

Landscape features drive insectivorous bat activity in Indian rice fields

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Abstract

Context

The conversion of natural land for agriculture is a crippling threat to biodiversity. The effect of this conversion can be minimised by understanding the habitat requirements of local species and incorporating them into agricultural landscapes. Insectivorous bats, which have been shown to control a number of agricultural insect pests, exhibit species-specific responses to the surrounding landscape, tied closely to their morphology and foraging mode. The activity and distribution patterns of bats are therefore influenced by the landscape characteristics.

Objectives

This study aimed to determine which features in the landscape surrounding rice fields influence the activity levels of insectivorous bats, and at what scales they were most influential.

Methods

We collected acoustic recordings to determine activity levels of seven bat sonotypes in rice fields surrounded by a variety of landcover types in the Nagaon district of Assam, India. Using this, we determined the most important set of features in the surrounding landscape, and the scales at which they were most predictive, for each sonotype.

Results

Our results suggest that variables related to tree cover are the most important predictors of bat activity in rice fields. Distance to nearest forest, area of forest within 1km, distance to nearest forest edge, and landscape heterogeneity influenced all five of the analysed bat sonotypes. Also important were the amount of urban land within 1km, which exerted a negative effect on the activity of one sonotype, and moonlight activity, which negatively influenced the activity levels of one sonotype.

Conclusion

Our results demonstrate that when in rice fields, bat activity is most influenced by presence and proximity of trees. Increasing tree cover in agricultural landscapes will increase bat activity and likely the level of pest control.

Introduction

Bats, of the order Chiroptera, are the second most diverse mammalian order on the planet, bringing with their diversity substantial ecological and financial value through their potential use as bioindicators (Jones et al. 2009; Russo et al. 2021), providers of fertilizer, and ecosystem services such as pest control, seed dispersal, and pollination (Kunz et al. 2011). Of the known > 1400 species of bats (Simmons and

Cirranello 2021), nearly two-thirds are insectivores, which thrive in a range of habitats – from deserts (Razgour et al. 2018) – to wetlands (Mas et al. 2021). In adapting to these environments, bats have evolved highly specialized acoustic and morphological characteristics that enable them to navigate different niches and hunt prey in a wide variety of conditions (Denzinger et al. 2016; Jones et al. 2016). These same specializations, however, also define the limits of their existence. As a result, bats adapted to a particular habitat cannot easily forage in another.

Interest in insectivorous bats in agricultural landscapes has risen dramatically in the last two decades, driven in part by the growing evidence of their value as pest suppression agents to crops such as rice (Puig-Montserrat et al. 2015), cotton (Cohen et al. 2020), cacao (Cassano et al. 2016), and corn (Maine and Boyles 2015). Their success as natural pest suppressors comes from a broad diet (Tournayre et al. 2021; Maslo et al. 2022), large energetic demands associated with flight, and, importantly, flexibility in foraging habitats. Insectivorous bats quickly switch to the most productive foraging habitat available. When an agricultural plot is fallow between seasons, bats can move to more productive regions elsewhere, to return when there are pest outbreaks (McCracken et al. 2012; Puig-Montserrat et al. 2015). This has led to the suggestion that bats might be uniquely suited to tackle the changing ranges of pests under climate change (Blažek et al. 2021).

A number of characteristics determine the suitability of a landscape to insectivorous bats. Chief among these is the composition of the wider landscape surrounding the crop fields. Studies of bats in agricultural landscapes consistently find that heterogeneous landscapes support a more species rich and diverse bat community than homogenous ones (Frey-Ehrenbold et al. 2013; Monck-Whipp et al. 2018; Rodríguez-San Pedro et al. 2019) and that higher levels of natural and semi-natural landcover within agricultural landscapes promotes bat activity (Kelly et al. 2016; Kahnonitch et al. 2018).

Linear elements such as hedgerows and lines of trees constitute a key type of natural landcover for echolocating bats. These are used both as landmarks for navigation, and for protection against avian predators and wind (Downs and Racey 2006). Even a single row of trees can be used for commuting and, if the trees are of the right structural form, for roosting (Fischer et al. 2010; Kalda et al. 2015). Increasing the width of the linear features is usually accompanied by larger insect communities, leading to higher bat activity (Russ et al. 2003). As a result, linear features around agricultural fields host bats in greater numbers and diversity than the field interiors do (Kelm et al. 2014; Finch et al. 2020). With many types of agriculture providing less-than-hospitable matrices between forest patches, the presence of suitable linear elements reaching into agricultural fields increases the permeability of such agricultural landscapes (Finch et al. 2020).

