



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

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ABSTRACT

Rice is widely consumed as a staple food, being cultivated worldwide. However, in West Africa, production is not enough to satisfy demand. Rice often suffers intensive damage by herbivorous arthropods that affect quality and quantity of the grain. Birds and bats have been shown to suppress arthropod pests, potentially enhancing rice productivity and food security. However, the degree to which these taxa provide nature-based solutions for mitigating pest-induced rice losses is poorly known, especially in West Africa. Here, we used experimental exclosures to investigate whether birds and bats reduce plant damage and boost rice yield by suppressing arthropod abundance. In a rural area in northern Guinea-Bissau, we established 14 sets of paired control and experimental exclosures parcels, precluding access of birds and bats to rice plants. We then quantified how the absence of birds and bats influenced arthropod communities, plant damage, and rice yield over a full rice production cycle (six months). Arthropod numbers in exclosures (10.1 ± 9.1 ind./plot) were nearly double those in control plots (5.8 ± 3.0 ind./plot), a result mostly due to a lower spider abundance in the controls. The percentage of leaf and grain damage showed no difference between exclosure and control. Using Structural Equation Models, we uncovered that the exclusion of birds and bats boosted arthropod abundance but had only marginal effects on rice damage and no detectable effect on yield. The exclusion of flying vertebrates led to a marked increase in spider abundance, suggesting an effect of mesopredator release, which in turn likely helped maintaining pest abundance low and potentially contributing to the small overall effect on rice damage and yield. Enhancing the abundance of birds and bats is an interesting option to suppress agricultural pests, but our results highlight the need for a better understanding of ecological interactions in agricultural landscapes in West Africa. We stress the need for more research to inform evidence-based policies using nature-based solutions that foster the natural consumption of pests by vertebrates, as a means to improve food security.

1. Introduction

Nature-based solutions are increasingly seen as a way to meet some of Humanity's key challenges (e.g., achieving food and health security), while supporting biodiversity and livelihood sustainability (Dainese et al., 2019; Seddon et al., 2020). For instance, arthropod pests heavily impact agriculture worldwide, diminishing both product quality and yield (Deutsch et al., 2018; Wanger et al., 2014). Biological pest suppression, such as that undertaken by birds and bats, is a strategy that is

increasingly advocated for decreasing yield loss and avoiding the use of pesticides (Kemp et al., 2019; Ocampo-Ariza et al., 2023; Tuneu-Corral et al., 2023).

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 is rapidly growing, challenging rice production and prompting imports. In West Africa, rice is the most nutritious and extensively consumed grain (Adjah et al., 2022). However, even though this region produces the most rice in the continent, it still needs to

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import ca. 50% of its supply (Medagbe et al., 2020; Tondel et al., 2020). Notably, rice productivity in West Africa has stagnated over the last decade, presumably related to agricultural pest pressure, and environmental factors that limit growth (Diagne et al., 2013).

In small-scale plantations, the amount of nutrients in the soil, water availability and temperature variations may lead to yield fluctuations (Haeefe et al., 2013; Nhamo et al., 2014; Senthilkumar et al., 2020; Tanaka et al., 2017). Multiple vertebrate species (e.g., rodents or granivorous birds) inflict damage on rice by eating grains or leaves (Moinina et al., 2021). However, arthropods have been confirmed as major contributors to the damage of rice and other crops across Africa (Dhaliwal et al., 2010). Indeed, arthropod-driven rice loss is estimated at ca. 10–15 % per year (IRRI, 2011), which is partly due to rice production occurring in warm and humid environments, which are ideal for insects to grow and prosper (Pathak and 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 and Barrion, 2004). The orders Hemiptera, Orthoptera, Coleoptera and Lepidoptera are responsible for several types of damage, mainly to leaves and panicles (Heinrichs and 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 and Roy, 2012). For instance, leaf yellowing can cause the loss of 10–100 % of the yield, depending on the development stage of the plant and on the extent of leaf area that is affected (Sekiya et al., 2022). 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 assess the degree of impact that arthropod damage may have on rice productivity at the local scale.

While there is a propensity for intensive use of chemical pesticides to control insect pests, their cost-effectiveness remains low (Wilson and Tisdell, 2001). Moreover, excessive use of pesticides causes risks to human health and to pest predators (Way and Heong, 1994). Inappropriate application and prolonged exposure to pesticides may also lead pests to develop resistance, lowering their efficiency (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). Pest consumption services provided by insectivorous bats and birds are a nature-friendly way of regulating pest populations as revealed by numerous studies conducted in different regions and agricultural systems (Karp et al., 2013; Maas et al., 2013; Xavier et al., 2023), including rice paddies (Puig-Montserrat et al., 2015; Tuneu-Corral et al., 2024; Wanger et al., 2014). However, a positive effect by these predators on rice yield is not always detected (e.g., Bhalla et al., 2023; Borkhataria et al., 2012).

