	0.180	-0.030	0.976
	Month	0.124	0.111	1.123	0.261
Coleoptera	Intercept	-4.384	0.410	-10.700	<0.001***
	Exclosure	0.518	0.313	1.653	0.098
	Month	-0.431	0.210	-2.056	<0.05*
Hymenoptera	Intercept	-4.588	0.315	-14.549	<0.001***
	Exclosure	-0.037	0.229	-0.162	0.871
	Month	0.187	0.140	1.333	0.182
Araneae	Intercept	-8.692	0.431	-20.150	<0.001***
	Exclosure	2.624	0.299	8.784	<0.001***
	Month	1.460	0.121	12.036	<0.001***

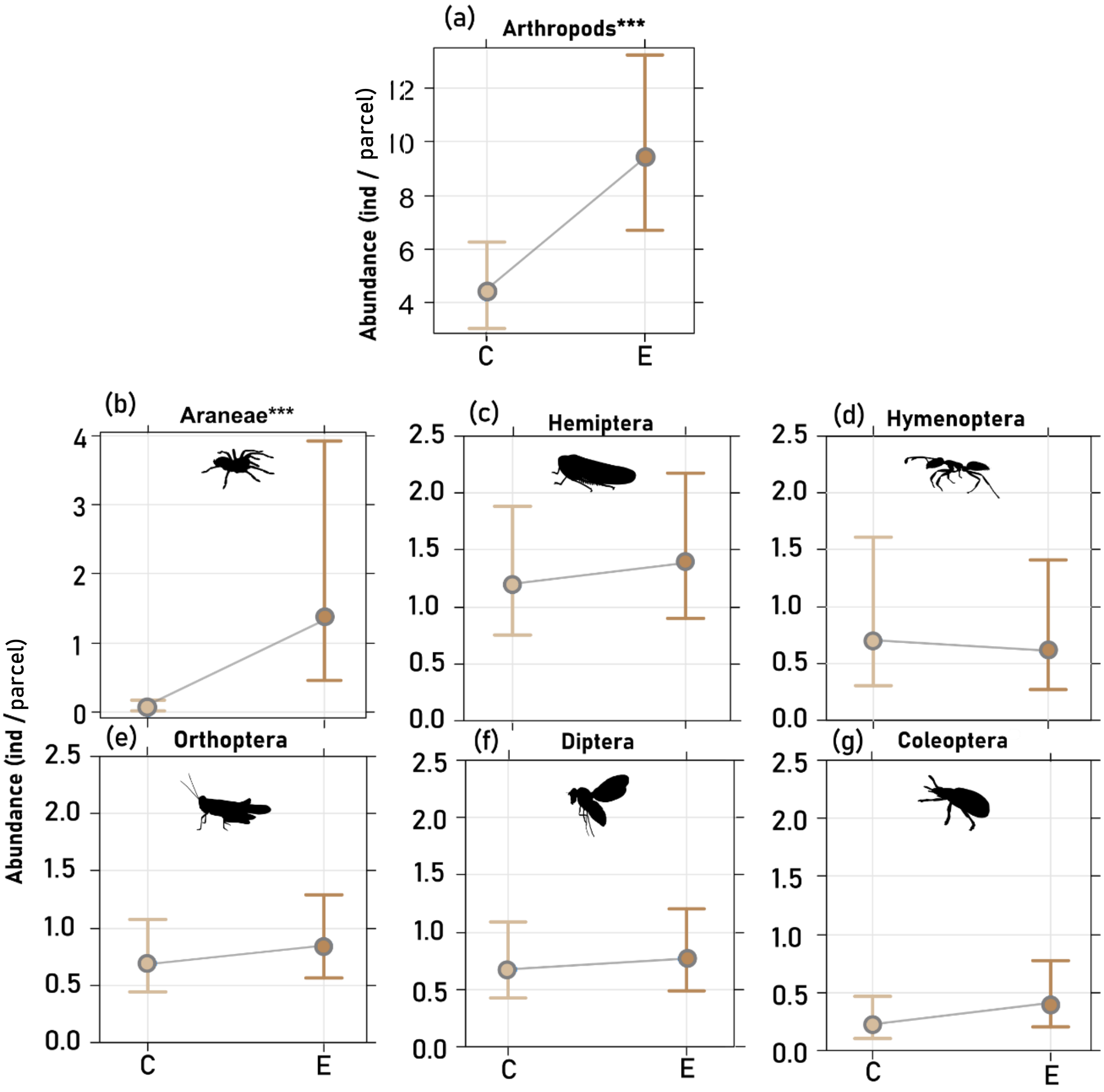

Figure 3.1. Partial effects of the GLMs of control-exclosure pairs, on (a) the arthropod abundance and the most frequent arthropods orders: (b) Araneae, (c) Hemiptera, (d) Hymenoptera, (e) Orthoptera, (f) Diptera, (g) Coleoptera, recorded per number of plants, during the survey. “C” denotes “Control” and represents areas where birds and bats were not excluded, whereas “E” stands for exclosures, and represents areas where these groups were excluded. The significance level is indicated as ***p < 0.001, and *p < 0.05. Notice that the y-scale of the graphs varies between taxa.

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3.2 | Leaf damage

The average percentage of defoliation observed was 11.0 ± 9.5 % per number of plants while yellowing accounted for 22.4 ± 15.9 % per number of plants. The damage classified as other marks recorded the highest average of 81.5 ± 27.6 % per number. of plants. The exclosure had no effect on leaf damage (Table 3, Fig. 3.2). However, month exhibited a negative effect on defoliation and a positive effect on other marks (Table 3).

