Article
Bat Activity in Organic Rice Fields Is Higher Than in Conventional Fields in Landscapes of Intermediate Complexity

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Abstract: The extent to which organic farming can support biodiversity has been extensively studied. However, most of the research has been conducted on organic farms in temperate regions, with the focus mainly being on birds, insects, and plants and rarely on insectivorous bats, especially in Southeast Asia. We studied pairs of matched organic and conventional rice fields along a gradient of landscape complexity in the Songkhla Lake Basin and conducted acoustic surveys using bat detectors to analyze the influence of farming system and landscape characteristics on bat activity and prey availability. We also tested the “intermediate landscape complexity” hypothesis, which states that local conservation efforts are most effective in landscapes of intermediate complexity compared to extremely simple or extremely complex landscapes. We detected no difference in bat species richness, total bat activity, feeding activity, and insect prey abundance between organic fields and conventional fields. Even though organic farming did not increase bat activity on its own, it was most beneficial to bat activity in landscapes of intermediate complexity. Our findings suggest that landscape traits contribute more to bat activity than farm management and that insectivorous bats have species- and guild-specific responses to various landscape contexts. We also found that disturbance caused by tropical storms negatively impacts the activity of insectivorous bat.

Keywords: agriculture intensification; conservation; farm management; landscape context; Southeast Asia

1. Introduction

Agricultural intensification is widely recognized as one of the main solutions to the world’s growing food security problems [1]. Intensive agricultural practices have considerably contributed to the loss of biodiversity and ecosystem services [2,3], particularly in Southeast Asia, which has had the fastest rate of tropical deforestation for agriculture in recent decades [4,5]. Globally, this region supports very high diversity of bats, accounting for about 30% of the world’s bat fauna, with nearly half of them being of conservation concern [6]. As a result, efforts to resolve the tension between crop production and biodiversity protection are crucial, and achieving this goal necessitates major changes to current agricultural systems, such as reducing pesticide use while maintaining crop yields [7]. In Europe, agri-environmental schemes (AESs) are key policies that attempt to increase biodiversity and ecosystem services in farmlands by rewarding farmers who use environmentally friendly techniques [8]. However, conservation programs aimed at mitigating the detrimental effects of intensive agriculture in Southeast Asia still require more concrete government support.

Organic farming is one of the most eco-friendly agricultural options. The Research Institute of Organic Agriculture (FiBL) stated that organic agricultural land covers over 6.1 million hectares or 0.4% of the Asian agricultural sector. Likewise, organic farming accounted for 0.4% of Thailand’s agricultural land in 2018, and more land continues to be converted to organic farming [9]. Studies comparing biodiversity between organic
and conventional fields are frequently cited to highlight the positive effects of organic farming on biodiversity conservation due to the wildlife-friendly management practices (e.g., no synthetic chemical pesticides or fertilizers and little land-use pressure). Biodiversity maintenance also results from the increased landscape heterogeneity and complexity that accompanies organic farming [10]. In contrast, several studies have found that organic farming on its own do not enhance biodiversity [11–13]. While most studies have found that organic farms have higher biodiversity than conventional farms, results vary between and within taxonomic groups [11,14–16], by scale, and by landscape context [15,17–19]. The “intermediate landscape complexity” hypothesis proposes that landscape complexity may influence the effects of local field management on biodiversity and ecosystem services in a nonlinear way [20–22]. It suggests that, at the field scale, organic farming should have the greatest impact in landscapes of intermediate complexity and the least impact in extremely simple or extremely complex landscapes. However, studies [11,23,24] testing this hypothesis have reported conflicting findings.

The effects of organic farming on biodiversity have primarily been studied in temperate annual crops, with the focus being on birds, plants, and insects. There have been limited studies on tropical areas, including Sundaland, which is a global biodiversity hotspot [25]. In addition, only one study has examined the effects of organic rice fields on bats [26], even though insectivorous bats are known bioindicators and pest control agents in rice production [27–29]. Little is known about how farm and landscape management affect bats in rice-dominated landscapes. At the field scale, organic rice farming could be less detrimental to insects than conventional practices, such as the use of synthetic agrochemicals [14], resulting in increased bat activity and species richness [30]. At the landscape scale, habitat use by bats in paddies is likely influenced by the existence of other foraging habitats (e.g., bodies of water and forests) and roost sites (e.g., trees, caves, and anthropogenic structures) [31].

In the present study, we examined whether organic farming promotes bat activity and species richness in paddies of the Songkhla Lake Basin in southern Thailand. We hypothesized that bat species richness, bat activity, and the number of nocturnal airborne insects would be higher in organic than in conventional paddies. Our second objective was to evaluate the validity of the “intermediate landscape complexity” hypothesis [21]. Our third objective was to examine how landscape features influence bat activity and species richness. We hypothesized that the distance to the nearest limestone outcrop and water bodies would affect the activity and richness of insectivorous bats in paddies.