A powerful way to investigate the role of birds and bats on arthropod pest consumption and overall crop yield is through exclusion experiments (Maas et al., 2019). These consist of pairing experimental enclosures with controls and evaluating the impacts that the enclosures have on arthropod abundance and diversity, and crop productivity. They have been successfully applied to various tropical crops, such as cacao (Ferreira et al., 2023; Vansynghel et al., 2022), macadamia (Bouarakia et al., 2023), and rice (Bhalla et al., 2023). We conducted an enclosure experiment on rainfed lowland rice fields in Guinea-Bissau, to examine the top-down effects of insectivorous aerial vertebrate predators (birds and bats) on arthropod diversity and abundance, pest-induced plant damage, and rice yield. Specifically, we addressed the following questions: (1) Does the exclusion of aerial vertebrate predators influence arthropod communities inhabiting rice paddies? (2) Do predator-induced differences in arthropod communities affect rice plant damage rates? and, (3) To what degree is rice yield affected by pest-associated plant damage? We hypothesised that insectivorous aerial vertebrate predators suppress some arthropod orders, which in turn reduces leaf damage and increases rice yield. We thus predicted that by excluding these predators, arthropod abundance and plant

damage (i.e., leaf yellowing and defoliation) would decrease, and rice yield would increase.

2. Methods

2.1. Study area and local rice production

This study was conducted between the cities of Farim and Mansaba (Oio region), in northern Guinea-Bissau, West Africa (Fig. 1). The six targeted rice fields were within the area surrounding the villages of Bereco, Djalicunda, Bironqui, Demba Só, Mambonco and Mansaba. All rainfed lowland rice fields in this region are situated along the flooding margins of small seasonal streams. Rice fields typically exhibit a narrow width, ranging between 150 m in Bereco and 510 m in Mambonco, with variable lengths. The surrounding landscape exhibits a gentle topography, reaching a maximum altitude of ca. 75 m. It is primarily characterized by a mosaic of cashew orchards interspersed with small forest remnants, highland rice fields, and a few small villages. Guinea-Bissau has a tropical semi-humid climate, with a rainy season between June and October/November. This period of rainfall contributes to a regional annual rainfall between 1200 and 1400 mm (Catarino et al., 2001).

In the study area, the rice is sown between July and August, depending on the onset of heavy rains. The growth cycle has three different stages: (1) a vegetative phase, in which plant germination takes place and the panicle starts growing (± 2 months); (2) a reproduction phase, leading the panicle to heading – i.e., panicles exit from the rice stem (± 1 month); and (3) a grain filling and maturation phase. Following this last stage, between December and January, the rice is ready to be harvested for peeling and consumption. After the harvest, rice fields are either left fallow for cattle to graze on the residual rice plants or, in some restricted areas where water is available, they are used as vegetable gardens. Each rice field consisted of a mosaic of 0.5 ha parcels. Within the same field, parcels differed in rice variety, development stages, and several other management options. However, each parcel was managed by a single farmer and subjected to uniform management practices and conditions.

In parallel studies, the composition of bird and bat assemblages, along with their dietary habits, has been examined in the study area. Preliminary, unpublished findings indicate that the bird diversity is substantial, with a recorded total of over 200 species (Lacerda, 2024). Granivorous birds such as the village weaver (*Ploceus cucullatus*) predominate in the rice fields, but more than 45 insectivorous species also occur (Tobias et al., 2022), some of which are common. More than 25 species of insectivorous bats were recorded in the area, with notable abundance in edge and open space foragers of the genera *Scotophilus*, *Scotoecus* and *Mops*, and gleaners such as *Nycteris* sp. Bird and bat species richness and abundance were similar across all the sampled rice fields (Coimbra, 2023; Lacerda, 2024). Preliminary unpublished data based on molecular analyses of the diets of 25 insectivorous bats and 34 granivorous and insectivorous bird species captured in the study area revealed a steady consumption of arthropod prey throughout the rice season. Several potential rice pests were identified (Heinrichs and Barrion, 2004), including the Asian rice gall midge (*Orseolia oryzae*) and the grass webworm (*Herpetogramma licarsisalis*).

2.2. Experimental enclosures

During the second half of June 2022, before rice seeding, we deployed a total of 14 enclosures (Fig. 1). Experimental enclosures were built using a bamboo frame (3 × 3 m in area and 2 m tall) secured with stainless steel cables. The excluded area was similar to that of recent studies on similar crops; smaller than the 9 × 9 m used by Bhalla et al. (2023) but closer to the 2.5 × 5 m enclosures used in Sow et al. (2020) and other studies listed by Maas et al. (2019). A commercial anti-bird black net with 2 cm mesh made with braided nylon was used to prevent bird and bat access to rice plants while allowing access to



Fig. 1. Map of the study area and on-site photographic examples of the enclosure structure: (a) 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; (b) study area when rice is seeding; and (c) study area at the rice reproductive stage.

arthropods. Enclosures were left open, with the nets fully retracted, until rice was sown. Afterward, enclosures were closed, only being opened to allow human access during sampling, weeding, and harvesting. The enclosures remained in the fields for six months, until the rice from all parcels was harvested, in December 2022.

Two parcels were sampled in each rice field, except in Bironqui where four parcels were sampled. Both enclosure and control plots were set within the same parcel, at least 10 m apart (average $\pm$ SD: 23.1 $\pm$ 11.9 m) and maintained under the same management conditions throughout the entire duration of the experiment (Fig. 1).