Table 3. Summary results of the GLMMs investigating the effects of the exclosure and month on the leaf damage. The exclosure effect was used as a binary variable, with Control as reference. The significance of the results is presented as: ***p < 0.001, **p < 0.01.

Category	Response variable	Parameters	Estimate	Std. Error	df	t value	Pr(>|t|)
Leaf damage	Defoliation	Intercept	17.588	2.620	42.651	6.711	<0.001***
		Exclosure	2.053	1.399	64.158	1.467	0.147
		Month	-3.890	0.882	64.944	-4.411	<0.001***
	Yellowing	Intercept	19.679	5.394	29.050	3.648	0.001**
		Exclosure	1.765	3.273	63.424	0.539	0.592
		Month	0.874	2.044	66.092	0.428	0.670
	Other marks	Intercept	54.699	7.878	9.444	6.943	<0.001***
		Exclosure	4.832	3.519	64.141	1.373	0.174
		Month	12.146	2.220	64.705	5.470	<0.001***

Table 4. Summary results of the GLMs investigating the effects of the exclosure and month on grain damage and yield. The exclosure effect was used as a binary variable, with Control as reference. The significance of the results is presented as: ***p < 0.001.

Category	Response variable	Parameters	Estimate	Std. Error	t value	P-value
Grain damage	Pecky rice	Intercept	49.367	9.641	5.12	<0.001***
		Exclosure	-3.948	13.941	-0.283	0.78
	Whiteheads	Intercept	8.542	1.524	5.606	<0.001***
		Exclosure	1.204	2.203	0.546	0.591
Yield	Grain Yield	Intercept	8.827	0.457	19.321	<0.001***
		Exclosure	-0.088	0.646	-0.136	0.893

