



# Batting for rice: The effect of bat exclusion on rice in North-East India

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## ABSTRACT

Insectivorous bats are gaining increasing attention for their potential as biological agents of pest suppression. Studies around the world have demonstrated their tendency to track and hunt agricultural pests over time and space, and thus to have a positive impact on reducing plant damage and protecting yield of agricultural crops. We documented the effect of insectivorous bats on the health and yield of a rice crop in Assam, India. Using six sets of paired experimental and control plots (of which five were analysed), where bats were selectively excluded from the experimental plots, we collected two measures of plant damage and one measure of total yield to assess the impact of bats on the crop. In parallel, bat activity at the six sites was recorded over the rice growing season using passive acoustic recorders. Our results show that the exclusion of insectivorous bats causes an increase in the degree of defoliation suffered by rice plants. We also report non-significant differences in the degree of yellowing of rice and of the total yield between the experimental and control plots. Bat activity levels showed a mono- or bimodal peak in activity over the growing season, which broadly tracked the maturity of rice, a pattern also seen in many insect pests. Our results strongly suggest that bats have suppressive impact on pest action in rice fields. The general trend in activity levels, as well as the significant difference in plant damage, would indicate that bats are hunting insect pests and that the non-significant difference in final yield was likely the result of methodological limitations. These findings suggest that bats add significant ecological and economic value to Indian rice ecosystems and hold great potential to be used in integrated pest management (IPM) strategies aimed at suppressing pests.

## 1. Introduction

Climate change, through increased temperatures, changing precipitation patterns and increasingly erratic weather (Shukla et al., 2019), has and will continue to decrease the reliability and profitability of agricultural industries (Lobell and Field, 2007; Rosenzweig et al., 2014). Pests add to this burden. The range of many insect pests, particularly in the higher latitudes, is predicted to increase (Vanhanen et al., 2007; Stange and Ayres, 2010), as is their metabolism and population growth rate (Deutsch et al., 2018). Rice (*Oryza sativa*) is consumed as a staple food by over half the world's population (Muthayya et al., 2014; IIRI, 2019). Increased pest action, which already severely affects yield (Pathak and Khan, 1994), is predicted to decrease global rice yield, for a two-degree Celsius increase in mean temperatures, by 19% (Deutsch et al., 2018).

The Green Revolution of the 1960 s transformed Indian agriculture

by means of the introduction of high yielding varieties of rice (Nelson et al., 2019). However, despite the disease- and pest-resistant nature of these varieties, pesticide use in India (Bowonder, 1979; Parayil, 1992) and indeed across much of Asia (Parveen and Nakagoshi, 2001; Normile, 2013; Huang et al., 2014; Wang et al., 2018), grew steadily, with conflicting evidence of its effect on pest populations. In the complex ecosystem of a rice field, indiscriminate pesticide use often does more harm than good, suppressing arthropod predator populations to a greater extent, and for longer, than the pest populations, leading to higher overall pest action and driving pests to evolve resistance (Way and Heong, 1994). In India, erstwhile minor pests, such as the brown planthopper, became prominent post the Green Revolution, causing widespread damage that continues to the present day (Bottrell and Schoenly, 2012). In response to this, Integrated Pest Management (IPM) strategies were developed as the sustainable alternative to chemical pesticides (Teng, 1994). Foremost among them was the use of natural

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enemies of pests such as fish (Halwart et al., 2012), frogs, parasitoids (Babendreier et al., 2020), and ducks (Zhang et al., 2009; Teng et al., 2016) to control pest populations. And, in the last decade, the potential of bats to be effective pest agents has emerged as a topic of attention.

Insectivorous bats have been shown to eat pests of cotton (Federico et al., 2008; Kolkert et al., 2020), corn (Maine and Boyles, 2015), rice (Puig-Montserrat et al., 2015; Kemp et al., 2019), cacao (Cassano et al., 2016), coffee (Classen et al., 2014), and other crops (Maas et al., 2019). They have been shown to reduce pest abundance (Kalka et al., 2008; Williams-Guillén et al., 2008), plant damage (Maine and Boyles, 2015) and loss in yield (Librán-Embú et al., 2017). They have also been shown to limit disease spread by limiting disease vectors like mosquitoes and other flies (Kervyn et al., 2012; Siemers et al., 2012; Puig-Montserrat et al., 2020).

Many insectivorous bats are generalists, eating any insects that they can catch and handle (Kunz et al., 2011). In addition to suppressing resident pest populations, this gives them the ability to buffer against sudden outbreaks, or the invasion of new pest species, against which existing pest control measures may be ineffective (Maas et al., 2016). The generalist diet of many bats is complemented by their high mobility, which allows them to change foraging grounds and survive on different prey when crop pests are not available (Lee and McCracken, 2005).

Several methods have been used to estimate the value of the pest suppression service provided by bats. Among them, diet analyses (McCracken et al., 2012) and exclusion experiments (Maas et al., 2019) dominate, with mathematical models (Federico et al., 2008) and experimental manipulation of bat populations (Puig-Montserrat et al., 2015) also making an appearance.

The largest estimates of pest suppression by bats are rooted in diet analyses that used either microscopic (Leelapaibul et al., 2005; Lee and McCracken, 2005; Wanger et al., 2014) or genetic (McCracken et al., 2012) tools to document the identity and proportion of agricultural pests in the diet of bats. These data can then be used to estimate the impact of bat predation on pest populations, and therefore yield, per unit of farmland (Cleveland et al., 2006). Some studies have gone further, to extrapolate these estimates to entire countries. One study estimated the pest suppression service of the Brazilian free-tailed bat (*Tadarida brasiliensis*) to the cotton industry of the U.S.A to be worth \$26.7 billion per annum (median) (Cleveland et al., 2006; Boyles et al., 2011), while another estimated that of the wrinkle-lipped bat (*Tadarida plicata*) to the rice industry of Thailand to be worth \$1.2 million per annum (Wanger et al., 2014). While diet analyses establish crucial links between bats and their prey, economic valuations based on this method are limited by assumptions concerning how an agricultural ecosystem will respond to the removal of a top predator. These assumptions are further stretched when extrapolating over an entire country (Fisher and Naidoo, 2011; Boyles et al., 2013; Maine and Boyles, 2015).

Many insect pests of rice, including planthoppers, leafhoppers, leaf folders, and stem borers, show an *r*-selected reproductive strategy, with fast reproductive rates and short generation times (Heong et al., 1992; Gurr et al., 2011). The primary limits on the population growth of these insects are set at the egg to larval and larval to adult stages, imposed by natural enemies other than bats (Heong et al., 1992; de Kraker et al., 1999). Bats prey primarily on the flying adult stages of these pests, while most of the crop damage is done by the larvae (Maine and Boyles, 2015). The impact of bat predation is therefore only felt in subsequent generations of pests.

Crops themselves have evolved alongside pests, and many are capable of compensating for pest damage, with some showing no decrease in yield for mild to moderate pest action (Hughes and McKinlay, 1988; Way and Heong, 1994; Lv et al., 2008). The impact of pest action on yield is further complicated when multiple pest species are acting on the same plant. While some studies have shown simultaneous attack by multiple pests on rice to have an additive or synergistic negative effect on plants (Litsinger et al., 2011a, 2011b), others have shown a less-than-additive effect (Pinnschmidt et al., 1995). Even if the

absence of bat predation was to increase the activity of some pests, it is by no means straightforward to determine the resulting contribution to plant damage or yield loss, particularly if the plants are under stress from other pests.

Rice fields, especially those managed in a non-intensive manner, are ecologically diverse and complex landscapes and host many non-pest arthropods (Drechsler and Settele, 2001; Bambaradeniya and Edirisinghe, 2009). Among these arthropods are predators like spiders and ants, which are also prey of insectivorous bats (Maas et al., 2013). The net effect of bat predation on pests therefore depends on their effect on mesopredators, as well as on their direct effect on the pests. Synergistic effects between bats and predatory arthropods may cause a net increase in pest suppression, leading to lower losses of yield (Mooney et al., 2010). On the other hand, bats may curtail the effect of mesopredators, leading to higher pest activity and plant damage than would be the case without bats (Karp and Daily, 2014).