2.3. Rice and arthropod sampling

Rice growth and damage and arthropod abundance were quantified monthly, from September to November. To mitigate potential margin effects within the enclosure, rice and arthropods were sampled in the two central rice rows (1 m along in each row) in both enclosures and controls. Each rice plant underwent thorough sampling to guarantee no arthropod was overlooked. To assess arthropod abundance, individuals were counted during the survey and photographed for later identification. Arthropods were identified to the order level. Instances of arthropods escaping were noted as unidentified. The survey was performed between 9 AM and 5 PM, to ensure similar arthropod activity (Ruttan et al., 2016). The survey alternated between morning and afternoon periods to capture the representative abundance of arthropods active during each part of the day. However, paired enclosure and control plots were consistently sampled within a half-hour period to ensure data comparability. Height of the rice plants and water depth were measured at six and two points, respectively, and values were then averaged. Rice damage was assessed at the leaf, stem, and grain levels (Supplementary Fig. S1). At the leaf level, two categories of damage were considered: yellowing and defoliation. At the grain level, two categories of damage were considered: pecky rice and whiteheads. It was also noted whether the panicles lacked any grain. Although 14 parcels were initially sampled, two were abandoned by the farmers for unknown reasons, resulting in missing data for the last monitoring and harvest. Additionally, one of the parcels was harvested by the farmer before the last data collection. Consequently, rice yield was assessed from a total of 11 parcels.

Once the rice was mature, 20 panicles were collected per enclosure

and per control plot. Rice panicles were sun-dried until attaining a stable weight for at least five days (Nwilene, 2018). Slightly adjusting the procedure used by Bhalla et al. (2023), in the lab, 500 rice grains were removed from each group of 20 panicles and dried for 24 h at 80°C. Grains were peeled using a pestle and a mortar, similar to the methods used locally, and then weighed to quantify yield.

2.4. Data analysis

All statistical analyses were conducted using R version 4.2.2 (R Core Team, 2022). Results were considered significant when $p < 0.05$.

We examined the effect of the exclusion on arthropod abundance, using negative binomial Generalised Linear Mixed Models (GLMM) with log as a link function. The total number and the number of individuals of each arthropod order was used as the dependent variable in different models, with the presence or absence of an enclosure and the month of the observations as independent variables. The number of sampled rice plants was included as an offset to accommodate slight variations in the number of rice plants sampled within each enclosure-control pair. The enclosure-control pairs were linked in the random term using an id-code. A similar procedure was used in modelling the effect of the exclusion on rice damage. In this case, we used a Gaussian GLMM with an identity link, with the percentage of rice plants exhibiting signs of yellowing and defoliation as dependent variables. The effect of the enclosures on grain damage and yield was also modelled using a Gaussian GLMM with an identity link, using the number of damaged grains and the dry weight of 500 grains as dependent variables. In these last two models, month was not included as a descriptor given that all rice was harvested in December. All models were fitted with the *lme4* (Bates et al., 2015) and *lmerTest* packages (Kuznetsova et al., 2017). We verified each model's assumptions using the package *DHARMa* (Hartig, 2018) and obtained each model's partial effects—estimated change in the response variable for each unit change in the independent variable, using the *Effects* package v. 4.2–2 (Fox, 2003). The statistical analysis concentrated exclusively on orders and damage representing more than 5% of the evidence in the sampled parcels.

To examine both the direct and indirect relationships between the enclosure effect and rice yield, we used the *piecewiseSEM* package (Lefcheck, 2016) to perform piecewise Structural Equation Models (SEMs)

with a set of GLMMs, using the data from the last month of sampling. SEMs consist of path analysis that tackles intricate multivariate relationships among a set of directly interrelated variables (Lefcheck, 2016). SEMs were employed as a complementary analysis, thereby providing a broader exploration of underlying mechanisms, potentially uncovering hidden constructs and insights into complex variable connections (Lefcheck, 2016).

SEMs were built considering separately the two types of leaf damage – yellowing and defoliation, and the two types of grain damage – whiteheads and pecky rice. In each SEM, we initially included the overall insect abundance (i.e., overall arthropod abundance, excluding spiders), and subsequently incorporated the insect order most strongly associated with the respective rice damage, either to leaf or grain. This was not possible for whiteheads due to the insufficient number of records of Lepidoptera, which is potentially the primary order responsible for this type of damage (Heinrichs and Barrion, 2004). In this case, we used only total insect abundance as a proxy. For each type of damage, the basis set of the SEM consisted of the following GLMMs: (1) the effect of the enclosure on spider abundance; (2) the effect of the enclosure and spider abundance on relevant insect order abundance; (3) the effect of insect order abundance on rice leaf and grain damage; (4) the effect of insect order abundance and leaf and grain damage on rice yield. Spider abundance was log-transformed to reduce data skewness. Gaussian LMMs with identity link were used in all models. The enclosure-control pairs were linked in the random term using an id-code. Non-saturated

models were used, and the model's goodness-of-fit was assessed using Fisher's C as the statistical test, combining the *p*-values of the set of GLMMs (Shipley, 2000).