2. Materials and Methods
2.1. Study Area

This study was conducted in the Songkhla Lake Basin in southern Thailand. The area includes the provinces of Phatthalung, Nakhon Si Thammarat, and Songkhla (65 × 150 km between 6°45′–8°05′ N and 99°50′–100°35′ E), with elevations ranging from 0 to 25 m above sea level (Figure 1). There are two seasons, namely the dry season (February–April) and the wet season (May–December), which are influenced by the northeast and southwest monsoons. January is a transition between wet and dry season, and it was wet in the study year (220 mm of rain) due to a tropical storm “Pabuk”, which hit the region from 31 December 2018 to 7 January 2019. Annual relative humidity ranges from 77.0 to 86.2%, and humidity is much higher during the late rainy season (November–December). Average annual rainfall is 1873.8 mm per year, and the average annual temperature is 27.4 °C.

The Songkhla Lake Basin is a predominantly agricultural landscape consisting primarily of rubber plantations, mixed fruit orchards, and palm oil plantations (44%) as well as rice paddies (17%), and forest cover barely exceeds 15% of this area [32]. Within southern Thailand, this basin is the largest rice-planting area. Adjacent to the paddies in this basin, there are limestone outcrops with caves that harbor colonies of insectivorous bat species.
Rice farming in the Songkhla Lake Basin is rain-fed, with planting starting in October and harvesting occurring in February–March, although rice is grown more than once a year in some areas depending on the amount of irrigated water, weather conditions, and the type of rice cultivar. Most paddies in this area are conventional, while only a few (<5%) are organic. In conventional paddies, synthetic agrochemicals and fertilizers are commonly used, whereas organic paddies are typically planted with indigenous rice cultivars and use biological materials to manage pests and provide nutrients to rice plants. Furthermore, to avoid chemical contamination from nearby farms, organic paddies are usually surrounded by woods or other seminatural habitats that serve as field boundaries.

2.2. Sampling Design and Site Selection

We employed a matched pair design, with each pair consisting of one organic and one conventional rice paddy. We identified organic paddies based on organic certification (by a government agency) recorded in the 2018 growing season. All organic rice paddies used in this study had been certified for 1 or 2 years. Farms are certified organic by the Department of Agriculture, National Bureau of Agricultural Commodity and Food Standards, and...
We then selected a conventional paddy that resembled each organic paddy in terms of its size, presence or absence of linear features (i.e., hedgerows and tree lines) at paddy boundaries, rice growth stage, and surrounding landscape composition (Table S1). To ensure paired sites in relatively similar landscape context, the organic and conventional paddies within each pair were separated by at least 0.5 km (mean distance: 707 m, range: 454–1317 m), and pairs of paddies were more than 1 km from each other (mean distance to next closest pair: 5.92 km, range: 1.01–31.84 km). Although the distance within paired sites used in this study is relatively close and may not be strongly independent, it is similar to the minimum distance within matched paired sites given in other studies (500 m in [11] and 600 m in [34]). We acknowledge that sites may not be fully independent as the information on foraging range of tropical bats is obviously limited.

We used ArcGIS 10.5 (ESRI, Redlands, CA, USA) to establish three buffers (1, 2, and 3 km radii) around each paddy to quantify the surrounding landscape composition. Using the 2017 Global Land Cover data from the European Space Agency [35], we computed the proportion of agricultural area, urban area, forested and seminatural area (i.e., small patches of natural growing trees and shrubs within farmland), and water bodies within each buffer for each field (Table S2). Based on the proportions obtained in the 3 km radius around each point, we classified each paddy to one of three levels of area complexity following Tscharntke et al. [21] and Froidevaux et al. [11]: (1) complex landscapes, which had a high percentage of noncrop habitat (>20% forest and seminatural); (2) simple landscapes, which were areas comprising 1–20% forest and seminatural areas and exhibited an intermediate level of landscape complexity; and (3) cleared landscapes (<1% forest and seminatural areas). Finally, for each sampling site, we calculated the distance to the nearest linear feature (hedgerow or tree line), the nearest main water body (canal, river, or lake), and the nearest limestone outcrop and building using Google Earth Pro.

2.3. Acoustic Sampling

We conducted bat acoustic sampling between November 2018 and February 2019 in the 28 pairs of paddies (56 detector nights in total) during the period of rice growing in this area. We simultaneously monitored bat activity from 18:00 to 06:00 in both paddies (organic and conventional) within a pair, thereby controlling for nightly variation in bat activity (following [36]). On each survey night, we used two RPA3 recorders (Peersonic Ltd., Windsor, UK), one at each paddy, connected to remote ultrasonic microphones mounted on poles 2 m above the ground, pointed at 45° towards the sky. We set up the detectors to record full-spectrum sounds at a sampling rate of 384 kHz, with an auto record threshold of −35 dB, an input gain of −2 dB, and a maximum recording duration of 15 s. We did not conduct acoustic sampling in heavy rain or during full moon (moon light >50%) (following [37]).