In theory, exclusion experiments can account for the above dynamics where methods rooted in diet analyses cannot. That is, a bat exclusion experiment can be designed to allow the biotic community within to reach a new equilibrium, which recreates the characteristics of the ecosystem minus bats (Boyles et al., 2013). The reality is more complicated.

Exclusion experiments involving bats are necessarily field based. This imposes practical restrictions on the size of the enclosures, and the control that one has over other variables such as weather, configuration of the enclosures, and management history of the chosen sites. Bats' nocturnality adds another complication: unless the barriers to access are removed during the day, the effect of bats will be confounded with those of birds. The logistical requirements of twice daily adjustment to the enclosure further limits the scale and extent of the enclosures. No doubt influenced by these considerations, the vast majority of bat exclusion experiments have focussed on tree/bush type crops, where individual trees/bushes can be used as a unit of replication and covered by netting (Maas et al., 2019). Links between bat pest suppression and row crops have therefore primarily come from diet analyses and these estimates tend to be larger than those calculated from exclusion experiments. Previous exclusion experiments have been conducted on crops such as coffee (Karp and Daily, 2014), cacao (Cassano et al., 2016) and corn (Maine and Boyles, 2015) and have been set primarily in North and South America. Despite the acknowledged potential of bats to regulate rice pests and the glaring need for sustainable pest control of a crop which loses 30% of its yield to pest and pathogen action (Savary et al., 2019), only two studies have attempted an economic evaluation of this dynamic (Wanger et al., 2014; Puig-Montserrat et al., 2015), neither of which were set in India or China, the two largest rice producing countries in the world.

This study reports the results of the first exclusion experiment of bats over rice fields. Set in Assam, India, five pairs of enclosures were used to compare the effect of excluding bats from rice. By pairing experimental plots with controls, this study documented the effect of removing these top predators from the rice food web on crop damage and total yield. We hypothesise that the exclusion of bats will result in increased insect pest activity, and therefore greater damage to the rice plant. We further hypothesise that the increased plant damage will affect the final yield of the crop, with the experimental plots producing a lower yield than the control plots. To the best of the authors' knowledge, this is the first experiment for a rice field that excluded bats, while leaving birds undisturbed, in their access to a crop.

## 2. Methods

### 2.1. Study site

The study was conducted in the rice fields of Puthimari, a village in the Sonitpur district of Assam. Rice is a major crop in Assam, grown on 2.43 million hectares of land (Directorate of Economics and Statistics,

2019). Of the three rice crops, Ahu (autumn), Boro (summer), and Sali (winter), planted in Puthimari each year, our field season was conducted over the Sali/winter rice season of 2019. This location was chosen because the fields to the east of the village were large and uninterrupted, and offered sites that were identical in management strategy, set approximately 100 m from each other (Fig. 1).

The individual 'fields', i.e plots of individual farmers, can vary in size and can be difficult to distinguish from that of their neighbours'. The fields studied extend to the east for several km before reaching the first village. To the south, they extend a few hundred metres to a river and to the north they extend around one km before reaching a highway.

The six sites chosen for our study were set in the fields of five farmers. Each farmer was compensated for use of their land, amounting to the maximum possible value that the crop within the experiment could be sold for. After the final weighing had been conducted, they were also given the grain collected from the plots. Permission for this work was granted by the owners of each field, as well as the District Agricultural Officer of Sonitpur, Tezpur, and the Divisional Forest Officer, Sonitpur West Division, Tezpur.

## 2.2. Experimental setup

Six pairs of experimental-control enclosures were constructed (though data from only five were eventually used), each set at least 100 m from its nearest neighbour and from the closest treeline. The fields were located west of the village, which features a mix of semi-forested areas and houses built of bamboo or concrete. Rice in Puthimari is grown in a mosaic of varieties and management strategies, depending in part on the religious and ethnic background of the landowner. While the fields selected for this study were not treated with pesticides or fertilisers, some of the surrounding fields were.

Each 'site' consisted of an experimental and control 'plot', set 8 m apart. The experimental enclosure was built using a bamboo frame 9 m x

9 m in area and 4 m tall (Fig. 2). Each frame consisted of eight vertical stilts and four horizontal beams on top. Nets used for cricket practice, with a 5 cm mesh size, were used for the walls and roof of the enclosures. These nets were ideal for enclosures because the mesh size allowed for the free movement of insects while excluding all bats and the stiffness of the material ensured that birds would not get entangled in them. Although birds routinely perched on the enclosures, they were never caught in the nets. With the aim of excluding only bats, each 'wall' and the 'roof' of the experimental plots had a pulley system that allowed it to



Fig. 2. One of the six pairs of experimental (left) and control (right) plots built in the rice fields of Puthimari village, Assam. The experimental enclosure was a 9 m x 9 m by 4 m bamboo frame with nets making up the walls and roof of the enclosure. The nets were retracted at dawn and extended again at dusk every day to exclude bats but not diurnal birds from the plants within. The control was an identical frame without any nets, set 8 m away from the experimental plot. Both plots of each pair were constructed on the land of the same farmer. The frame in the control plot accounted for the effect of birds using it as a perch.

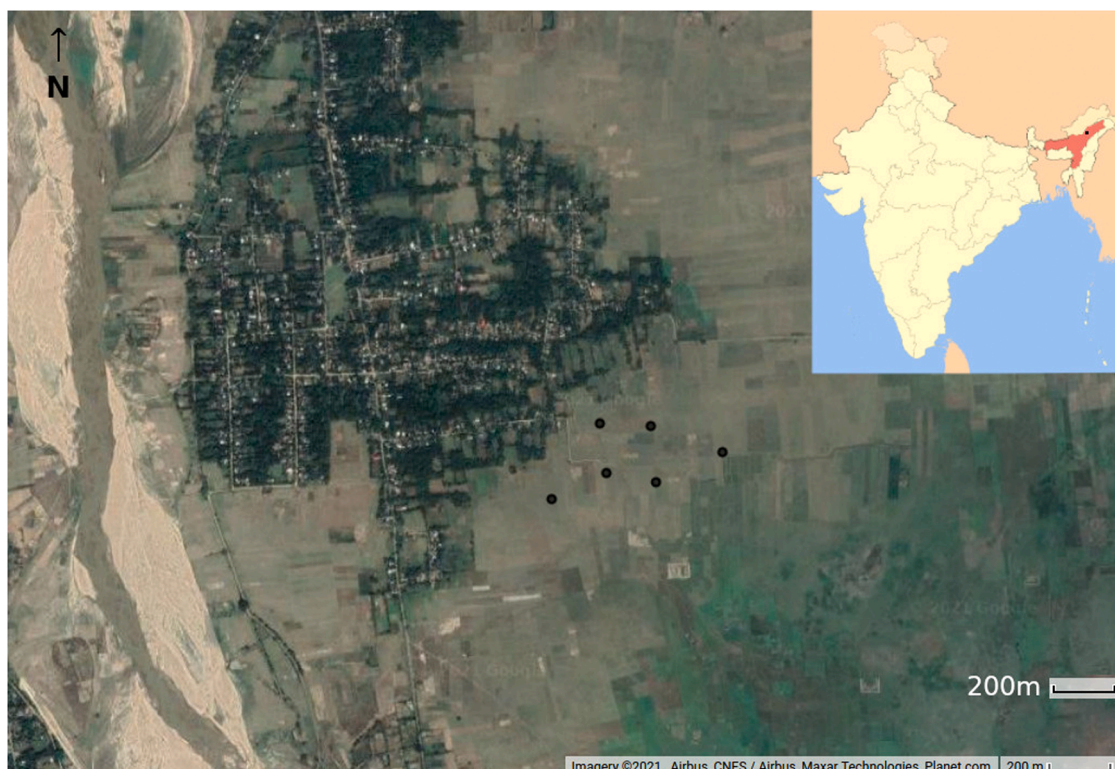


Fig. 1. Six sites chosen for the six experimental-control plots of the exclusion experiment. Located in Puthimari village, Assam, these sites were to the east of the village, and were part of a larger rice landscape in which rice were grown, within a mosaic of different varieties and management strategies. Source: Map of India by Ganeshk (GFDL&cc-by-sa-2.5,2.0,1.0); Airbus, CNES/Airbus, Maxar Technologies, Planet.com.

be retracted. The walls retracted upward and were pulled tight to the top frame. The net that comprised the roof was attached at one end to the enclosure frame, and at the other end to a sliding bamboo rod. Ropes attached to this sliding rod were used to pull the net across the top of the enclosure. Smaller ropes tied intermittently to the sides of the 'roof' net were used to ensure that, when extended, it was taut and left no space for bats to enter (Fig. 2).