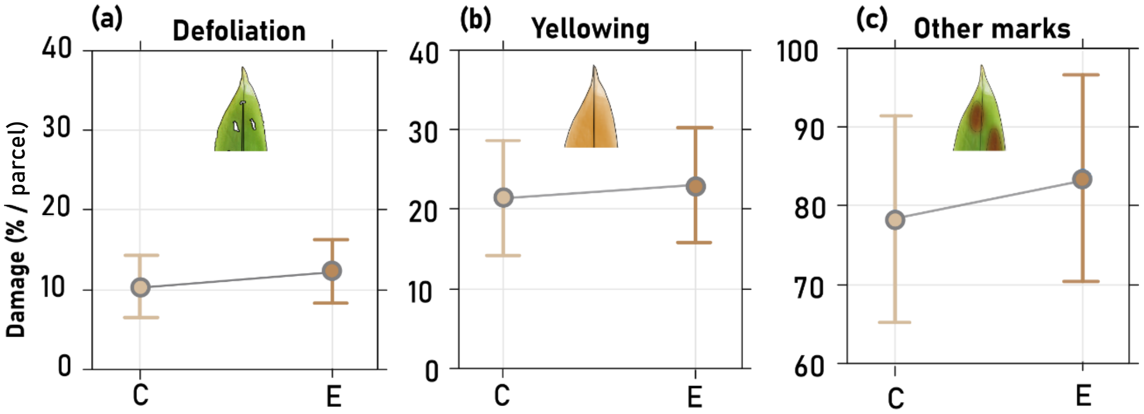

Figure 3.2. Partial effects of the GLMMs of control-exclosure pairs on the percentage of leaf damage observed in rice leaves. The three types of damage recorded were: (a) defoliation, (b) yellowing and (c) other marks. "C" denotes "Control" and represents areas where these groups were absent. Notice that the y-scale of the graphs varies between taxa.

3.3 | Grain damage

On average 54.2 ± 34.7 % of the panicles had damage, with pecky rice showing on 47.5 ± 32.0 % of the panicles. Additionally, whiteheads, on average, were present on 9.1 ± 5.1 % of the panicles. No significant difference was found, in both types of damage, between exclosures and controls (Table 4, Fig. 3.3).

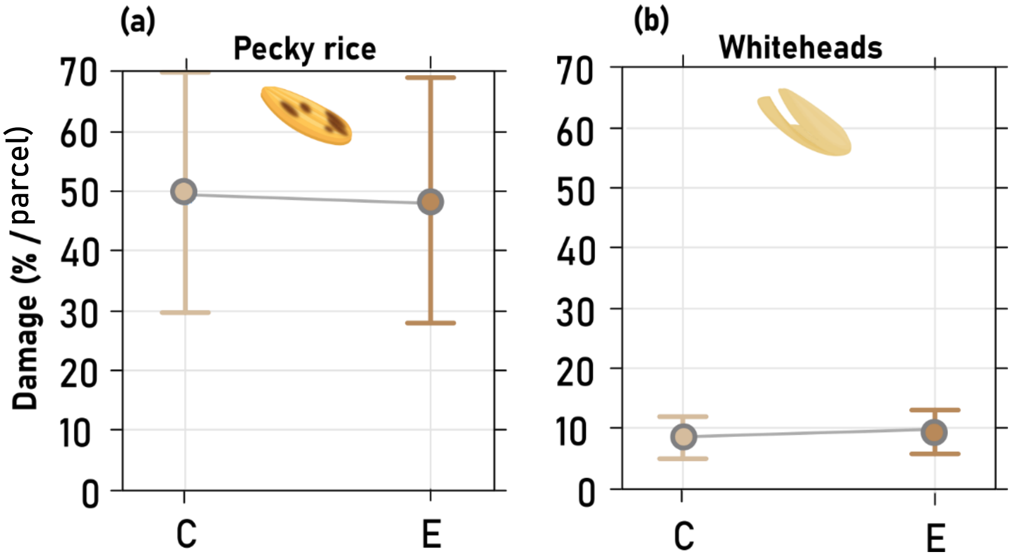

Figure 3.3. Partial effects of the GLM of control-exclosure pairs on grain damage. The two types of grain damage surveyed were: (a) pecky rice and (b) whiteheads. "C" denotes "Control" and represents areas where birds and bats were not excluded, whereas "E" stands for exclosures, and represents areas where these groups were excluded.

3.4 | Rice Yield

Rice yield varied between 5.5 and 11.0 g per parcel (8.8 ± 1.5 g/parcel). No yield differences were detected between exclosure and control areas (β = -0.008, p = 0.860, Fig. 3.4).

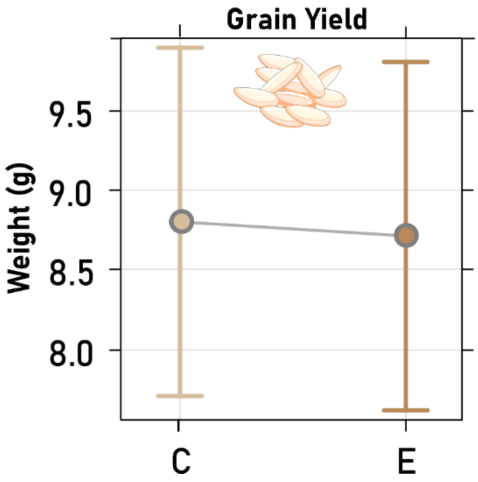

Figure 3.4. Partial effects of the GLM of control-exclosure pairs on the weight of 500 rice grains. “C” denotes “Control” and represents areas where birds and bats were not excluded, whereas “E” stands for exclosures, and represents areas where these groups were excluded.