Acoustic sampling sites were located near the center of the rice field. Although tree lines or hedgerows, which are known to influence the flight activity of bats if present, were relatively far from the paddies, we tried to be as far from these features as possible by placing a bat detector at least 30 m away from hedgerows and tree lines (mean distance: 105 m, range: 30–650 m). For the same reason, we discarded areas in close proximity to buildings to avoid bias generated by the possible presence of bat roosts [26], with bat detectors being placed more than 150 m from settlements (mean distance: 405 m, range: 150–1454 m). Each site was also more than 500 m from major rivers as such water bodies can influence bat activity [38–40]. We placed recording points at least 150 m away from artificial lighting. We also measured temperature and relative humidity at dusk each sampling night. During the sampling period, in early January 2019, our study area was hit by tropical storm “Pabuk”, which we predicted may affect insectivorous bat activity. Thus, we compared bat activity before and after the storm.
2.4. Analysis of Echolocation Calls

We analyzed recorded calls using Bat-Sound Pro 4.2.1 (Pettersson Elektronik AB, Uppsala, Sweden) and identified each bat pass to species level by comparing call characteristics (including frequency of maximum energy, minimum frequency, call duration, call interval, number of harmonic, and used harmonic) with the call library of the Bats, Small Mammals, and Birds Research Unit, Prince of Songkla University [41]. To quantify bat activity, we counted bat passes per night, which we defined as a series of at least two consecutive pulses [11] and separated from the next pulse by more than one second. We grouped insectivorous bats according to foraging habitat and corresponding echolocation call characteristics [42–44] into three foraging guilds: open-space foragers (Scotophilus kuhlii and Taphozous melanopogon), which forage at high altitudes and far from vegetation; edge-space foragers (Myotis horsfieldii, M. muricola, and Hipposideros larvatus), which forage near the edges of vegetation in vegetation gaps; and narrow-space bats (Rhinolophus spp.), which forage close to surfaces such as leaves or the ground. We calculated the guild night activity by combining the number of passes for each species in each guild. To estimate foraging activity, we recorded the number of feeding buzzes, which we defined as the final terminal-phase calls that are emitted immediately before attack on an insect prey [45,46]. Feeding buzzes can be another quantitative measure of bat foraging activity but it may not represent capture success.

2.5. Insect Sampling

We sampled insects using two modified light-suction traps (0.4 w LED light traps, each with a fan that sucks insects into a plastic container containing detergent) set 1.5 m above the ground in each paddy. This trap was designed to collect samples of small, weak flying insects throughout the night in agricultural areas without electricity [29]. We placed each modified light trap at least 50 m from bat detectors and as far as possible from streetlights on the same night that bat activity was observed. We trapped insects from 18:00 to 06:00 h. Trapped insects were stored in 70% alcohol. We counted and identified trapped insects to the level of order following Triplehorn and Johnson [47]. After identification, we also measured the body length of each insect from the front of the labrum to the tip of the abdomen [48]. We used the body length of the insect to categorize insect specimens into 12 size classes (0.1–2.0, 2.01–4.00, 4.01–6.00, . . . and 22.01–24.0 mm) [49,50]. Insect biomass was estimated according to Rogers et al. [51]: \[ W = 0.0305 L^{2.62} \] where \( W \) is dry mass (mg) and \( L \) is body length (mm).

2.6. Data Analysis

We applied generalized linear mixed-effect models (GLMMs; “glmmTMB” package; [52]) with the appropriate distribution (Poisson, negative binomial, or Gaussian) to investigate the influence of farming system (organic vs. conventional) and the potential interaction between farming system and landscape complexity on insectivorous bats and their insect prey. We treated bat species richness, total bat activity, number of feeding buzzes, numbers of feeding buzzes per pass (buzz ratio), insect abundance, and insect biomass as response variables. Independent variables included farming type, landscape complexity, and the farming type by landscape interaction. We classified landscape complexity as a factor with three levels: cleared, simple, and complex landscapes (defined above). For all models, we treated site pair as a random effect. We used a Poisson distribution for bat species richness. We used a negative binomial distribution for bat activity, number of feeding buzzes, and insect abundance as we found overdispersion of the count data. While we used Gaussian distribution for buzz ratio and insect biomass. Using Wald chi-squared tests, we determined the statistical significance of fixed effects and interaction factors. We used the “emmeans” package [53] to evaluate the effect size (marginal means and 95% confidence intervals) of each response at variable levels of landscape complexity to test the hypothesis that the impacts of organic farming are dependent on the features of the surrounding landscape. Furthermore, we used Spearman’s correlation test to verify our
prediction that bat activity should be positively associated with insect abundance and insect biomass.

To determine the influence of farming system (organic vs. conventional) and different landscape variables on bat species richness, bat activity (of the whole assemblage, of each foraging guild, and of each species), feeding buzzes, and buzz ratio, we included one local-scale variable (farming system) and other landscape-scale variables (distance to linear feature, water body, limestone outcrop, and building; proportion of agricultural areas, urban areas, forests and seminatural areas, and water bodies at three different radii; see Section 2.2 for descriptions) as independent variables. We treated field pair as a random effect. We added the effect of extreme environmental disturbance (data collected before and after tropical storm “Pabuk” in January 2019) as a potential confounding variable. We explored spatial autocorrelation in the residuals using a Mantel test (“ade4” Package; [54]) and detected no spatial autocorrelation ($p > 0.05$ in all models).