Every experimental plot was paired to a control plot, which was an identical bamboo frame, sans nets. They accounted for the influence of birds using the frame as a perch, which may have biased their activity around the enclosures (Boyles et al., 2013).

It was clear that the daily process of retracting and extending the nets would entail disturbing the rice immediately adjacent to the plot. To ensure that conditions at both plots were standardised, a 0.5 m wide buffer around every enclosure, both experimental and control, was cleared of plants to permit access. In addition, within every enclosure, both experimental and control, the first three rows closest to the edge were treated as a 'buffer zone', and not considered. Only plants situated more than three rows from the edge - in the 'core zone' - were harvested.

The six pairs of experimental-control plots were constructed on the land of five farmers, with both experimental and control plots of each set being constructed on the same farmers' land. This way, both plots of a site enclosed rice that was under the same management strategy - treated with neither pesticides nor fertilisers.

Rice in all six fields was planted in the last ten days of July, 2019. Construction of the enclosures began on the 17th of August and was completed on the 10th of September. Beginning on the 10th of September, the nets of all six experimental plots were retracted at dawn and extended at dusk every day. This continued every day until the rice within the enclosure was harvested and removed, which took place between the 11th and 28th of November.

### 2.3. Acoustic monitoring

In parallel to the exclusion experiment, the activity patterns of insectivorous bats were also monitored over the rice season using six AudioMoth passive acoustic recorders (Hill et al., 2018). On 48 nights between 27th August and 9th December 2019, these six recorders were placed adjacent to the control plot of the six exclusion experiments at a height of 1 m, programmed to record from dusk till 4:30 am with a sampling rate of 384 kHz and gain set to medium.

The raw acoustic data amounted to 2576.5 h of recordings, with some nights seeing logistical or technical difficulties that prevented recording for the scheduled period of time. Using Python version 2.7 (Rossum and Drake Jr, 1995), bat orientation calls were isolated and extracted based on the following measurements.

(i) Frequency of maximum energy (FMAXE) - the frequency containing the most energy in the call (Wordley et al., 2014). (ii) Minimum and maximum frequencies - The lowest and highest frequencies that contained 5% of the energy of FMAXE. (iii) Bandwidth - Difference in frequency between the minimum and maximum frequencies. (iv) Call length - the time interval between the point that the call first crosses 5% FMAXE, and when it last crosses FMAXE. (v) Average amplitude - The average amplitude of the call.

Using manually verified calls to form a template, a linear discriminant analysis in the MatLab Classification learner (The MathWorks Inc., 2019) was used to build a classifier that classified all the remaining calls into sonotypes. The classified calls were then processed in R version 3.63 (R Core Team, 2020) to reclassify based on FMAXE and bandwidth those calls which had been misclassified. The calls were also filtered to remove false positives arising from heavy rain, instrument failure, or bats that were recorded prior to the start time.

There are limited acoustic libraries for Indian bats, none extending as far as Assam. Without such a library to use as reference, and with a dataset too large to check manually, the isolated calls were classified to the sonotype level, rather than the species level. These were defined

based on FMAXE and bandwidth into: (i) Constant Frequency calls (CF), (ii) Frequency modulated - Quasi Constant frequency calls (FM-QCF), and (iii) Quasi-Constant frequency calls (QCF). Pure Frequency Modulated (FM) and FM-CF-FM calls were not recorded. A few CF calls were recorded, but could not be separated from insect noises and so were excluded from the analysis. QCF calls were recorded in the same frequency range as another FM-QCF call, frequently changing from QCF to FM-QCF within a pass. These were therefore considered to be the same sonotype and were recorded as FM-QCF. All the calls used for the analysis, therefore, had FM-QCF characteristics. Henceforth, sonotypes will be identified by 'S' followed by the frequency at which they called. For example, FM-QCF calling at 20 kHz is S20. It was our intention to measure feeding activity using feeding buzzes. However, the lack of characteristic features in feeding buzzes (as compared to orientation calls), and their considerable intra-pass variation made it difficult for our classifier to accurately isolate feeding buzzes from the many types of ultrasonic noise present in the recordings. We therefore used the orientation calls described previously as a proxy for feeding activity, since general activity (as measured by orientation calls) and foraging are known to correlate (Davy et al., 2007; Puig-Montserrat et al., 2015; de Oliveira et al., 2015).

All recordings were divided into five-second intervals. One bat pass was defined as an interval containing more than two orientation calls of the same sonotype (Millon et al., 2015). Using a random number generator, ten percent of the extracted passes were selected for manual verification. The classifier accurately identified > 90% of the passes. At a minimum of 100 m apart, the six sites were not independent. A certain amount of pseudoreplication was therefore unavoidable when the same bat flew from one site to another.

### 2.4. Rice data

To test the two hypotheses, rice was sampled twice during the season, once in the middle of the season, to assess plant damage due to pests, and once at the end, to assess yield. Site three was removed from consideration when it was discovered, late in the season, that it had been sowed with a different strain of rice. As a result, only data from five sites were used for the analysis.

#### 2.4.1. Mid-season data

A unit of rice, transplanted to the field at the seedling stage, is composed of one to several plants, each bearing tillers, leaves and panicles. Such a unit is known as a hill.

Between the 9th and 22nd of October, roughly midway through the rice growing season, 30 hills were sampled from the 'core zone' of three pairs of experimental and control plots (plants from the remaining two pairs having unfortunately been found to have dried out after collection). Hills were chosen by mapping each 'core zone' as a grid and using a random number generator in Python version 2.7 (Rossum and Drake Jr, 1995) to identify the row and column number of the 30 plants. Since the hills were removed by hand and then washed to remove the mud, it was assumed that insect pests on the hill may have been jostled or washed off and that those that remained would be unrepresentative of the level of infestation and so they were not counted for analyses.

To test our first hypothesis, the 30 hills were analysed for the following measures of insect damage:

- Yellowing of leaves, caused by green leafhoppers (IRRI, 2014).
- Defoliation of leaves, caused by caseworms (IRRI, 2014), caterpillars (Tanwar et al., 2010) and grasshoppers (NICRA, 2011).

Both measures were documented as proportion of affected leaves per hill.

#### 2.4.2. End-season data

To test our second hypothesis, up to 900 hills were harvested from

the core zone of five pairs of plots, by hand, at the end of the rice growing season (between 11th of November and 28th December). If the core zone had fewer than 900 hills in one of the treatments, then the same number of hills was harvested from the other treatment of that site. The hills at each site were harvested on the date that the farmer harvested the rest of his field.

The full 900 hills were collected from sites one, five, and six and 800 hills were collected from site two. It was only possible to harvest 400 hills from site four because while the experimental plot had 900 hills of the correct variety, the control plot had only 400 hills of the correct variety, so 400 hills were harvested from both.

Two types of data were collected from these hills.

- a. Total yield: Grain from the harvested rice was removed from the hill by hand and placed into metal tins. The grain from every plot, both experimental and control, was dried for two days by spreading them on a plastic tarp, under a net to prevent birds from eating them, in the sun. After two days of drying, the grain was weighed.
- b. 1000 grain weight: After the final weighing, a small box of grain from each plot was retained for the calculation of 1000 grain weight, which is another measure of yield (Huang et al., 2013). A handful of grain was dried at 80°C for 24 h, and from this handful 1000 full grains were removed and weighed on a high precision balance.

## 2.5. Statistical analysis

### 2.5.1. Mid-season data

To test for the effect of treatment on plant damage caused by insects, a generalised linear mixed model (GLMM) was built using the 'glmmTMB' function (Brooks et al., 2017) in R version 3.63 (R Core Team, 2020). Two types of damage – defoliation and yellowing – were modelled separately as indicators of the action of two groups of pest. The data did not need to be transformed prior to being used in the model, but outliers were removed using the 'check\_outliers' function from the 'performance' package (Lüdtke et al., 2020).