3.5 | Indirect effects of the exclosure in the rice yield

Considering the model including yellowing, arthropod abundance increased within exclosures ($\beta = 0.4$, $p > 0.05$), which promoted an increase in the yellowing of leaves ($\beta = 0.5$, $p < 0.01$), which had no direct influence on yield. Nevertheless, the abundance of arthropods had a direct, negative effect on rice yield ($\beta = -0.5$, $p < 0.01$) (Fig. 3.5a, Table. A1a). In the model that included defoliation, arthropod abundance had neither influence on defoliation nor yield. Defoliation was also not related to yield (Fig. 3.5b, Table. A1b). When the SEM was repeated considering the grain damage in the place of either of the leaf damage types, no significant relationships were observed as well as for the abundance of insects (Fig. A2, Table. A2).

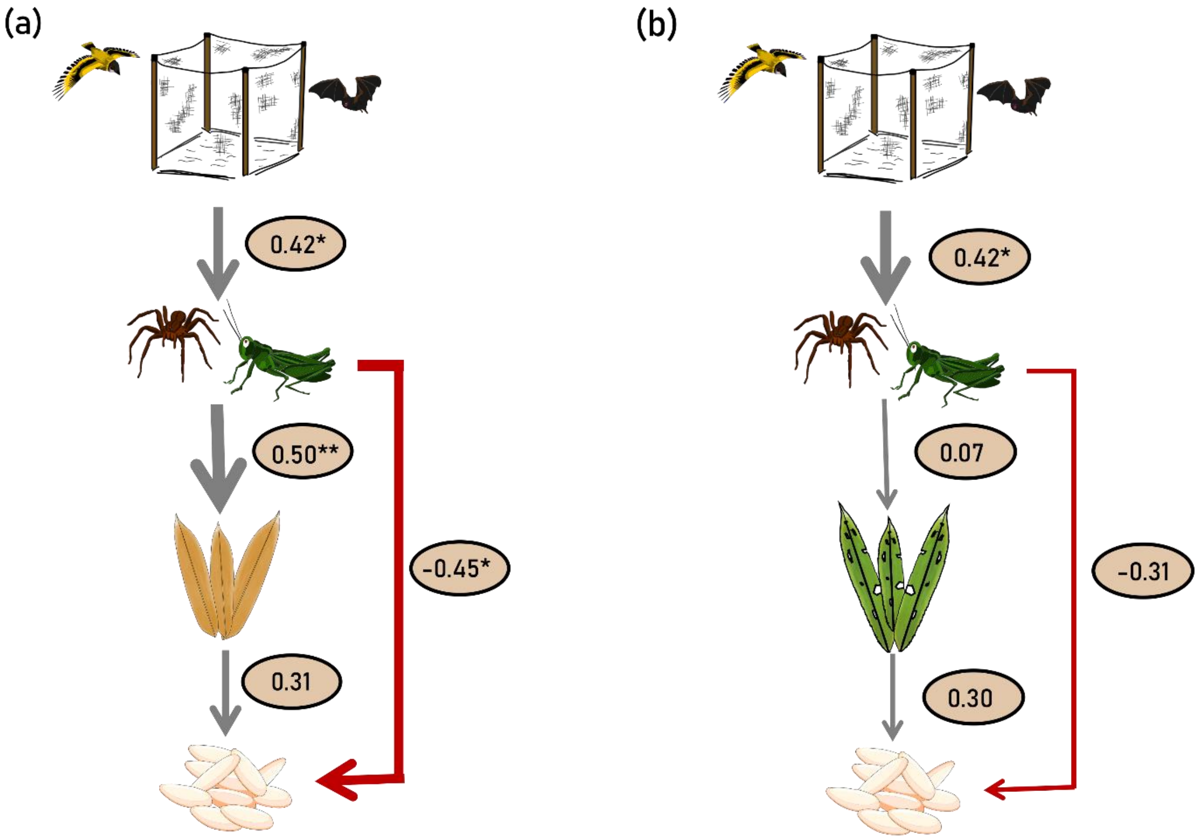

Figure 3.1. Results of the piecewise Structural Equation Model indirectly relating exclosure and yield, as mediated by arthropod abundance and leaf damage, i.e. (a) yellowing and (b) defoliation. The standardized coefficients for each relationship are indicated, with asterisks representing significant relationships (*P < 0.05; **P < 0.01). The strength of the effect is represented by the arrows thickness. Grey arrows represent direct and positive relationships while red arrows represent negative relationships.