3. Results

3.1. Arthropod abundance

A total of 635 arthropods from 10 orders were identified, with an average ($\pm$ SD) of 7.9 ± 7.1 individuals per parcel (Supplementary Table S1). Total arthropod abundance was higher inside the enclosures ($\beta = 0.4$, $p = 0.007$, Fig. 2a, Supplementary Table S2): 405 individuals were observed in the enclosures (10.1 ± 9.1 ind./ enclosure) and 230 in the controls (5.8 ± 3.0 ind./ control). Insect abundance was similar under both conditions, with 218 individuals observed in the enclosures (5.5 ± 2.7 ind./per enclosure) and 187 in the controls (4.7 ± 2.8 ind./ per control, Fig. 2b, Supplementary Table S2). 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%).

An increase in arthropod abundance was recorded throughout the rice production cycle ($\beta = 0.5$, $p < 0.001$, Fig. 3a, Supplementary Table S2) while insect abundance showed less clear pattern ($\beta = 0.2$, $p = 0.077$, Fig. 3b, Supplementary Table S2). In most instances, enclosure and month had no effect on the abundance of individual arthropod orders (Supplementary Table S2), except for Araneae for which abundance

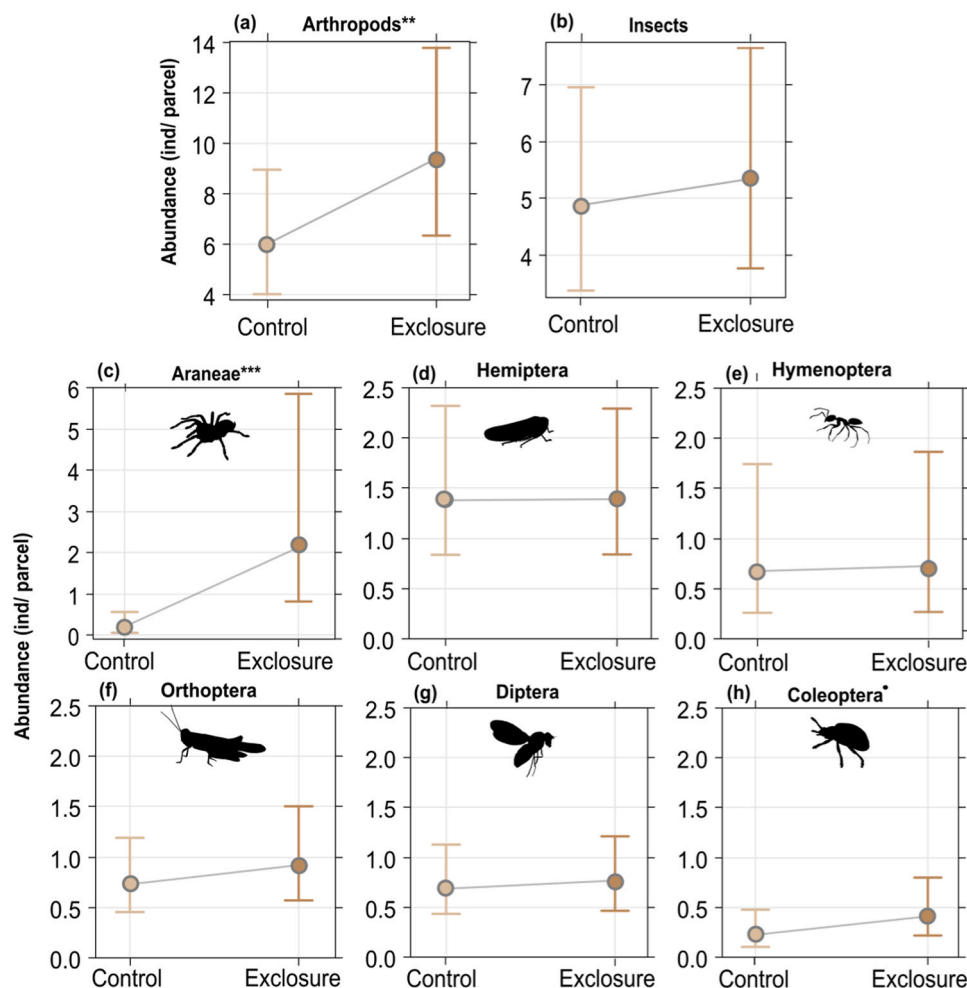


Fig. 2. Partial effects of the GLMMs of control-enclosure pairs on the abundance of (a) arthropods, (b) insects, and the most frequent arthropods orders: (c) Araneae, (d) Hemiptera, (e) Hymenoptera, (f) Orthoptera, (g) Diptera, and (h) Coleoptera. Control represents areas where birds and bats were not excluded, whereas Enclosure represents areas where these groups were excluded. The significance levels are indicated as ** $p < 0.01$ and *** $p < 0.001$. A dot denotes near significance. Notice that the y-scale of the graphs varies between taxa.