The response variable for both types of damage were in the form of proportion of leaves affected per hill, warranting the use of the binomial GLMM. The treatment – experimental and control – was taken as the explanatory variable and to account for non-independence of samples within each site, site number was taken as a random effect.

A generalised linear model was also built, without the random effect of site, and compared to the final mixed models of both types of damage. For both types of damage, the GLMMs had AICc scores more than two units lower than the corresponding GLMs, which justified the inclusion of site as a random effect. Model residuals were plotted and visually analysed for patterns. Neither of the two models showed any patterns in the residuals.

### 2.5.2. End-season data

To test the effect of the treatment on total yield and 1000 grain weight, the two sets of data were checked for normality using a QQ plot and for comparable variances using an F test. Having ascertained that both sets of data are normally distributed and with comparable variances, a paired Student's t-test was used to compare the difference between the two treatments. All statistical analyses were performed in R version 3.63 (R Core Team, 2020).

## 3. Results

### 3.1. Acoustic monitoring

In total, 18,890 passes were identified across six locations over 48 nights of sampling. In addition four sonotypes (S34, S38, S48, S65) showed a clear bimodal pattern in activity over the season, peaking once in early-mid September, and again in mid-October.

### 3.2. Mid-season data

The exclusion of bats in the experimental treatment contributed to significantly greater defoliation, indicative of damage by grasshoppers, caseworms, and caterpillars, in experimental plots (where bats were excluded) than in the control plots (Estimate = 0.168, standard error = 0.059,  $P = 0.004$ ; Table A.1). Proportion of leaves yellowing, indicative of leafhopper damage, was not influenced by experimental treatment (Estimate = 0.101, standard error = 0.078,  $P = 0.198$ ; Table A.1).

### 3.3. End-season data

Total yield was not significantly different between the experimental and control plots ( $t = -1.4361$ ,  $P = 0.1903$ ; Fig. 4). There was also no significant difference in the 1000 grain weight between the experimental and control plots ( $t = -0.31746$ ,  $P = 0.7586$ ; Fig. 4).

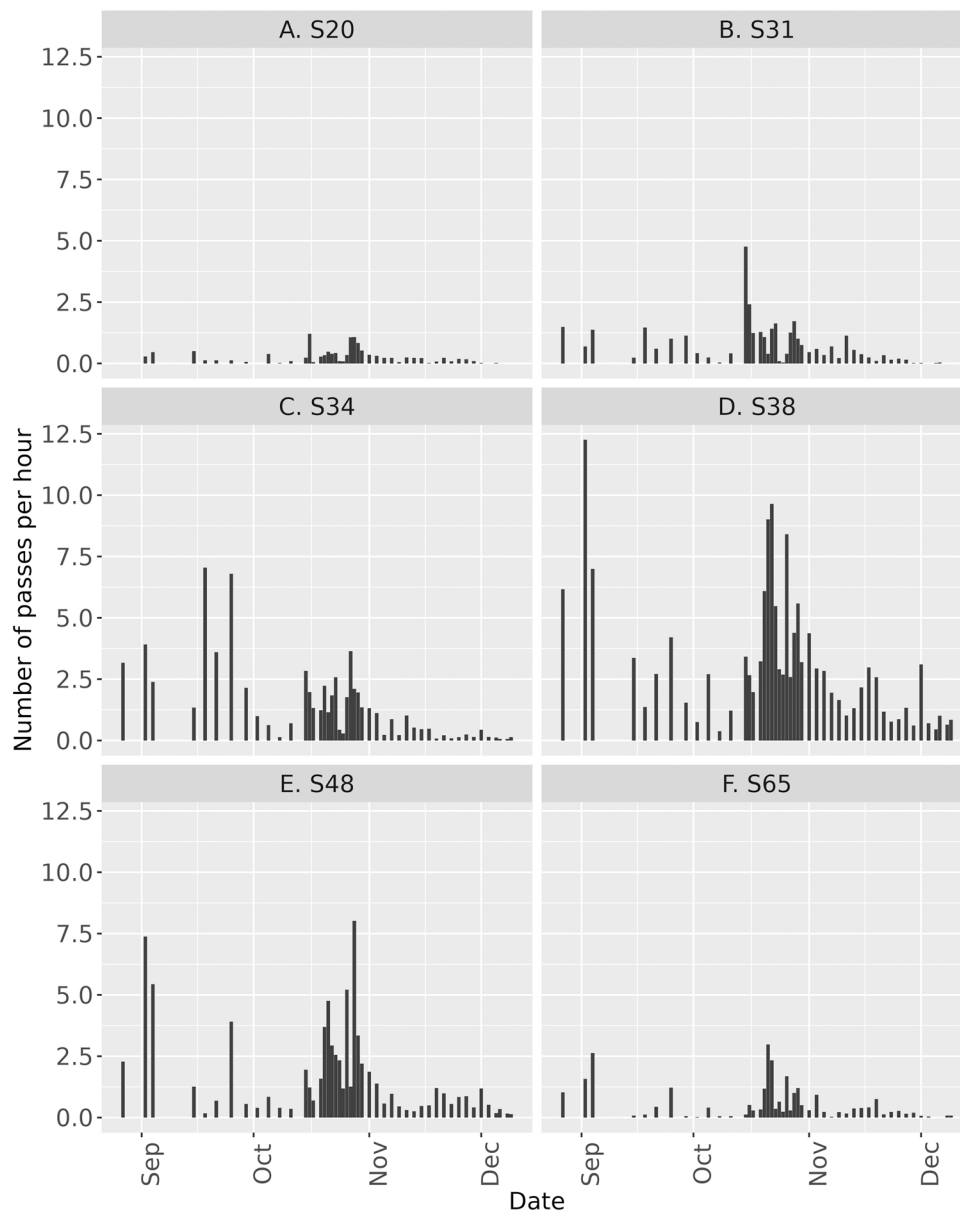
## 4. Discussion

Our acoustic monitoring demonstrated that insectivorous bats were highly active in the landscape and that over the rice growing season their activity mirrored the known activity patterns of multiple rice pests (Zhong-xian et al., 2006; Sharma et al., 2018). With over 18,000 passes recorded at the six sites, even allowing for multiple records of the same individual, it is reasonable to assume that bats did consistently hunt insects over the rice crop, and that these insects must have included pests.

From an ecosystem services point of view, the most important metric is arguably final yield, as this speaks to a demonstrable value of the pest suppression service provided by bats to farmers. Contrary to our second hypothesis, we found non-significant differences in final yield between the experimental and control plots of the exclusion experiment. A similar result was reported by the only other exclusion experiment involving bats and rice. Set in Florida, this study was focussed on blackbirds, but by keeping the nets in place throughout the experiment, they inadvertently also excluded bats (Borkhataria et al., 2012). They also reported a non-significant difference in final yield between the experimental and control plots. Similar non-significant differences in final yield have also been reported from other crops like cacao (Gras et al., 2016), and coffee (Karp and Daily, 2014).

At face value, the results of our study would imply that the absence of bats from rice fields in Assam had no effect on rice yield, a conclusion that would be at odds with the observed patterns in bat activity. As seen in Fig. 3, four out of six sonotypes peaked in activity (standardised to sampling effort) in the second half of October, corresponding to the mid-season peak characteristic of many herbivorous insect pests of rice (Zhong-xian et al., 2006; Sharma et al., 2018), and also to the activity of vocal insects in the study area (Bhalla, 2022). Assuming for the moment that the exclusion experiment functioned as expected, a number of biological mechanisms could still have resulted in a non-significant difference in yield between the two treatments. For instance (i) pest populations with and without bats might be comparable if bat predation is not a primary limitation on pest survival; (ii) mesopredators in the experimental plots, released from predation by bats, could have increased their activity resulting in similar overall levels of pest suppression; (iii) the rice plants themselves might compensate for damage by pests well enough that lower pest action did not bring about an increase in yield; or (iv) the effect of bat activity may bring a general benefit to the level of infestation at the field level, bringing down crop damage *inside* the enclosures as well as in the rest of the field where the control sites were located.

In southern Illinois, Maine and Boyles (2015) also conducted an exclusion experiment on a row crop. Excluding bats from corn, they reported a non-significant difference in yield between their control and experimental plots. With six replicates, their final non-significant difference in yield weight was attributed to limited statistical power.