4 | Discussion

This study – one of the first to use exclosure experiments to examine bird and bat ecosystem services on rice fields in West Africa, through a pathway analysis – demonstrates the probable role of birds and bats as controllers of arthropod populations and possibly of rice pests, which enhances rice productivity. Results showed a significant effect of the exclosure on arthropod abundance; however, neither plant damage nor yield was affected by the exclosure. Over the months, arthropod abundance and other marks exhibited positive variations, whereas defoliation showed a decrease. Further analysis, produced by structural equation models, revealed a positive relationship between the exclusion of insectivorous birds and bats and arthropod abundance, supporting the hypothesis of arthropod predation existence when birds and bats are not excluded. Additionally, as predicted, we showed that arthropod abundance was positively linked to yellowing and directly diminished yield. Yet, we did not observe any direct impact of defoliation or grain damage on rice yield.

4.1 | Arthropod abundance

The abundance of arthropods was higher inside exclosures compared to nearby controls, as predicted (Fig. 3.1a). Studies conducted using exclosures for birds and bats in cacao plantations (Ferreira et al., 2023) and in coffee plantations (Greenberg et al., 2000) demonstrated similar results, showing a higher abundance of arthropods when these predators were absent. However, this result was mostly driven by the abundance of Araneae (Fig. 3.1b). Predatory arthropods such as spiders may favour the control of pests under bird and bat absence due to mesopredator release (Karp & Daily, 2014; Ritchie & Johnson, 2009). Furthermore, the exclosure structure can promote spider web building, which in turn can enhance spider survival and proliferation (Greenstone, 1984). Possibly, spider abundance was favoured by the net protection and support, averting a decline in rice yield primarily due to their predatory pressure on pests. Nevertheless, during the surveys, spiders were also seen building shelter by folding the rice leaves or constructing webs and nests around several rice plants, which may prevent the rice from growing and properly maturing, affecting yield (Fig. A3). When producing the pathway analysis focusing solely on the impact of insects on leaf damage and yield, no effects were found on yield, or any other variable (Table A3). This outcome suggests a possible pitfall of the methodology applied by promoting the proliferation of spiders. In comparison, the abundance of insects might have remained low in the area (Table 1), producing no effect when in exclusion conditions.

The most abundant insect orders (Hemiptera, Coleoptera, Diptera, Hymenoptera, and Orthoptera) are known to include multiple known rice pests in West Africa (Heinrichs & Barrion, 2004). However, the recorded abundance of arthropods in each parcel was low and the taxonomic resolution was weak, indicating that it may not be statistically suitable for a comprehensive functional analysis (Fig. 3.1). This stands in contrast to the findings of Ferreira et al., (2023) and Greenberg et al., (2000), in which higher recorded abundances facilitated a successful functional analysis of the present orders. Greenberg et al., (2000) observed that, within the exclosure, all the sampled Orders showed an increase in the abundance. However, Ferreira et al., (2023)'s findings are in agreement with our study recording a higher abundance of spiders within the exclosure.

Arthropod abundance changed throughout the rice production cycle. When rice was nearly mature, a greater number of arthropods were detected on the sampled parcels (Table 2). This result is not surprising since during the end of the rainy season, the rice fields are still watered creating a favourable environment for insect growth (Pathak & Khan, 1994). This aligns with findings from Settle et al., (1996) on rice fields in Java, Indonesia. The increase in arthropod abundance during this timeframe may be alarming as it aligns with the period when grains are approaching maturity, which can directly affect yield. Nevertheless, it is important to mention that our study did not detect an increase in grain damage when arthropod abundance was higher. Furthermore, it is worth noting that closely related groups of avian and chiropteran exhibit a propensity to adjust their diet with seasonal variations rather than relying on immediate insect prey availability (Yard & Kearsley, 2004).