Prior to building candidate models, we went through several steps. First, we tested the effects of mean temperature at night, mean relative humidity, and Julian day on response variables independently and then used an information theoretic approach to determine the importance of these variables as covariates in our models [55]. Second, we tested multicollinearity using the Spearman’s correlation test for all independent variables and found that all the proportions of distinct landscape cover categories at three different radii were significantly correlated (based on Spearman’s rank correlation tests; $|r| > 0.7$) [56]. Thus, we ran models with each proportion of different landscape cover variable separately to avoid possible collinear predictor effects. For each response variable, we built 49 candidate models (including a null one). Then, we used the “DHARMa” package [57] to validate the candidate models. Lastly, we ranked and selected the most parsimonious model using AICc values (Akaike information criterion with a correction for small sample sizes; “AICcmodavg” package; [58]). When multiple models were equivalent ($\Delta$AICc < 2), we selected the model with the fewest number of parameters (df) and the lowest AICc. We performed all analyses with R version 3.6.1 [59] and RStudio version 1.2.1335 (RStudio, Inc., Boston, MA, USA). The level of significance for all tests was 0.05.

3. Results

We recorded a total of 9975 bat passes and 459 feeding buzzes within the 28 pairs of paddies (56 detector nights; Table 1). We identified nearly all (99.89%) of the bat echolocation calls to species. There was a minimum of 12 species present in the study area: *Myotis horsfieldii* (40.47%), *Scotophilus kuhlii* (13.20%), *Taphozous melanopogon* (13.07%), *Rhinolophus lepidus* (11.75%), *M. muricola* (9.40%), *Hipposideros larvatus* (7.55%), *R. stheno* (3.35%) and other species (1.21%). Bat activity in this agricultural area was dominated by edge-space (57.2%) and open-space species (26.3%).

We captured a total of 12,872 insects from 112 insect sampling events at the 56 rice fields. Insect orders observed included Diptera (38.96%), Coleoptera (38.54%), Hemiptera (13.49%), Lepidoptera (8.01%), and others (1.00%). The highest proportion of total insect biomass belonged to Lepidoptera, followed by Diptera, Coleoptera, Hemiptera, Hymenoptera, and other insect orders (Table 2).

While farming type and landscape complexity were not significant on their own for any of the response variables (i.e., bat species richness, total bat activity, number of feeding buzzes, insect abundance, and insect biomass), we did observe an interaction between both independent variables for two of the response variables (Table 3). Total bat activity and the number of feeding buzzes were impacted by the interaction between farming type and landscape complexity ($\chi^2 = 8.168$, df = 2, $p = 0.017$; $\chi^2 = 7.828$, df = 2, $p = 0.020$). Meanwhile, bat species richness, insect abundance, and insect biomass revealed no significant effect by the interaction between farming type and landscape complexity ($\chi^2 = 0.235$, df = 2, $p = 0.689$; $\chi^2 = 2.517$, df = 2, $p = 0.284$). The significant interactions revealed that bat activity, the number of feeding buzzes, and buzz ratio were significantly higher in organic rice fields than in conventional rice fields within simple landscapes. In contrast, bat activity
and feeding buzzes were significantly higher in conventional fields than in organic fields within cleared landscapes (Figure 2). Bat activity was not correlated with either total insect abundance (Spearman’s rank correlation, $R_s = 0.071$, $p > 0.05$; Figure 3A) or total insect biomass (Spearman’s rank correlation, $R_s = 0.003$, $p > 0.05$; Figure 3B).

Figure 2. Effect sizes (mean ± 95% confidence interval) are shown with black triangles and black solid lines, respectively, for bat richness (A), total bat activity (B), number of feeding buzzes (C), buzz ratio (D), insect abundance (E), and insect biomass (F) based on the difference in marginal means between organic rice fields and conventional rice fields across a gradient of landscape complexity (complex, simple, and cleared landscapes). Values on the right side of the dotted line suggest greater bat activity, number of feeding buzzes, species richness, or insect abundance in organic rice fields, while values on the left side of the dotted line suggest greater bat activity, number of feeding buzzes, species richness, or insect abundance in conventional rice fields. Asterisks denote effect sizes that are significantly different from zero ($p < 0.05$).
Table 1. Total bat activity (no. of bat passes) and feeding activity (total no. of feeding buzzes) by rice farming type for each bat species and the foraging guild they belong to.