**Fig. 3.** The activity patterns of six sonotypes of insectivorous bats over a rice season. Data was collected at six locations between 27th August and 9th December 2019 in Puthimari, Assam. Recording began each night at dusk, and ended by 4:30 am over 48 nights of recording. Activity at all six locations was summed and standardised to number of hours sampled.

However, their analysis of multiple measures of plant damage and pest abundance did show significant differences between the two treatments, based on which they concluded that bats were providing a pest suppression service.

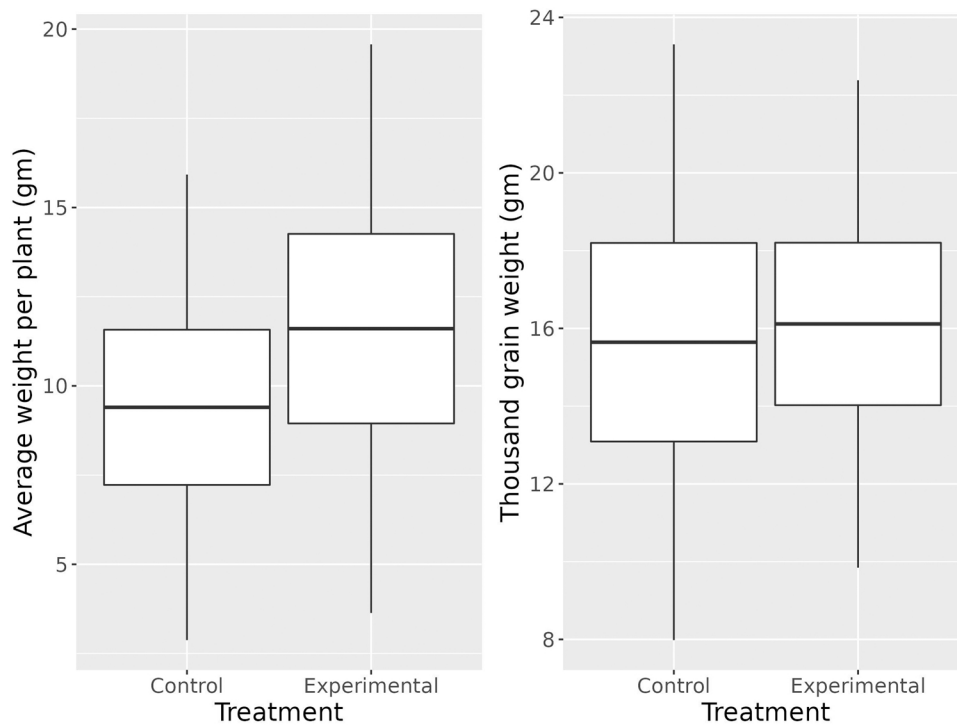
Our study showed a similar pattern. We report a significant difference in one type of plant damage – degree of defoliation – between the two treatments, in line with our first hypothesis, accompanied by a non-significant difference in total yield.

Assuming that limited replication contributed to the non-significant result in total yield, a significant difference in plant damage strongly suggests that bats are reducing the effect of insect pest activity on the rice crop. This would support rice-based studies such as [Wanger et al. \(2014\)](#) and [Puig-Montserrat et al. \(2015\)](#) that indicate the same. It would also be in line with exclusion experiments involving bats and other crops ([Maas et al., 2013](#); [Rodríguez-San Pedro et al., 2020](#)) that reported significant changes to yield and plant health as a result of bat- or bird- and bat- exclusion. However, while insufficient statistical power might have resulted in the non-significant difference in final yield, the

same result might also have arisen from limitations in the methodology. Bat exclusion experiments function under the assumption that the ecosystem within the experimental enclosures are perfectly insulated against the influences of bats, but identical in all other respects to the controls. This assumption is not watertight, and merits examination.

Bat exclusion experiments need to be manipulated twice daily, a logistic challenge that imposes limits on the number of replicates and, perhaps more importantly, the dimensions of the enclosures. Most enclosures aren't higher than 7 m, which makes it impossible to control for the hunting that is occurring above the enclosure, where insects fly and bats follow.

Many insect prey of bats have evolved behavioural and physical adaptations to reduce the risk of predation. Tympanate moths, many of which are agricultural pests, can detect the ultrasonic calls of bats through typanal organs evolved for this purpose ([Zha et al., 2009](#); [Miller, 2009](#)). These moths alter their foraging and reproductive behaviour when they hear bat calls, which increases their survival rate, but decreases fitness. For these insects, the mere presence of echolocating bats



**Fig. 4.** The difference in average yield per plant and 1000 grain weight between the control and experimental plots of the exclusion experiment, showing average (black horizontal line), one standard deviation (white box), and three standard deviations (vertical line). Comparing the effect on yield of excluding bats from rice fields, the experiment selectively excluded bats from five experimental plots using retractable nets that were extended between dusk and dawn. Yield was calculated as the weight of grain per plant from all ten plots, and the weight of a 1000 full grains after they had been dried in an oven for 24 h. The difference between control and experimental treatment was non-significant for both total yield ( $t = -1.4361$ ,  $p = 0.1903$ ) and 1000 grain weight ( $t = -0.31746$ ,  $p = 0.7586$ ).

creates a 'landscape of fear' (Russo et al., 2018), and because the insects need only to hear the outgoing call of the bat, where a bat needs to hear the returning echo, the range at which tympanate insects hear bats is much greater than the range at which bats can detect them (Kunz et al., 2011). One study predicted that tymanate insects could detect the insectivorous bat *Cormura brevirostris* as far as 50 m away (Surykke and Kalko, 2008). Were this range even 15 m, tympanate insects at the very centre of most exclusion experiments would detect bats foraging around and above the enclosures and switch to less efficient foraging patterns. Adding to this, the nets used to exclude bats create acoustic edges. Edge-space bats that make use of edges to hunt might spend more time near these nets, creating a biased 'landscape of fear' near the experimental plots of the experiments.

Flying insects are, by their nature, mobile. Even if the absence of bat predation created a hotspot of pests within the enclosures, those with flying adult stages would almost certainly spread outside the enclosures, diluting the effect caused by a local absence of bats. Taking such mobility into account, the effect of bats on yield may only be measurable at the field level, if average pest populations sizes are significantly reduced due to consistent predation by bats. All these factors may reduce the accuracy with which exclusion experiments can measure the impact of bats on pest communities. The final results, however, must also be taken in the context of the landscape they came from.

Rice in India is grown on more than 43 million hectares of land (Directorate of Economics and Statistics, 2019). Rice farms, however, are still typically small in size (Wang et al., 2015) (the average operational farm size in India is 0.83 ha) and they are farmed using labour-intensive methods (compared to China's more mechanised approach) (Wang et al., 2015). While the fields chosen for this study all grew the same strain of rice and were not treated with chemical pesticides or fertilisers, they were set in a mosaic of other fields, each with a different management strategy, from which the effect of pesticides may have carried over.

The small scale and often traditional farming practices are also often accompanied with poor documentation. The lack of historical records on yield, tilling and cropping patterns, and pesticide and fertiliser use detract from our ability to standardise all extraneous variables when

conducting an exclusion experiment. A case in point, the experimental plot at site two produced nearly double the yield of the control. The most plausible explanation for this was that the land of the experimental plot received six more passes by the tractor during tilling than the land of the control plot, and that this resulted in plants in the experimental plot being grown on more nutritious soil. This information was provided post-facto, by the neighbour who had driven the tractor.

In considering the effectiveness of bat pest-suppression over rice, there also arises the question of seasonality. Rice is a highly seasonal crop, and rice fields are very different ecosystems at different times of the year (Toffoli and Rughetti, 2017). The arthropod communities in rice fields show seasonal patterns of invasion, establishment, and decline in response to these changes (Settle et al., 1996). Insectivorous bats are strongly influenced by the availability of insect prey (Lang et al., 2006; Taylor et al., 2013) (Bhalla et al. Unpublished manuscript), but also broader patterns in the weather and their reproductive cycle (Rydell, 1993; Chaverri and Vonhof, 2011; Barros et al., 2014). The energetic demands of a lactating bat have been reported to be double that during pregnancy (Kunz et al., 1995). This increased demand is managed through changes in their hunting behaviour (Duvergé et al., 2000). The food webs in rice ecosystems are likely, therefore, to have very different dynamics over different seasons. An ideal estimation of this service would require, at a minimum, a year-long study, to account for the different dynamics arising from changes in abiotic conditions and biotic communities over the different rice seasons.