The edges between forest and non-forest habitats also provide productive feeding grounds for bats that offer (comparative) safety from predators. The relative safety and higher foraging success for the generally rich guild of edge-space foragers (Denzinger et al. 2016), results in significantly higher bat activity at edges or in close proximity to linear features compared to open and cluttered habitats (Jantzen and Fenton 2013; Finch et al. 2020).

Compounding the requirements for foraging habitats are the requirements for roosting and water. While many bats are capable of commuting long distances to forage, such movements are often along edges. Many bats will avoid open spaces, which bring higher risks of predation, colder temperatures, and faster winds (Downs and Racey 2006). Landscape elements providing bats with access to water bodies support greater bat activity (Heim et al. 2018).

The carrying capacity of a landscape is therefore not solely determined by its composition, but also by the configuration of the elements within it, which shape a bat's access to food, roosts, and water (Heim et al. 2015). Landscape complementation – whereby close proximity of different landscape elements, and their resulting ease of access, increase the abundance of a species – is particularly evident in bats due to the often contrasting requirements of roosting (in mature trees) and foraging (in more open spaces). A study in Canada found that when the area of different landcover is kept constant, increased fragmentation led to increased bat activity (Ethier and Fahrig 2011).

Across the world, the intensification and homogenization of agricultural practices (Robinson and Sutherland 2002; Wang et al. 2015) are having severe impacts on bat populations (Park 2015). Given the strong preference of bats for specific landscape structures, changes which reduce treecover disproportionately affect those species that forage in dense natural vegetation. The general trend shows a greater decline of clutter foragers than open-space foragers with reduced treecover (Heim et al. 2016; Mtsetfwa et al. 2018).

As agricultural systems worldwide come under increased production pressure, the need for sustainable pest control has bolstered studies of natural pest control measures. Given that bats are valuable pest suppression agents, and that India is striving to increase agricultural production (Hinz et al. 2020), it is important to understand the relationship of bats and agricultural landscapes.

This study focussed on the insectivorous bats in rice-dominated landscapes of Assam, India. In India, rice makes up 22.01% of the gross cropped area (Directorate of Economics and Statistics 2019). A small rice farm can offer an ideal habitat for a broad community of insectivorous bats, boasting an abundance of insects (Puig-Montserrat et al. 2015), edges (Harms et al. 2020), roosting sites (in trees and anthropogenic structures) (Kusuminda et al. 2021), and water bodies. As a matrix, rice is a harsh habitat, providing no landmarks, edges, tree cover, or resting sites. The larger the fields are, therefore, the less accessible we expect their interiors to be, as bats foraging in them are then further from water sources, shelter, edges, or roosting sites (Rainho and Palmeirim 2011; Frey-Ehrenbold et al. 2013).

This study used passive acoustic recordings from rice fields within the Nagaon district of Assam (26°21'0"N, 92°40'60"E) to investigate the importance and scales at which different landscape features drive the activity of insectivorous bats. By identifying how bats use the agricultural landscape, this study can contribute to designing agricultural landscapes for the protection of bats and the promotion of their ecosystem services.

Methods

Study site:

The study was conducted in the Nagaon district of Assam. Although the typical operational holding of agricultural land in Nagaon (of which rice is the primary crop) is 0.5-1.0 hectares (Saikiam et al. 2020), rice plots usually lie adjacent to one another, so the size of an uninterrupted stretch of rice varies considerably. Nagaon tends to have hot and wet summers. For the months of May and June 2019, the average temperature was 28°C, with a minimum of 21°C and a maximum of 35°C (accessed on 15 Jan 2022 from timeanddate.com). The lack of irrigation leaves many farmers relying on the rains to water their crops. Historically, the months of May and June see among the highest rainfall of the year, averaging 219 and 311mm, respectively (accessed on 15 Jan 2022 from timeanddate.com).