| Taxon                  | Foraging Guild | Total Activity | Bat Activity (Feeding Activity) |
|------------------------|----------------|---------------|---------------------------------|
|                        |                |               | Organic                        | Conventional                   |
| *Myotis horsfieldii*   | Edge-space     | 4037          | 2459 (228)                     | 1578 (105)                     |
| *Myotis muricola*      | Edge-space     | 938           | 508 (24)                       | 430 (19)                       |
| *Scotophilus kuhlii*   | Open-space     | 1317          | 895 (9)                        | 422 (4)                        |
| *Taphozous melanopogon*| Open-space     | 1304          | 555 (7)                        | 749 (16)                       |
| *Rhinolophus lepidus*  | Narrow-space   | 1172          | 661 (18)                       | 511 (15)                       |
| *Rhinolophus affinis*  | Narrow-space   | 56            | 32 (1)                         | 24                             |
| *Rhinolophus stheno*   | Narrow-space   | 334           | 214 (7)                        | 120 (5)                        |
| *Rhinolophus acuminatus*| Narrow-space   | 10            | 5                             | 5                              |
| *Hipposideros larvatus*| Edge-space     | 753           | 350 (1)                        | 403                            |
| *Hipposideros bicolor* | Narrow-space   | 8             | 1                             | 7                              |
| *Hipposideros lekaguli*| Narrow-space   | 26            | 8                             | 18                             |
| *Hipposideros galeritus*| Narrow-space   | 9             | 9                             | -                              |
| Bat unknown            |                | 11            | 8                             | 3                              |

Table 2. Total insect abundance (no. of individuals) and total insect biomass (mg) by rice farming type for each order.

| Order              | Total Abundance | Insect Abundance (Insect Biomass) |
|--------------------|-----------------|-----------------------------------|
|                    | Organic         | Conventional                      |
| Coleoptera         | 4961 (4141.10 mg) | 2095 (1892.59)                     | 2866 (2248.51)               |
| Lepidoptera        | 1031 (4783.78 mg) | 598 (2646.06)                     | 433 (2137.72)                |
| Hemiptera          | 1737 (1651.37 mg) | 864 (875.24)                      | 873 (776.13)                 |
| Diptera            | 5015 (4564.60 mg) | 2620 (2523.09)                     | 2395 (2041.51)               |
| Hymenoptera        | 123 (136.67 mg)  | 36 (41.06)                        | 87 (95.61)                   |
| Thysanoptera       | 3 (3.15 mg)     | 3 (3.15)                          | 0 (0)                        |
| Orthoptera         | 1 (43.56 mg)    | 1 (43.56)                         | 0 (0)                        |
| Blattodea          | 1 (20.50 mg)    | 1 (20.50)                         | 0 (0)                        |

Figure 3. Correlations between total bat activity (number of bat passes) with insect abundance (A) and insect biomass (B). Each plotted point represents data from a single survey event at a given sampling location.
Table 3. Results of statistical analyses showing the effects of farming type, landscape complexity, and the interaction between farming type and landscape complexity on bat species richness, bat total activity, total number of feeding buzzes, buzz ratio, insect abundance, and insect biomass.

| Response Variable                  | Independent Variable                                      | χ²   | df  | p-Value |
|-----------------------------------|-----------------------------------------------------------|------|-----|---------|
| Bat species richness              | Farming type (organic vs. conventional)                   | 1.224| 1   | n.s.    |
|                                   | Landscape complexity                                     | 5.809| 2   | n.s.    |
|                                   | Interaction (farming type × landscape complexity)        | 0.235| 2   | n.s.    |
| Total bat activity                | Farming type (organic vs. conventional)                   | 0.729| 1   | n.s.    |
|                                   | Landscape complexity                                     | 1.787| 2   | n.s.    |
|                                   | Interaction (farming type × landscape complexity)        | 8.168| 2   | *       |
| Feeding buzzes                    | Farming type (organic vs. conventional)                   | 0.960| 1   | n.s.    |
|                                   | Landscape complexity                                     | 0.601| 2   | n.s.    |
|                                   | Interaction (farming type × landscape complexity)        | 7.828| 2   | *       |
| Buzz ratio                        | Farming type (organic vs. conventional)                   | 4.008| 1   | *       |
|                                   | Landscape complexity                                     | 2.155| 2   | n.s.    |
|                                   | Interaction (farming type × landscape complexity)        | 0.540| 2   | n.s.    |
| Total insect abundance            | Farming type (organic vs. conventional)                   | 0.425| 1   | n.s.    |
|                                   | Landscape complexity                                     | 1.753| 2   | n.s.    |
|                                   | Interaction (farming type × landscape complexity)        | 2.517| 2   | n.s.    |
| Total insect biomass              | Farming type (organic vs. conventional)                   | 0.717| 1   | n.s.    |
|                                   | Landscape complexity                                     | 2.111| 2   | n.s.    |
|                                   | Interaction (farming type × landscape complexity)        | 1.561| 2   | n.s.    |

Abbreviations: n.s., nonsignificant; *, p < 0.05; χ², chi-square score; df, degrees of freedom.