The idiosyncrasies of rice stand in stark contrast to crops such as cacao and coffee, which show lower seasonal variation and pose fewer logistical challenges to the construction of enclosures. Since these challenges are not likely to change significantly, exclusion experiments may not be the most appropriate method to conduct an economic valuation of insectivorous bats in rice. Such an evaluation would need to be landscape-scale, where bat populations are bolstered at select sites to bring about differences in their numbers between sites. Given the comparatively slow life history of insectivorous bats, studies doing so with the intention of extrapolating in time and space must continue until the bat populations have stabilised, which would also allow seasonal differences to be discerned (Maas et al., 2013). Comparisons can then be

made between sites and within a site over time. Coupled with long term monitoring of arthropod communities, rice health and yield, and bat activity, such a study would provide a thorough exploration of the potential for bats to be effective pest suppressors in rice farms.

In 1999, one team in Northern Iberia deployed bat boxes to increase the resident population of the soprano pipistrelle bat. At the end of the ten years, the population of rice stem borers had dropped to below the threshold required to trigger aerial spraying of pesticides (Puig-Montserrat et al., 2015). Supporting the conclusions of Wanger et al. (2014), the multi-pronged approach of Puig-Montserrat et al. (2015), combining diet analyses and bat and pest monitoring, proved the potential of bats as pest suppression agents over rice.

A similar study is needed in Asia, which hosts diverse communities of bats and pests, and where most of the world's rice is grown and consumed (FAO, 2019). An accurate assessment of this service, coupled with investigations of bat diet, distribution, and activity patterns would allow conservationists and agriculturalists to devise strategies to protect bat populations and maximise the value of their ecosystem services.

### 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. Supplementary material

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.agee.2022.108196](https://doi.org/10.1016/j.agee.2022.108196).

### References

- Babendreier, D., Hou, M., Tang, R., Zhang, F., Vongsabouth, T., Win, K.K., Kang, M., Peng, H., Song, K., Annamalai, S., Horgan, F.G., 2020. Biological control of lepidopteran pests in rice: a multi-nation case study from Asia. *J. Integr. Pest Manag.* 11, 5.
- Bambaradeniya, C.N.B., Edirisinghe, J.P., 2009. Composition, structure and dynamics of arthropod communities in a rice agro-ecosystem. *Ceylon J. Sci.* 37, 23–48.
- Barros, M.A.S., Pessoa, D.M.A., Rui, A.M., 2014. Habitat use and seasonal activity of insectivorous bats (Mammalia: Chiroptera) in the grasslands of southern Brazil. *Zoologia* 31, 153–161.
- Bhalla, I.S., 2022. The ecology and ecosystem services of insectivorous bats in rice dominated landscapes. Doctoral thesis. Oxford University, Oxford.
- Borkhataria, R.R., Nuessly, G.S., Pearlstine, E., Cherry, R.H., 2012. Effects of blackbirds (*Agelaius phoeniceus*) on stink bug (Hemiptera: Pentatomidae) populations, damage, and yield in Florida rice. *Fla. Entomol.* 95, 143–149.
- Bottrell, D.G., Schoenly, K.G., 2012. Resurrecting the ghost of green revolutions past: the brown planthopper as a recurring threat to high-yielding rice production in tropical Asia. *J. Asia-Pac. Entomol.* 15, 122–140.
- Bowonder, B., 1979. Impact analysis of the green revolution in India. *Technol. Forecast. Soc. Change* 15, 297–313.
- Boyles, J.G., Cryan, P.M., McCracken, G.F., Kunz, T.H., 2011. Economic importance of bats in agriculture. *Science* 332, 41–42.
- Boyles, J.G., Sole, C.L., Cryan, P.M., McCracken, G.F., 2013. On estimating the economic value of insectivorous bats: prospects and priorities for biologists. In: Adams, R.A., Pedersen, S.C. (Eds.), *Bat Evolution, Ecology, and Conservation*. Springer, New York, NY, pp. 501–515.
- Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R. J.* 9, 378–400.
- Cassano, C.R., Silva, R.M., Mariano-Neto, E., Schroth, G., Faria, D., 2016. Bat and bird exclusion but not shade cover influence arthropod abundance and cocoa leaf consumption in agroforestry landscape in northeast Brazil. *Agric. Ecosyst. Environ.* 232, 247–253.
- Chaverri, G., Vonhof, M.J., 2011. Reproduction and growth in a neotropical insectivorous bat. *Acta Chiropterologica* 13, 147–155.
- Classen, A., Peters, M.K., Ferger, S.W., Helbig-Bonitz, M., Schmack, J.M., Maassen, G., Schleunig, M., Kalko, E.K.V., Böhning-Gaese, K., Steffan-Dewenter, I., 2014. Complementary ecosystem services provided by pest predators and pollinators increase quantity and quality of coffee yields. *Proc. R. Soc. B Biol. Sci.* 281, 20133148.
- Cleveland, C.J., Betke, M., Federico, P., Frank, J.D., Hallam, T.G., Horn, J., López, J.D., McCracken, G.F., Medellín, R.A., Moreno-Valdez, A., Sansone, C.G., Westbrook, J.K., Kunz, T.H., 2006. Economic value of the pest control service provided by Brazilian free-tailed bats in south-central Texas. *Front. Ecol. Environ.* 4, 238–243.
- Davy, C.M., Russo, D., Fenton, M.B., 2007. Use of native woodlands and traditional olive groves for foraging bats on a Mediterranean island: consequences for conservation. *J. Zool.* 273, 397–405.
- de Kraker, J.D., van Huis, A., Heong, K.L., van Lenteren, J., Rabbinge, R., 1999. Population dynamics of rice leaf folders and their natural enemies in irrigated rice in the Philippines. *Bull. Entomol. Res.*, 89, pp. 411–421.
- Deutsch, C.A., Tewksbury, J.J., Tigchelaar, M., Battisti, D.S., Merrill, S.C., Huey, R.B., Naylor, R.L., 2018. Increase in crop losses to insect pests in a warming climate. *Science* 361, 916–919.
- Directorate of Economics and Statistics, 2019. *Agricultural Statistics at a Glance 2019*. Ministry of Agriculture, Government of India.
- Drechler, M., Settele, J., 2001. Predator–prey interactions in rice ecosystems: effects of guild composition, trophic relationships, and land use changes — a model study exemplified for Philippine rice terraces. *Ecol. Model.* 137, 135–159.
- Duvergé, P.L., Jones, G., Rydell, J., Ransome, R.D., 2000. Functional significance of emergence timing in bats. *Ecography* 23, 32–40.
- FAO, 2019. FAOSTAT Statistical Database. Food and Agriculture Organization of the United Nations, Rome.
- Federico, P., Hallam, T.G., McCracken, G.F., Purucker, S.T., Grant, W.E., Correa-Sandoval, A.N., Westbrook, J.K., Medellín, R.A., Cleveland, C.J., Sansone, C.G., López, J.D., Betke, M., Moreno-Valdez, A., Kunz, T.H., 2008. Brazilian free-tailed bats as insect pest regulators in transgenic and conventional cotton crops. *Ecol. Appl.* 18, 826–837.
- Fisher, B., Naidoo, R., 2011. Concerns about extrapolating right off the bat. *Science* 333, 287. LP – 287.
- Gras, P., Tschamtké, T., Maas, B., Tjoa, A., Hafsa, A., Clough, Y., 2016. How ants, birds and bats affect crop yield along shade gradients in tropical cacao agroforestry. *J. Appl. Ecol.* 53, 953–963.
- Gurr, G.M., Liu, J., Read, D.M.Y., Catindig, J.L.A., Cheng, J.A., Lan, L.P., Heong, K.L., 2011. Parasitoids of Asian rice planthopper (Hemiptera: Delphacidae) pests and prospects for enhancing biological control by ecological engineering. *Ann. Appl. Biol.* 158, 149–176.
- Halwart, M., Litsinger, J.A., Barrion, A.T., Viray, M.C., Kaule, G., 2012. Efficacy of Common Carp and Nile Tilapia as biocontrol agents of rice insect pests in the Philippines. *Int. J. Pest Manag.* 58, 330–346.
- Heong, K.L., Aquino, G.B., Barrion, A.T., 1992. Population dynamics of plant- and leafhoppers and their natural enemies in rice ecosystems in the Philippines. *Crop Prot.* 11, 371–379.
- Hill, A.P., Prince, P., Piña Covarrubias, E., Doncaster, C.P., Snaddon, J.L., Rogers, A., 2018. AudioMoth: evaluation of a smart open acoustic device for monitoring biodiversity and the environment. *Methods Ecol. Evol.* 9, 1199–1211.
- Huang, R., Jiang, L., Zheng, J., Wang, T., Wang, H., Huang, Y., Hong, Z., 2013. Genetic bases of rice grain shape: so many genes, so little known. *Trends Plant Sci.* 18, 218–226.
- Huang, S., Wang, L., Liu, L., Fu, Q., Zhu, D., 2014. Nonchemical pest control in China rice: a review. *Agron. Sustain. Dev.* 34, 275–291.
- Hughes, G., McKinlay, R.G., 1988. Spatial heterogeneity in yield-pest relationships for crop loss assessment. *Ecol. Model.* 41, 67–73.
- IRRI, 2014. *Standard Evaluation System for Rice*, fifth ed. International Rice Research Institute, Los Baños, Philippines.
- IRRI, 2019. *World Rice Statistics*. International Rice Research Institute.
- Kalka, M.B., Smith, A.R., Kalko, E.K.V., 2008. Bats limit arthropods and herbivory in a tropical forest. *Science* 320, 71.
- Karp, D.S., Daily, G.C., 2014. Cascading effects of insectivorous birds and bats in tropical coffee plantations. *Ecology* 95, 1065–1074.
- Kemp, J., López-Baucells, A., Rocha, R., Wangenstein, O.S., Andriatafika, Z., Nair, A., Cabeza, M., 2019. Bats as potential suppressors of multiple agricultural pests: a case study from Madagascar. *Agric. Ecosyst. Environ.* 269, 88–96.
- Kervyn, T., Godin, M.-C., Jocque, R., Grootaert, P., Libois, R., 2012. Web-building spiders and blood-feeding flies as prey of the notch-eared bat (*Myotis emarginatus*). *Belg. J. Zool.* 142, 59–67.
- Kolkert, H., Smith, R., Rader, R., Reid, N., 2020. Insectivorous bats foraging in cotton crop interiors is driven by moon illumination and insect abundance, but diversity benefits from woody vegetation cover. *Agric. Ecosyst. Environ.* 302, 107068.