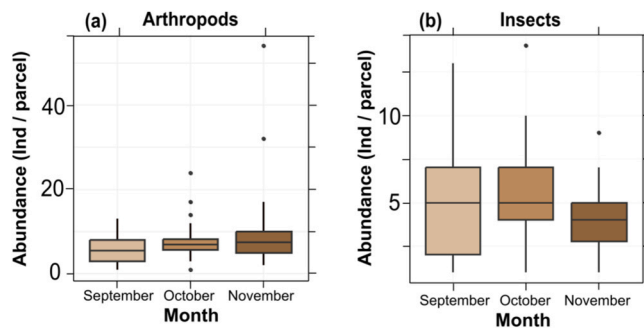


Fig. 3. Partial effects of the GLMMs of the month effect on the abundance of (a) arthropods, and (b) insects. The study covers the months of September, October and November and the data collected at both exclusions and controls. Notice that the y-scale of the graphs varies between taxa.

was higher inside the exclusions ($\beta = 2.5$, $p < 0.001$, Fig. 2c, Supplementary Table S2) and increased over time ($\beta = 1.1$, $p < 0.001$, Supplementary Table S2). Additionally, Coleoptera showed an increase in abundance inside the exclusions ($\beta = 0.6$, $p = 0.053$, Fig. 2h, Supplementary Table S2) and a temporal decrease in abundance ($\beta = -0.4$, $p < 0.04$, Supplementary Table S2). Diptera showed an opposite pattern over time ($\beta = 0.3$, $p = 0.04$, Supplementary Table S2).

3.2. Leaf damage, grain damage, and rice yield

On average, $11.0 \pm 9.5\%$ of the rice plants evaluated showed defoliation, and $22.4 \pm 15.9\%$ had yellowing. Vertebrate exclusion had no effect on any type of leaf damage (Fig. 4a and b, Supplementary Table S3), but month exhibited a negative effect on defoliation ($\beta = -3.9$, $p < 0.001$, Supplementary Table S3).

On average $54.2 \pm 34.7\%$ of the panicles had grain damage, with pecky rice showing on $47.5 \pm 32.0\%$ of the panicles. Additionally, whiteheads were present at a rate of $9.1 \pm 5.1\%$ per panicle. No significant difference was found, in both types of grain damage, between exclusions and controls (Fig. 4c and d, Supplementary Table S3).

Rice yield varied between 5.5 and 11.0 g per plot (8.8 ± 1.5 g/plot). No yield differences were detected between exclusion and control areas ($\beta = -0.1$, $p = 0.9$, Supplementary Table S3, Fig. 4e).

3.3. Direct and indirect exclusion effects on rice yield

In all SEMs, Araneae increased inside the exclusions ($\beta = 0.5$, $p = 0.013$, Supplementary Tables S4 and S5, Fig. 5), while no other relationships between the sampled variables were significant (Supplementary Table S5). All models focusing on insect orders most strongly linked to each type of damage showed an R^2 below 50%, except whiteheads, evidencing 66% (Fig. 5d, Supplementary Table S4).

4. Discussion

This is one of the first studies to use experimental exclusions to examine agricultural ecosystem services provided by birds and bats in West Africa. Aligning with previous research in multiple tropical crops (Bhalla et al., 2023; Ferreira et al., 2023; Karp et al., 2013), arthropod abundance was higher in the exclusions than in the control plots. However, our results failed to unveil any exclusion effects on insect abundance, rice damage or rice yield either due to the actual absence of such effects or to limitations imposed by the experimental method used. One of these limitations has been imposed by the exclusion structure which increased spider abundance inside exclusions, giving rise to confounding effects. Indeed, it is possible that the higher abundance of spiders might increase insect predation inside exclusions, contributing to offset any eventual difference with control plots.

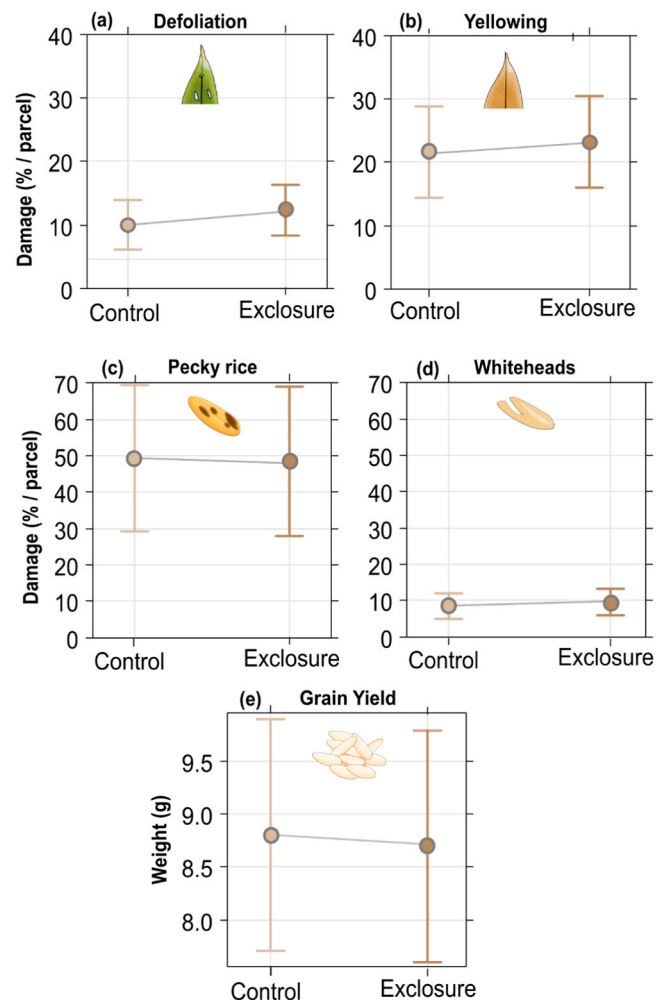


Fig. 4. Partial effects of the GLMMs of control-exclusion pairs on leaf and grain damage and rice yield. The two types of leaf damage recorded were: (a) defoliation and (b) yellowing. Grain damage was measured as (c) pecky rice and (d) whiteheads, while yield (e) was measured as the weight of 500 dry rice grains. Control represents areas where birds and bats were not excluded, whereas Exclusions represents areas where these groups were excluded. Notice that the y-scale of the graphs varies between taxa.