When combining farming system (organic vs. conventional) and different landscape characteristics predicted to affect bat activity, our models revealed different results for different response variables (Table 4 and Table S3, Figures 4–7). The top models showed that landscape features had larger impacts on bat activity than farming management and abiotic factors (temperature, humidity, and Julian day). Our models indicated a strong positive effect of the proportion of forest and seminatural areas within a 1 km radius on total bat activity, the activity of narrow-space foraging bats (Rhinolophus spp.), and the activity of edge-space foragers (i.e., H. larvatus). Our analyses also demonstrated a negative impact of distance to the nearest limestone outcrop on the total number of feeding buzzes and buzz ratio as well as a negative effect of distance to the nearest linear feature on T. melanopogon, suggesting higher bat activity in areas near these landscape features. Our models also suggested that the activity of open-space foraging bats and the activity of M. muricola increased near bodies of water. Moreover, we found a negative influence of the proportion of agricultural areas within a 2 km radius on bat species richness and the activity of M. horsfieldii. In addition to these landscape features that influenced bat activity, the tropical storm negatively affected total bat activity, the total number of feeding buzzes, and the activity of edge-space foragers (i.e., M. horsfieldii; Figure 8).

Table 4. Results of statistical analyses showing the effects of landscape characteristics on bat species richness, total bat activity, total number of feeding buzzes, activity of each bat species, and activity of each foraging guild.

| Response Variable                  | Independent Variable                                      | Estimate (±SE) | z-Value | p-Value |
|-----------------------------------|-----------------------------------------------------------|----------------|---------|---------|
| Bat species richness              | Percentage of agricultural area within 2 km radius        | −0.02 (±0.01)  | −2.19   | *       |
| Total bat activity                | Percentage of forest and seminatural area within 1 km radius | 0.09 (±0.03)  | 3.07    | **      |
|                                   | Tropical storm disturbance                               | 1.65 (±0.39)  | 4.23    | ***     |
Table 4. Cont.

| Response Variable | Independent Variable                                | Estimate (±SE)          | z-Value | p-Value |
|-------------------|-----------------------------------------------------|-------------------------|---------|---------|
| Feeding buzzes    | Distance to nearest limestone outcrop               | −0.14 (±0.04)           | −3.66   | ***     |
|                   | Tropical storm disturbance                          | 1.07 (±0.37)            | 2.86    | **      |
|                   | Tropical storm disturbance                          | −0.002 (±0.001)         | −2.02   | *       |
| Buzz ratio        | Distance to nearest limestone outcrop               | 1.07 (±0.37)            | 2.86    | **      |
|                   | Percentage of forest and seminatural area within 1 km radius | 0.13 (±0.04)           | 2.99    | **      |
|                   | Tropical storm disturbance                          | 1.93 (±0.56)            | 3.46    | ***     |
| M. horsfieldii activity | Percentage of agricultural area within 2 km radius | −0.16 (±0.06)           | −2.72   | **      |
|                   | Tropical storm disturbance                          | 1.96 (±0.80)            | 2.44    | *       |
| M. muricola activity | Distance to nearest water body                     | −0.16 (±0.05)           | −2.93   | **      |
| H. larvatus activity | Percentage of forest and seminatural area within 1 km radius | 0.17 (±0.05)           | 3.43    | ***     |
| Open-space foragers | Distance to nearest water body                     | −0.14 (±0.05)           | −2.86   | **      |
| S. kuhlii activity | Distance to nearest water body                     | −0.15 (±0.05)           | −2.97   | **      |
| T. melanopogon activity | Distance to nearest water body                     | −0.14 (±0.06)           | −2.29   | *       |
|                   | Distance to linear feature                          | −12.49 (±5.64)          | −2.22   | *       |
| Narrow-space foragers | Percentage of forest and seminatural area within 1 km radius | 0.13 (±0.04)           | 3.17    | **      |
| Rhinolophus spp. activity | Percentage of forest and seminatural area within 1 km radius | 0.13 (±0.04)           | 3.03    | **      |

Abbreviations: *, p < 0.05; **, p < 0.01; ***, p < 0.001; SE, standard error.

Figure 4. Effects of significant landscape factors on bat species richness, total bat activity and total number of feeding buzzes. (A) Percentage of agricultural cover within a 2 km radius had a significant negative effect on bat richness, (B) proportion of forest and seminatural habitat cover within a 1 km radius had a significant positive effect on bat activity, and distance to the nearest limestone outcrop had a significant negative effect on the number of feeding buzzes (C) and buzz ratio (D). All regressions are plotted with 95% confidence intervals.
Figure 5. Effects of significant landscape factors on edge-space foraging bats. (A) Percentage of forest and seminatural habitat cover within a 1 km radius had a significant positive effect on the activity of edge-space foraging bats, (B) proportion of agricultural cover within a 2 km radius had a significant negative effect on *M. horsfieldii* activity, (C) distance to the nearest water body had a significant negative effect on *M. muricola* activity, and (D) percentage of forest and seminatural habitat cover within a 1 km radius had a significant positive effect on the activity of *H. larvatus*. All regressions are plotted with 95% confidence intervals.