4.2 | Plant damage

Our initial analyses, based on GLMs suggested that neither of the leaf damages was affected by the presence of the exclosure (Table 3). However, the results of SEMs linked arthropod abundance with yellowing but not with defoliation. These findings are not supported by those of Bhalla et al., (2023) when examining the effects of bat exclusion on leaf damage (i.e. yellowing and defoliation) in an exclosure experiment in India. Bhalla et al., (2023)'s findings reveal a positive effect of the exclusion of bats on defoliation while having no effect on leaf yellowing. Besides leaf yellowing possibly being caused by multiple insects (Dale, 1994), a possible explanation for this outcome may rely on potentially being caused by a virus commonly transmitted by beetles, which is known to occur in Africa but not in India (Kouassi et al., 2005; M. Wopereis et al., 2009). Rice cultivation spans multiple countries; however, the presence of pests and their associated damage may vary across different regions (Edde, 2022; Hajjar et al., 2023).

Our study uncovered variations during the rice cycle in leaf damage, with higher defoliation observed in the vegetative stage and a greater prevalence of other marks when rice reached maturity (Table 3). The decline in defoliation could be attributed to the presence of arthropod Orders that tend to damage rice in earlier stages of growth. Coleoptera order is known to defoliate rice leaves at the beginning of the rice development (Heinrichs & Barrion, 2004) and in our study it evidenced a decrease in abundance during the sampled months. Notably, leaf-feeding insects commonly found in rice fields primarily belong to the hemipteran, coleopteran and lepidopteran Orders and are known to inflict damage on rice at various stages of the rice cycle (Heinrichs & Barrion, 2004).

Grain damage was evident in similar percentages inside the exclosures and on the control, having no effect on rice yield (Fig. 3.3 and Fig. A2). Our study further included another variable regarding grain damage, the percentage of whiteheads, which was not considered in other similar studies. Whiteheads may be responsible for high yield losses derived from empty rice grains (Heinrichs & Barrion, 2004). The similar percentage of damage under both conditions is not surprising concerning whiteheads since they are mostly caused by stem borers that feed within the stem, being protected from exterior predators. Regarding pecky rice, it can be caused by sucking insects, hemipterans, followed by fungi or bacteria that get installed on the sucking entrance, damaging progressively the grain (Lee et al., 1993). The lack of differences between exclosure and control might be justified by the action of these organisms that cannot be predated by birds and bats, while the responsible insect may be predated after damaging the grain. For instance, Borkhataria et al., (2012) when implementing bird exclosures focusing on the effect of blackbirds on Florida's rice fields, had similar results concerning pecky rice.

4.3 | Rice yield

The productivity of rice remained unaltered by the exclusion of birds and bats, contrary to the decrease initially hypothesized inside the exclosure (Fig. 3.4). (Heinrichs & Barrion, 2004). However, when considering leaf yellowing, only the arthropod abundance had a negative effect on yield. By directly feeding on the plant, arthropods may greatly decrease yield (Heinrichs &

Barrion, 2004). Thus, our findings show a potential contribution of birds and bats in sustaining and enhancing rice yield due to their predatory pressure on pests although this effect may not be statistically significant in all aspects of our analysis. Comparable results emerged from birds and bats exclosure experiments conducted in coffee plantations on Mount Kilimanjaro, increasing the quantity and quality of the grain produced (Classen et al., 2014). In Classen's study (2014), a combined effect of pest predation and pollination culminated in an increase in yield. Similarly, in cacao orchards in Indonesia, a decrease in yield was recorded in canopy covers exceeding 40% under bird absence, whereas, in the lower shade, a productivity increase was found, probably attributed to a mesopredator release (Gras et al., 2016). Studies conducted on rice plantations showed no effect of the exclosure on rice productivity, however.

4.4 | Conclusions

Our results contribute to understand the importance that birds and bats have to the human population in this specific agriculture system, and supports the need to conserve these vertebrates. As shown in other studies, increasing the abundance of birds and bats could amplify their possible role in controlling pest populations, consequently minimising the need for pesticide use and agricultural intensification. As a result, this approach is an important nature-based solution, which may avert landscape alteration arising from the agricultural boundary between rice fields and native woodland.