- Kunz, T.H., Whitaker Jr., J.O., Wadanoli, M.D., 1995. Dietary energetics of the insectivorous Mexican free-tailed bat (*Tadarida brasiliensis*) during pregnancy and lactation. *Oecologia* 101, 407–415.
- Kunz, T.H., Braun de Torrez, E., Bauer, D., Lobova, T., Fleming, T.H., 2011. Ecosystem services provided by bats. *Ann. N. Y. Acad. Sci.* 1223, 1–38.
- Lang, A.B., Kalko, E.K.V., Römer, H., Bockholdt, C., Dechmann, D.K.N., 2006. Activity levels of bats and katydids in relation to the lunar cycle. *Oecologia* 146, 659–666.
- Lee, Y.-F., McCracken, G.F., 2005. Dietary variation of Brazilian free-tailed bats links to migratory populations of pest insects. *J. Mammal.* 86, 67–76.
- Leelapabul, W., Bumrungsri, S., Pattanawiboon, A., 2005. Diet of wrinkle-lipped free-tailed bat (*Tadarida plicata* Buchanan, 1800) in central Thailand: insectivorous bats potentially act as biological pest control agents. *Acta Chiropterologica* 7, 111–119.
- Librán-Embíd, F., De Coster, G., Metzger, J.P., 2017. Effects of bird and bat exclusion on coffee pest control at multiple spatial scales. *Landsc. Ecol.* 32, 1907–1920.
- Litsinger, J.A., Bandong, J.P., Canapi, B.L., 2011a. Effect of multiple infestations from insect pests and other stresses on irrigated rice in the Philippines: I. Damage functions. *Int. J. Pest Manag.* 57, 93–116.
- Litsinger, J.A., Bandong, J.P., Canapi, B.L., 2011b. Effect of multiple infestations from insect pests and other stresses to irrigated rice in the Philippines: II. Damage and yield loss. *Int. J. Pest Manag.* 57, 117–131.
- Lobell, D.B., Field, C.B., 2007. Global scale climate-crop yield relationships and the impacts of recent warming. *Environ. Res. Lett.* 2, 14002.
- Lüdtke, D., Makowski, D., Waggoner, P., Patil, I., 2020. Performance: Assessment of Regression Models Performance. CRAN.
- Lv, J., Wilson, L., Longnecker, M., 2008. Tolerance and compensatory response of rice to sugarcane borer (Lepidoptera: *Crambidae*) injury. *Environ. Entomol.* 37, 796–807.
- Maas, B., Clough, Y., Tschamtké, T., 2013. Bats and birds increase crop yield in tropical agroforestry landscapes. *Ecol. Lett.* 16, 1480–1487.
- Maas, B., Karp, D.S., Bumrungsri, S., Darras, K., Gonthier, D., Huang, J.C.-C., Lindell, C. A., Maine, J.J., Mestre, L., Michel, N.L., Morrison, E.B., Perfecto, I., Philpott, S.M., Şekercioğlu, Ç.H., Silva, R.M., Taylor, P.J., Tschamtké, T., Van Bael, S.A., Whelan, C. J., Williams-Guillén, K., 2016. Bird and bat predation services in tropical forests and agroforestry landscapes. *Biol. Rev.* 91, 1081–1101.
- Maas, B., Heath, S., Grass, I., Cassano, C., Classen, A., Faria, D., Gras, P., Williams-Guillén, K., Johnson, M., Karp, D.S., Linden, V., Martínez-Salinas, A., Schmack, J.M., Kross, S., 2019. Experimental field closure of birds and bats in agricultural systems — methodological insights, potential improvements, and cost-benefit trade-offs. *Basic Appl. Ecol.* 35, 1–12.
- Maine, J.J., Boyles, J.G., 2015. Bats initiate vital agroecological interactions in corn. *Proc. Natl. Acad. Sci. USA* 112, 12438–12443.
- McCracken, G.F., Westbrook, J.K., Brown, V.A., Eldridge, M., Federico, P., Kunz, T.H., 2012. Bats track and exploit changes in insect pest populations. *PLoS One* 7, e43839–e43839.
- Miller, L., 2009. How some insects detect and avoid being eaten by bats: tactics and counterattacks of prey and predator. *BioScience* 51, 570–581.
- Millon, L., Julien, J.-F., Julliard, R., Kerbiriou, C., 2015. Bat activity in intensively farmed landscapes with wind turbines and offset measures. *Ecol. Eng.* 75, 250–257.
- Mooney, K.A., Gruner, D.S., Barber, N.A., Van Bael, S.A., Philpott, S.M., Greenberg, R., Schoener, T.W., 2010. Interactions among predators and the cascading effects of vertebrate insectivores on arthropod communities and plants. *Proc. Natl. Acad. Sci. USA* 107, 7335–7340.
- Muthayya, S., Sugimoto, J., Montgomery, S., Maberly, G., 2014. An overview of global rice production, supply, trade, and consumption. *Ann. N. Y. Acad. Sci.* 1324.
- Nelson, A.E., Ravichandran, K., Antony, U., 2019. The impact of the Green Revolution on indigenous crops of India. *J. Ethn. Foods* 6, 8.
- NICRA, 2011. Manual for rice pest surveillance. NICRA Team of Rice Pest Surveillance. National Centre for Integrated Pest Management, New Delhi, Central Research Institute for Dryland Agriculture and Directorate of Rice Research, Hyderabad.
- Normile, D., 2013. Vietnam turns back a “tsunami of pesticides”. *Science* 341, 737–738.
- de Oliveira, L.Q., Marciente, R., Magnusson, W.E., Estefano, P., Bobrowicz, D., 2015. Activity of the insectivorous bat *Pteronotus parnellii* relative to insect resources and vegetation structure. *J. Mammal.* 96, 1036–1044.
- Parayil, G., 1992. The green revolution in India: a case study of technological change. *Technol. Cult.* 33, 737–756.
- Parveen, S., Nakagoshi, N., 2001. An analysis of pesticide use for rice pest management in Bangladesh. *J. Int. Dev. Coop.* 8, 107–126.
- Pathak, M.D., Khan, Z.R., 1994. Insect Pests of Rice. International Rice Research Institute, Manila, Philippines.
- Pinnschmidt, H.O., Batchelor, W.D., Teng, P.S., 1995. Simulation of multiple species pest damage in rice using CERES-rice. *Agric. Syst.* 48, 193–222.
- Puig-Montserrat, X., Torre, I., López-Baucells, A., Guerrieri, E., Monti, M.M., Ràfols-García, R., Ferrer, X., Gisbert, D., Flaquer, C., 2015. Pest control service provided by bats in Mediterranean rice paddies: linking agroecosystems structure to ecological functions. *Mamm. Biol.* 80, 237–245.