4.1. Arthropod abundance

As anticipated, arthropod abundance was higher inside exclusions than in nearby controls. Several studies found similar results for other tropical crops (e.g., Ferreira et al., 2023 for cacao, Greenberg et al., 2000 for coffee). However, in our case this pattern was mostly driven by the abundance of Araneae. Predatory arthropods such as spiders may benefit from the absence of birds and bats through mesopredator release (Karp and Daily, 2014; Ritchie and Johnson, 2009). Furthermore, the structure of the exclusion can provide support and protection for spider webs, which in turn can enhance spider survival and proliferation (Greenstone, 1984). Increased spider abundance might have reduced insect pest abundance, and this in turn might have softened pest-induced declines in rice yield. Furthermore, when generating SEMs to incorporate insect variables at the order level, we did not account for the insect trophic level. Importantly, as noted by Sadou et al. (2017) while insect predators may damage rice, spiders typically only prey upon the insects, posing no direct threat to the plant (Sadou et al., 2017).

Path analysis revealed a positive influence of vertebrate exclusion on spider abundance, also suggesting a release of spiders when birds and bats are absent. This underscores the complexity of the trophic webs in this system, and the need to incorporate intermediary relationships that

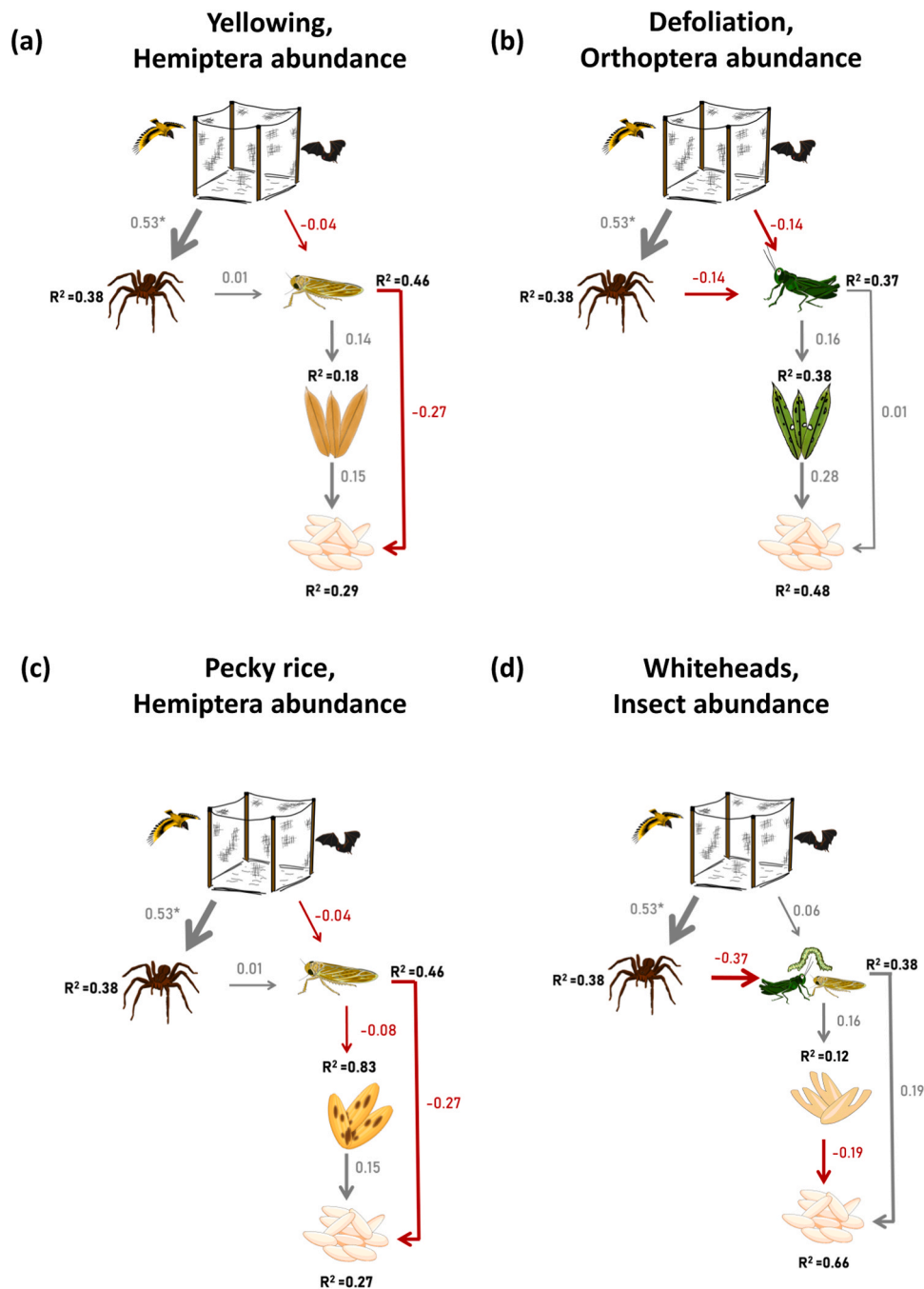


Fig. 5. Results of the piecewise Structural Equation Model relating enclosure and yield, as mediated by the rice plant observed damage and the insect order most strongly associated with each type of damage: (a) yellowing and Hemiptera abundance (Fisher's C = 10.374 with p-value = 0.240); (b) defoliation and Orthoptera abundance (Fisher's C = 9.946 with p-value = 0.269); (c) pecky rice and Hemiptera abundance (Fisher's C = 9.062 with p-value = 0.337); and (d) whiteheads and total insect abundance (Fisher's C = 4.735 and with p-value = 0.785). The standardized coefficient for each relationship is indicated, with asterisk representing significant relationships (* $p < 0.05$). The strength of the effect is represented by the arrows' thickness. Grey arrows represent positive relationships while red arrows represent negative relationships.

affect the lower levels. It also highlights a potential pitfall in the use of enclosures, as they may inadvertently promote the proliferation of mesopredators, corresponding mainly to spiders in our study, but also potentially other predator species such as Odonata, Orthoptera, or Coleoptera (Heinrichs and Barrion, 2004), offsetting the effects of the absence of birds and bats. Although Araneae and Coleoptera were the only orders showing a significant increase under bird and bat exclusion, future studies should consider the potential proliferation of natural enemies of pests inside the enclosures, which could compromise the efficacy of the method (Schmitt et al., 2021). Other studies have arrived at

similar conclusions, highlighting the potentially greater impact of mesopredators on insect communities inside the enclosures (Cassano et al., 2016; Ferreira et al., 2023; Karp and Daily, 2014).

The most abundant insect orders (Hemiptera, Coleoptera, Diptera, Hymenoptera, and Orthoptera) include multiple rice pests in West Africa (Heinrichs and Barrion, 2004). However, the low arthropod abundance in each parcel and weak taxonomic resolution hindered the possibility of conducting a comprehensive functional analysis. Although night sampling could potentially enhance our arthropod dataset, it was deemed infeasible due to safety concerns and the strong local cultural and