The overall lack of significance in our results mays be a consequence of some of the limitations of this study, namely its small sample size and the reduced dimensions of the exclosure. Additionally, the exclosure structure promoted spider proliferation, potentially reducing which may the effect of bird and bat exclusion, since spiders might have preyed on insects inside the exclosure. The limited taxonomic resolution and the lack of knowledge of rice pests in the area further hindered our ability to detect the presence of pests on our sampled sites and understand their effects. Given the lack of knowledge in the area, forthcoming studies should prioritize the identification of rice pests within these plantations, allowing a deeper comprehension of whether they were preyed on by birds and bats as well as distinguish the periods of higher activity and damage to the crop in the targeted area. Furthermore, analyzing the effects of biotic factors such as fungi as well as abiotic factors like soil composition will enable a comprehensive understanding of the extent of their impact on yield. Considering the high human dependence on rice, urgent action is needed to protect and increase arthropod pest predators so that their pest suppression services can mitigate crop losses and increase yield. The methodology applied on the present study has facilitated an effective comprehension of the impacts of excluding these aerial vertebrate predators from the rice fields. Further studies in larger rice fields could allow an increase in the dimensions of the subjected area to expand the number of affected plants. Mitigating the exclosure effect on spiders poses a considerable challenge since most strategies would involve restricting other arthropods from entering. A future option is trying to balance their effect on the control by delimiting the control area with a bamboo frame. Caution must be taken when attempting this technique since birds may exploit it as resting sites, possibly facilitating the predation on the control area.

It is important to align conservation measures, such as building nest and roosting areas to favour predator's abundance, with a dialogue involving farmers regarding the importance these vertebrates may have on rice (Maas et al., 2021). The farmer's perspectives, whether negative or positive, are likely to manifest in their land management practices (Kross et al., 2018). Implementing policies to conserve aerial vertebrate predators holds significant potential to increase arthropod population control and, consequently, rice pest suppression, enhancing food security.

5 | Appendix

Figure A1. Example of a sampling parcel with the exclosure and control plots. Controls represented unnetted areas where birds and bats were not excluded, whereas areas inside the experimental exclosures were not accessible to flying vertebrates.

Table A1. Summary results of the Structural Equation Model relating exclosure and yield, as mediated by arthropod a bundance and leaf damage, i.e. (a) yellowing (Fisher's C = 3.482 with P-value = 0.481) and (b) defoliation (Fisher's C = 2.009 with P-value = 0.734).

(a)

Response variable	**Predictor**	**Std.Error**	**Std.Estimate**	**P. value**	**R^2**
Arthropod abundance	Exclosure	4.326	0.415	0.054	0.27
Yellowing	Arthropod abundance	0.186	0.503	0.016	0.54
Yield	Yellowing	0.028	0.314	0.165	0.50
Yield	Arthropod abundance	0.028	-0.454	0.047	

(b)

Response variable	**Predictor**	**Std.Error**	**Std.Estimate**	**P. value**	**R^2**
Arthropod abundance	Exclosure	4.326	0.415	0.054	0.27
Defoliation	Arthropod abundance	0.115	0.069	0.731	0.47
Yield	Defoliation	0.044	0.304	0.151	0.52
Yield	Arthropod abundance	0.023	-0.312	0.106	

Table A2. Summary results of the Structural Equation Model relating exclosure and yield, as mediated by arthropod abundance and grain damage, i.e. (a) whiteheads (Fisher's C = 3.757 with P-value = 0.44) and (b) pecky rice (Fisher's C = 3.957 with P-value = 0.412).