- Puig-Montserrat, X., Flaquer, C., Gómez-Aguilera, N., Burgas, A., Mas, M., Tuneu, C., Marquès, E., López-Baucells, A., 2020. Bats actively prey on mosquitoes and other deleterious insects in rice paddies: potential impact on human health and agriculture. *Pest Manag. Sci.* 76, 3759–3769.
- R Core Team, 2020. R: A Language and Environment for Statistical Computing. Vienna, Austria.
- Rodríguez-San Pedro, A., Allendes, J.L., Beltrán, C.A., Chaperon, P.N., Saldarriaga-Córdoba, M.M., Silva, A.X., Grez, A.A., 2020. Quantifying ecological and economic value of pest control services provided by bats in a vineyard landscape of central Chile. *Agric. Ecosyst. Environ.* 302, 107063.
- Rosenzweig, C., Elliott, J., Deryng, D., Ruane, A.C., Müller, C., Arneth, A., Boote, K.J., Folberth, C., Glotter, M., Khabarov, N., 2014. Assessing agricultural risks of climate change in the 21st century in a global gridded crop model intercomparison. *Proc. Natl. Acad. Sci. USA* 111, 3268–3273.
- Rossum, V.G., Drake Jr, F.L., 1995. Python Reference Manual. Centrum voor Wiskunde en Informatica Amsterdam.
- Russo, D., Bosso, L., Ancillotto, L., 2018. Novel perspectives on bat insectivory highlight the value of this ecosystem service in farmland: research frontiers and management implications. *Agric. Ecosyst. Environ.* 266, 31–38.
- Rydell, J., 1993. Variation in foraging activity of an aerial insectivorous bat during reproduction. *J. Mammal.* 74, 503–509.
- Savary, S., Willocquet, L., Pethybridge, S.J., Esker, P., McRoberts, N., Nelson, A., 2019. The global burden of pathogens and pests on major food crops. *Nat. Ecol. Evol.* 3, 430–439.
- Settle, W., Ariawan, H., Astuti, E., Cahyana, W., Hakim, A.L., Hindayana, D., Lestari, A., Pajarningsih, 1996. Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. *Ecology* 77, 1975–1988.
- Sharma, K., Raju, S., Jaiswal, D., 2018. Influence of environmental effect on the population dynamics of brown plant hopper, *Nilaparvata lugens* (Stal) and White-backed plant hopper, *Sogatella furcifera* (Hovarth) in Varanasi region. *J. Entomol. Res.* 42, 339.
- Shukla, P.R., Skea, J., Buendia, E.C., Masson-Delmotte, V., Pörtner, H.-O., Roberts, D.C., Zhai, P., Slade, R., Connors, S., van Diemen, R., Ferrat, M., Haughey, E., Luz, S., Neogi, S., Pathak, M., Petzold, J., Pereira, J.P., Vyas, P., Huntley, E., Kissick, K., Belkacemi, M., Malley, J., 2019. IPCC 2019: summary for policymakers. Climate Change and Land: An IPCC Special Report on Climate Change, Desertification, Land Degradation, Sustainable Land Management, Food Security, and Greenhouse Gas Fluxes in Terrestrial Ecosystems.
- Siemers, B., Kriner, E., Kaipf, I., Simon, M., Greif, S., 2012. Bats eavesdrop on the sound of copulating flies. *Curr. Biol.* 22, R563–4.
- Stange, E.E., Ayres, M.P., 2010. Climate Change Impacts: Insects. eLS.
- Surlykke, A., Kalko, E.K.V., 2008. Echolocating bats cry out loud to detect their prey. *PLoS ONE* 3, e2036.
- Tanwar, R.K., Prakash, A., Panda, S.K., Swain, N.C., Garg, D.K., Singh, S.P., Kumar, S.S., Bambawale, O.M., 2010. Rice swarming caterpillar (*Spodoptera mauritia*) and its management strategies. Technical Bulletin 24. National Centre for Integrated Pest Management, New Delhi.
- Taylor, P.J., Monadjem, A., Steyn, J.N., 2013. Seasonal patterns of habitat use by insectivorous bats in a subtropical African agro-ecosystem dominated by macadamia orchards. *Afr. J. Ecol.* 51, 552–561.
- Teng, P.S., 1994. Integrated pest management in rice. *Exp. Agric.* 30, 115–137.
- Teng, Q., Hui, X.-F., Cheng, C., Luo, Z., Luo, F., Xue, Y., Jiang, Y., Mu, Z., Liu, L., Yang, M., 2016. Ecological effects of rice-duck integrated farming on soil fertility and weed and pest control. *J. Soils Sediments* 16, 2395–2407.
- The MathWorks Inc., 2019. MATLAB and Statistics Toolbox Release 2019b. Natick, Massachusetts.
- Toffoli, R., Rughetti, M., 2017. Bat activity in rice paddies: organic and conventional farms compared to unmanaged habitat. *Agric. Ecosyst. Environ.* 249, 123–129.
- Vanhänen, H., Veteli, T.O., Paivinen, S., Kellomaki, S., Niemela, P., 2007. Climate change and range shifts in two insect defoliators: gypsy moth and nun moth—a model study. *Silva Fenn.* 41, 621.
- Wang, J., Chen, K.Z., Das Gupta, S., Huang, Z., 2015. Is small still beautiful? A comparative study of rice farm size and productivity in China and India. *China Agric. Econ. Rev.* 7, 484–509.
- Wang, J., Chu, M., Ma, Y., 2018. Measuring rice farmer’s pesticide overuse practice and the determinants: a statistical analysis based on data collected in Jiangsu and Anhui provinces of China. *Sustainability* 10, 677.
- Wanger, T., Darras, K., Bumrungsri, S., Tschamtké, T., Klein, A.-M., 2014. Bat pest control contributes to food security in Thailand. *Biol. Conserv.* 171, 220–223.
- Way, M.J., Heong, K.L., 1994. The role of biodiversity in the dynamics and management of insect pests of tropical irrigated rice—a review. *Bull. Entomol. Res.* 84, 567–587.
- Williams-Guillén, K., Perfecto, I., Vandermeer, J., 2008. Bats limit insects in a neotropical agroforestry system. *Science* 320, 70.
- Wordley, C.F.R., Foui, E.K., Mudappa, D., Sankaran, M., Altringham, J.D., 2014. Acoustic identification of bats in the Southern Western Ghats, India. *Acta Chiropterologica* 16, 213–222.
- Zha, Y.-P., Chen, Q., Lei, C., 2009. Ultrasonic hearing in moths. *Ann. Soc. Entomol. Fr.* 45, 145–156.
- Zhang, J., Zhao, B., Chen, X., Luo, S., 2009. Insect damage reduction while maintaining rice yield in duck-rice farming compared with mono rice farming. *J. Sustain. Agric.* 33, 801–809.
- Zhong-xian, L.U., Villareal, S., Xiao-ping, Y.U., Heong, K.L., Cui, H.U., 2006. Biodiversity and dynamics of planthoppers and their natural enemies in rice fields with different nitrogen regimes. *Rice Sci.* 13, 218–226.