Figure 6. Effects of significant landscape factors on open-space foraging bats. Distance to the nearest water body had a significant negative effect on the activity of open-space foraging bats (A) and *S. kuhlii* (B), while two landscape factors, namely distance to the nearest water body (C) and distance to the nearest linear feature (D), had a significant negative effect on *T. melanopogon* activity. All regressions are plotted with 95% confidence intervals.
Contrary to our predictions, there were no differences in bat species richness, total bat activity, feeding activity, or insect prey abundance between organic and conventional rice fields, similar to some previous studies [11–13]. These studies stated that the proximity of structured linear habitat (e.g., hedgerow) and water bodies and the size of organic farmland are more important factors than farm management in supporting bat activity. However, the present study demonstrates for the first time the effect of farming system (organic vs. conventional) and landscape features on insectivorous bats in rice fields of Southeast Asia. The effects of significant landscape factors on narrow-space foraging bats. Percentage of forest and seminatural habitat cover within a 1 km radius had a significant positive effect on the activity of narrow-space foraging bats (A) and Rhinolophus spp. (B). All regressions are plotted with 95% confidence intervals.

**Figure 7.** Effects of significant landscape factors on narrow-space foraging bats. Percentage of forest and seminatural habitat cover within a 1 km radius had a significant positive effect on the activity of narrow-space foraging bats (A) and Rhinolophus spp. (B). All regressions are plotted with 95% confidence intervals.

**Figure 8.** Mean (±SE) values of total bat activity (A), total number of feeding buzzes (B), activity of edge-space foraging bats (C), and activity of M. horsfieldii (D) in matched organic and conventional rice fields before (pre) and after (post) tropical storm disturbance. Asterisks indicate significant differences between pre and post tropical storm disturbance (p < 0.05).

4. Discussion

4.1. The Effects of Organic Farming on Bats and Insects

The present study demonstrates for the first time the effect of farming system (organic vs. conventional) and landscape features on insectivorous bats in rice fields of Southeast Asia. Contrary to our predictions, there were no differences in bat species richness, total bat activity, feeding activity, or insect prey abundance between organic and conventional rice fields, similar to some previous studies [11–13]. These studies stated that the proximity of structured linear habitat (e.g., hedgerow) and water bodies and the size of organic farmland are more important factors than farm management in supporting bat activity. However,
most previous reports in temperate farmland have indicated that organic farming has a positive effect on bat activity and their insect prey [14,16,30,60–62]. Wickramasinghe et al. [30] mentioned that the high foraging activity of insectivorous bats in organic farms indicates high-quality foraging habitat in terms of prey availability. In the present study, prey availability was similar in organic and conventional rice fields, suggesting that there is no reason for bats to have greater feeding activity in one type of rice field compared to the other. Furthermore, the fact that farm management did not significantly affect insect availability and insectivorous bats may raise some concerns about potential agrochemical contamination of organic rice fields from nearby conventional ones, as was found in organic vegetable farms in adjacent areas [63]. Organic farms can be contaminated with agrochemicals through floodwater during unusually heavy rain.

Our findings that total bat activity, the number of feeding buzzes, and buzz ratio in organic versus conventional fields depend on the level of landscape complexity support the “intermediate landscape complexity” hypothesis. This hypothesis states that local conservation management (e.g., organic farming) within the agricultural matrix is most effective in landscapes of intermediate complexity (1–20% noncrop habitats) compared to cleared landscapes (where source populations are nearly absent) or highly complex landscapes (potentially due to high local diversity; [20,21]). The significantly higher bat activity, number of feeding buzzes, and buzz ratio in organic rice fields in simple landscapes indicate that patches of forest and seminatural habitat can promote bat activity in organic fields in landscapes of intermediate complexity. Meanwhile, there were no significant differences between bat activity in the organic and conventional fields in complex landscapes, indicating that high landscape complexity can support insectivorous bats even in conventional fields. The significantly higher bat activity and number of feeding buzzes in conventional rice fields in the cleared landscapes are probably due to the presence of water bodies (50–100 m in diameter) that were adjacent to two of the sampling sites, where the two most common bat species, namely *M. horsfieldii* and *T. melanopogon*, were found actively foraging at these sites. The importance of water bodies to bats in agricultural landscapes is discussed below.

### 4.2. Response of Insectivorous Bats to Landscape Characteristics

Our findings that the presence of landscape features had larger impacts on bats than farming practice corroborate those of previous studies [11,13]. As we found a positive relationship between total bat activity and the proportion of forest and seminatural area within a 1 km radius, it is very probable that bat activity was enhanced by trees cover. Several studies in temperate areas have also highlighted the benefit of tree cover to insectivorous bats [64–66]. In a tropical study, Harvey et al. [67] reported that retaining tree cover within agricultural landscapes had clear positive impacts on species richness and abundance of bats. Indeed, bats use forest and seminatural habitat for foraging, roosting, and commuting due to the great abundance and diversity of food resources (i.e., insects) and protection from predation [68]. In this study, activity of *T. melanopogon* increased with distance to linear feature. Studies in farmland and vineyard have shown linear features enhance bat activity [11,69]. Bats use this element for commuting, foraging, and as shelter from predators [70]. Authors have suggested that bats with short-range echolocation will benefit from hedgerow [11,70]. Further studies on the impact of linear feature to long-range echolocation bats such as *T. melanopogon* should be carried out. In general, research on linear feature and tropical bats are currently limited.