societal discouragement against nocturnal activities in the rice fields. In Ferreira et al. (2023) and Greenberg et al. (2000), higher abundances facilitated a successful functional analysis of the different orders. Greenberg et al. (2000) observed that all orders showed an increase in abundance in the enclosures, whereas, similar to our study, Ferreira et al. (2023) found spiders to be more abundant in the enclosures. Mitigating the enclosure effect on spiders poses a considerable challenge since most strategies would involve restricting other arthropods from entering. A potential future approach could involve trying to balance their effect on the control plots by delimiting the control area with a bamboo frame similar to the one used in the enclosure. However, caution must be taken when attempting this technique, as birds may exploit the frames to perch, potentially facilitating predation inside the controls. Another approach could involve adding small pieces of net into the control area, ensuring that no plants are enclosed, thus creating similar web-building opportunities as those found within the enclosure (Gunnarsson, 2007).

4.2. Plant damage and rice yield

Our initial analyses, based on GLMMs suggested that over time neither of the leaf damage types was affected by the enclosure. These findings further supported by the SEM analysis, differ from those of Bhalla et al. (2023), who examined the effects of bat exclusion on leaf damage (i.e., yellowing and defoliation) in India. While conducting night-time only exclusions, Bhalla et al. (2023) found a positive effect of the exclusion of bats on defoliation but no effect on leaf yellowing. Leaf yellowing might be caused by multiple insects (Dale, 1994), either by directly affecting the plant or by transmitting viruses (commonly by beetles) (Kouassi et al., 2005).

Grain damage, considering both pecky rice and whiteheads (which may be responsible for high yield losses derived from empty rice grains; Heinrichs and Barrion, 2004), was similar in enclosures and in control plots, seemingly having no effect on rice yield. Whitehead damage is mostly caused by stem borers that feed within the stem (thus protected from exterior predators), while pecky rice is mostly due to sucking insects, such as hemipterans, which allow for fungal or bacterial infections, progressively damaging the grain (Lee et al., 1993). The lack of differences between enclosure and control plots might be explained by the overall low abundance of these insects, which might circumvent flying vertebrate predators from focusing on them. For instance, Bor-khataria et al. (2012) when implementing bird enclosures focusing on the effect of blackbirds on rice fields in Florida, obtained similar results with no differences concerning pecky rice.

Rice yield remained unaltered by the exclusion of birds and bats. In the study of Bhalla et al. (2023), the enclosure also had no effect on rice yield. Once again, this outcome may stem from various factors, including the limited sample size alongside the confounding effect of increased spider abundance, potentially impeding a further rise in insect pest populations. However, other unaccounted factors could have influenced this outcome. In most of our SEM models, less than 50% of the yield variation was explained by the variables, suggesting the possibility of additional factors, such as fungi, diseases or soil nutrient deficiencies should be considered, as these can impact rice yield by disrupting essential nutrient uptake and impairing plant health (Heinrichs and Barrion, 2004; Saito et al., 2019).