(a)

Response variable	**Predictor**	**Std.Error**	**Std.Estimate**	**P. value**	**R^2**
Arthropod abundance	Exclosure	4.326	0.415	0.054	0.27
Pecky rice	Arthropod abundance	0.29	0.183	0.107	0.89
Yield	Pecky rice	0.01	0.325	0.165	0.47
Yield	Arthropod abundance	0.024	-0.305	0.121	

(b)

Response variable	**Predictor**	**Std.Error**	**Std.Estimate**	**P. value**	**R^2**
Arthropod abundance	Exclosure	4.326	0.415	0.054	0.27
Whiteheads	Arthropod abundance	0.097	0.154	0.490	0.20
Yield	Whiteheads	0.057	-0.102	0.617	0.49
Yield	Arthropod abundance	0.025	-0.268	0.185	

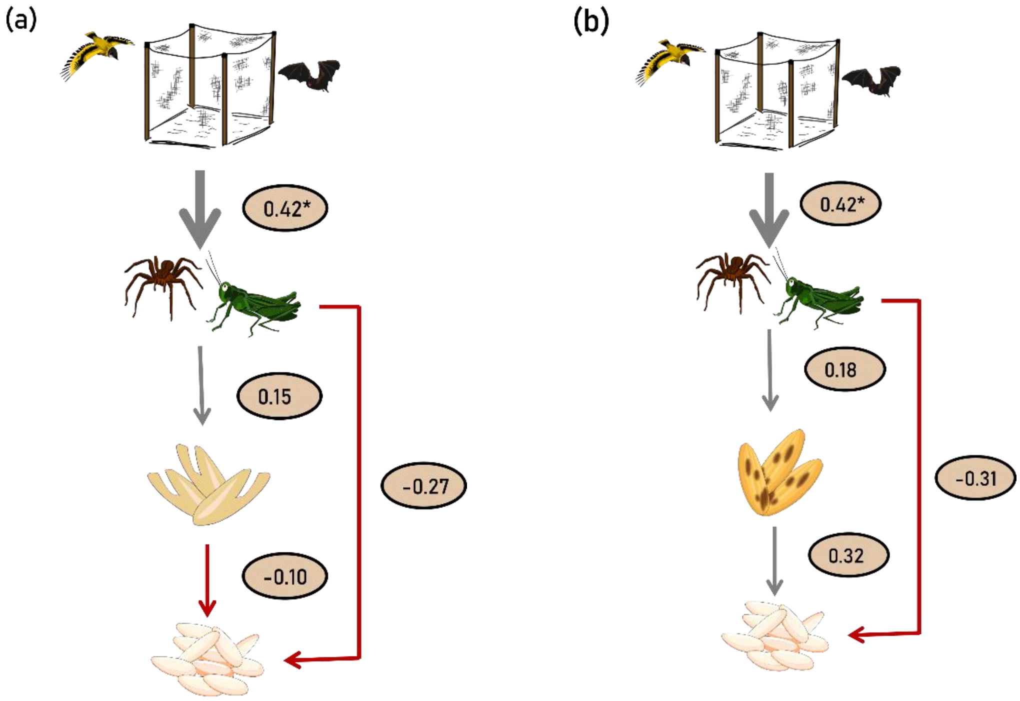

Figure A2. Results of the piecewise Structural Equation Model indirectly relating exclosure and yield, as mediated by arthropod abundance and grain damage, i.e. (a) whiteheads and (b) pecky rice. The standardized coefficients for each relationship are indicated, with asterisks representing significant relationships (*P < 0.05). The strength of the effect is represented by the arrows thickness. Grey arrows represent direct and positive relationships while red arrows represent negative relationships.

Table A3. Summary results of the Structural Equation Model relating exclosure and yield, as mediated by insect abundance and leaf damage, i.e. (a) yellowing (Fisher's C = 1.013 with P-value = 0.908) and (b) defoliation (Fisher's C = 1.925 with P-value = 0.75).

(a)

Response variable	Predictor	Std.Error	Std.Estimate	P. value	R^2
Insect abundance	Exclosure	1.096	-0.129	0.522	0.24
Yellowing	Insect abundance	0.891	-0.132	0.559	0.06
Yield	Yellowing	0.025	0.048	0.814	0.56
Yield	Insect abundance	0.107	0.116	0.586	

(b)

Response variable	Predictor	Std.Error	Std.Estimate	P. value	R^2
Insect abundance	Exclosure	1.096	-0.129	0.522	0.24
Defoliation	Insect abundance	0.502	-0.014	0.951	0.45
Yield	Defoliation	0.047	0.266	0.282	0.56
Yield	Insect abundance	0.107	0.096	0.671	

Figure A3. Photographic example of a spider nest and web around rice plants.

6 | References

Following the guidelines of Agriculture, Ecosystems & Environment

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