### 4.3. The Differential Response of Bats According to Species and Guild

We discovered that insectivorous bats have species- and guild-specific responses to different landscape features. Such responses may be influenced by their wing morphology, foraging strategy, and echolocation call characteristics [71–73]. Our finding that the activity of narrow-space foragers is positively correlated with the proportion of forest and seminatural area within a 1 km radius is easily explained as these bats (such as *Rhinolophus* spp.)
have broad wings and low wing loadings, making them highly maneuverable and able to forage in cluttered vegetation [76]. In contrast, the activity of open-space foragers, which have wings with high aspect ratio, high wing loading, and low-frequency echolocation calls, tends to increase near bodies of water. The strong association between the activity of open-space foraging bats and the nearest water body underlines the importance of riparian habitats for bats, both as commuting routes [77,78] and as foraging grounds [79,80]. Previous studies [81] in Malaysia and in Tanzania [82] have shown that riparian vegetation along rivers and water bodies in agricultural land promotes insectivorous bat activity. Freshwater bodies also provide bats with a source of drinking water and insect prey, including dipterans, which emerge and swarm over water bodies or near vegetation structures [83].

Previous studies on insectivorous bats in central Thailand have revealed that open-space foraging bats, especially *Taphozous* spp., mainly consume dipteran insects [84,85].

Edge-space foraging bats, the most common guild, exhibited a variety of responses to landscape features. The overall activity of edge-space species increased with the proportion of seminatural habitats, implying that natural environments benefit this foraging guild. Moreover, the feeding activity of insectivorous bats, especially *M. horsfieldii* (which accounted for 72.5% of all feeding buzzes), notably increased closer to limestone outcrops. These outcrops harbor remnants of natural forest within large agricultural landscapes and can provide vital feeding grounds within the relatively hostile monoculture farmlands. Based on this study, the increasing conversion of these isolated natural habitats to agriculture areas could deleteriously impact *M. horsfieldii*. The activity of another edge-space forager, *M. muricola*, increased with proximity to the nearest body of water, which is similar to many other *Myotis* species that are reported to forage in freshwater habitats [86]. This bat is flexible in its foraging habitats, with authors previously reporting that it forages over streams and rivers and in farmland and fields [85]. We also found a positive relationship between the activity of *H. larvatus* and the proportion of forest and seminatural habitats. Previous studies have reported that hipposiderid bats mostly forage in understorey that includes both closed and edge vegetation. Thus, this group of bats displays great flexibility in habitat use and is able to occupy a range of foraging habitats [84,87].

### 4.4. Response of Insectivorous Bats to Extreme Environmental Disturbance

The extreme environmental disturbance caused by a tropical storm had a significant negative impact on bat populations as total bat activity, activity of edge-space foraging bats, and total number of feeding buzzes all decreased significantly after disturbance of the tropical storm “Pabuk” during our study period. Severe storms can cause direct mortality and can also alter habitats, which can affect food and roost availability [88]. Bat population declines have also been observed following severe storms in Montserrat [89], Puerto Rico [90,91], Guam [92], Rodrigues [93], and Samoa [94]. Bat species that are most vulnerable to storm disturbance are species that make use of trees for roosting. Sustaining primary forest and patches of secondary forests is critical for mitigating the effects of significant natural disturbances on biodiversity [95]. Within two months after a tropical storm, bats reduce their foraging activity by more than 50%. With the prediction that storms will be more intense and more frequent [96], bats in continental areas are inevitably prone to disturbance from cyclonic storms. Little is known about their response to storms in continental regions, including the Thai–Malay peninsula. Documentation on the impacts of extreme climatic occurrences, which can have both short-term and long-term effects on bat populations, is needed.

### 5. Implications for Conservation

In conclusion, organic rice fields appear to be more effective in promoting insectivorous bat activity in moderately complex landscapes (classified as simple landscapes in this study) than in extremely complex or cleared landscapes. Thus, landscapes of intermediate complexity should be emphasized for local bat conservation management. Conservation efforts for bats should concentrate on the construction and maintenance of critical land-
scape characteristics, such as woodlands and freshwater bodies, as well as enhancing roost availability within agricultural landscapes, i.e., installing bat boxes [11]. Agroecology agriculture schemes, such as agroforest farming, could also enhance biodiversity and offer economic feasibility in already disturbed environments. Ecologically friendly farming practices, such as organic rice farming, may be ineffective in enhancing bat activity on their own. This farming approach is suggested to benefit biodiversity in general [97], although it is not conclusive [11–13]. Overall, organic farming provides significant environmental benefits, including reduced carbon and ecological footprints, the elimination of harmful chemicals and their spread in the environment and throughout the food chain, and improved biological control and pollination services [98]. However, due to 19–25% lower yield per unit of land, organic farming requires 23–33% more land, which in turn may result in higher natural habitat loss. Thus, sustaining crop productivity while protecting the environment likely requires smart integration of conventional and organic agriculture [97].

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d14060444/s1, Table S1: General information about study sites, Table S2: Description of the reclassified land cover data, Table S3: Summary of generalized linear mixed model selection.

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