This may also indicate that pests responsible for rice damage are not present in high enough numbers to impact crop productivity in the study area. Notably, our study encompassed three rice development stages, surveying arthropod assemblages and plant-level damage. Thus, it is unlikely that we overlooked quantifying such insects. Instead, it is possible that an exclusion effect on rice yield would become significant in a scenario where pest abundance is high.

4.3. Birds and bats as pest suppressors

Despite the abundance of insectivorous birds and bats in the study area (Coimbra, 2023; Lacerda, 2024), and confirmed predation of several potential pest insects (authors' own data), there was no evident impact on rice damage or yield. However, the consumption of pest prey does not always result in a reduction of crop damage, and this study adds to several others that, using enclosures, also failed to demonstrate the top-down effects of birds and bats on agricultural crops (Maas et al., 2016; Tuneu-Corral et al., 2023).

The non-significant results of this study concerning the effect of the exclusion of birds and bats on crop damage and yield may be attributed to its low sample size and small enclosure dimensions. While the number of sampled enclosure-control plots surpasses the eight recommended by Maas et al. (2019), the lower number of surveys conducted in each plot may justify the overall lack of significance in our findings. However, as discussed by Bhalla et al. (2023), predator exclusion, while a widely used method, has inherent limitations, and may not fully isolate the area of the enclosure. Factors such as the mesopredator release mentioned above, but also potential effects of enclosures on insects and rice plants (e.g., shading or edge effects), or insufficient predation pressure to limit pest survival, could contribute to the absence of effects resulting from the exclusion of birds and bats. Furthermore, despite our cautious approach in sampling only the two inner rice rows, enclosures might not effectively prevent predation by birds and bats foraging near the enclosure (Maas et al., 2019; Tuneu-Corral et al., 2023), potentially resulting in observable predator effects inside the enclosure. In fact, many insect pests have flying stages and may still be preyed upon by open- or edge-foraging birds and bats despite the enclosure (Russo et al., 2018). It is plausible to expect higher predation rates of flying insects over enclosures that do not extend significantly above the crop like the ones we used, even if similar difficulties were found in studies with larger enclosures (Bhalla et al., 2023; Tuneu-Corral et al., 2024). Conversely, some pest stages, usually the most damaging, live inside the plant stems (Heinrichs and Barrion, 2004) and are thus not accessible to either bats or birds (Tuneu-Corral et al., 2024). The enclosures may in fact be more effective in preventing predation by gleaners.

Gleaning birds such as *Cisticola* are common in the studied area, foraging either in the vegetation or on the ground. Their diet is diversified, including insects (and their larvae) as well as spiders (Ryan, 2020; Ryan and Dean, 2020). Similarly, some species of gleaning bats are present. Those most frequently encountered belong to the genus *Nycteris*, of which several breeding colonies are known to occur near the rice fields. These species prey on various insects, including some pests; however, they reportedly favor soft-bodied arthropods such as spiders as their primary prey (authors' data; Happold and Happold, 2013). The exclusion of these gleaning species might have thus further contributed to the increased abundance of these mesopredators inside the enclosures.

In this region, most lowland rice is cultivated in less than six months. During this period, the landscape undergoes dramatic changes - from almost barren, dry land with minimal grassy vegetation to lush, green flooded fields of rice. These transformations are expected to significantly impact the region's fauna composition and phenology, particularly insects (whether pests or not), birds, and bats (Rainho et al., 2023). Further fluctuations are anticipated over the years as climatic variations and aridity increase (Lickley and Solomon, 2018). However, the seasonal and annual dynamics of both predators and prey are poorly understood. While we suspect that pest abundance levels during our study period were atypically low, the absence of consistent historical data or even collective memory of past pest peaks hinders our ability to fully confirm these suspicions. In agreement with Bhalla et al. (2023), we argue that a more comprehensive approach is necessary to address the knowledge gaps in rice production in such dynamic landscapes, and to determine whether birds and bats exert a top-down effect on rice pests or if this effect depends on other factors such as landscape context or

seasonality.

5. Conclusions

The role of insectivorous birds and bats as pest suppressors was not evident in our study, potentially due to mesopredator release increasing the abundance of spiders inside the experimental enclosures. Considering the acute lack of knowledge in the area, forthcoming studies should prioritise the identification of rice pests within these plantations. To elucidate the intricate dynamics among key insect predators like bats and birds and their pest-insect prey, it is essential to untangle the complex interactions within the entire food web. This entails considering the influence of other participants, including spiders, additional predators, competitors, as well as accounting for factors such as fungi and bacterial infections. Furthermore, analysing the effects of abiotic factors like seasonality and soil composition would contribute to a more holistic understanding of the multiple factors impacting rice yield in West Africa.

CRedit authorship contribution statement

Madalena Sottomayor: Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis. **Ricardo F. de Lima:** Writing – review & editing, Investigation. **Ricardo Rocha:** Writing – review & editing, Validation, Supervision, Investigation, Conceptualization. **Ana Filipa Palmeirim:** Writing – review & editing, Visualization, Validation, Supervision, Methodology, Investigation. **Christoph F.J. Meyer:** Writing – review & editing, Investigation, Conceptualization. **Ana Rainho:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

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.2024.109067](https://doi.org/10.1016/j.agee.2024.109067).

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