A typical farming village in Assam has a central road with many branches, dotted on either side with buildings, both concrete and wood. Hubs in a village centre have the highest density of buildings and artificial light, which decrease as one moves further away. Forested or semi-forested vegetation is present in pockets and surrounding most structures. Data for this study came from rice fields surrounding such villages near the city of Nagaon.

Field Data:

Acoustic data were collected using six Audiomoth 1.0.0 full spectrum recorders (Hill et al. 2018) with a sampling rate of 384kHz and a medium gain. Data were collected over 18 nights between 9 May and 8 June 2019, with the six recorders placed as far away from each other as was feasible. Sites were chosen by a combination of logistical feasibility, diversity of the surrounding landscape, and contacts with local communities. Uniform data collection in this landscape proved difficult, and site locations and sampling effort were influenced significantly by logistical, cultural, and safety considerations. As a result, not every site was revisited, nor were recorders always in place by dusk. To account for difference in sampling effort, any recorder that collected less than 90 minutes of audio in a night was excluded from the analysis, and sampling effort was included in the global model of each sonotype. To account for potential spatial autocorrelation introduced by clustering of sites, both the raw data and the residuals of final models were tested for spatial autocorrelation at all relevant scales.

Acoustic data analysis

Acoustic recordings totalling 481 hours were processed using custom built code in Python version 2.7 (Rossum et al. 1995). From these recordings bat calls were isolated and extracted based on the following measurements. All code used during analysis will be uploaded to a git repository.

- (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 few calls that 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 recorders being put in place.

There are limited acoustic libraries for Indian bats, none extending as far as Assam. Without such a library to use as reference, 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), (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. One QCF call was 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. Calls were classified into sonotype based on FMAXE values, resulting in one pure QCF call at 28kHz, and six FM-QCF calls at 20kHz, 31kHz, 34kHz, 38kHz, 48kHz, and 65kHz, respectively.

All recordings were divided into five-second intervals. One bat pass was defined as an interval containing more than two 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.

Spatial data analysis

Landscape data used for the analysis came from Level-2A of Copernicus Sentinel data [2019], accessed on 13 January 2022. Different studies choose different radii around sites within which to calculate landscape statistics. These vary based on the objective of the study, bat species in question, and landscape. They range between 0.1km–1km (Kahnonitch et al. 2018) to 1km–5km around each site (Rodríguez-San Pedro et al. 2019). Due to lack of data on the home and foraging ranges of India bats, we chose intermediate scales of analysis for landscape variables, using scales of 500m, 1000m, 2000m, and 3000m, to account for difference in range sizes between different species. The landscape in a radius of 3km around every site was classified at a 10m resolution using a random forest supervised classifier in Google Earth Engine (Gorelick et al. 2017). Training data were collected using Google Earth Engine and classified landscapes were verified using Google Earth imagery from January 2019, and the first author's knowledge of the fieldsites. The classification of rice fields was also ground-truthed.

Four bands were used for the classification, B3, B4, B8 and B11, which correspond to green, red, near infrared (NIR), and short-wave infra-red (SWIR), respectively. In addition to the above bands, the following three indices were calculated for use in the classifier. NDVI and NDWI (Xue and Su 2017) and one additional index (Mayer and Scribner 2002) were calculated using the formulae below.

1. NDVI: $(\text{NIR}-\text{Red})/(\text{NIR} + \text{Red})$
2. NDWI: $(\text{Green}-\text{NIR})/(\text{Green} + \text{NIR})$
3. $(\text{SWIR} - \text{Red})/(\text{SWIR} + \text{RED})$.

To increase the accuracy of the classifier, the least cloudy image, selected using the 'CLOUDY_PIXEL_PERCENTAGE' band from data for each of January and May were considered. These two months represent the landscape before and during the rice season, respectively. The difference in the values of the above three metrics between the months of January and May exploited changes in the spectral characteristic of rice prior to and during the season, increasing the accuracy of the classifier.

Each 10m-10m pixel was classified into one of nine landscape types.

1. Dry Rice: Rice planted in dry fields.
2. Wet rice: Rice planted in waterlogged fields.
3. Water: Pixels covered completely with water that was not covered by any algae/plants.
4. Bank: Pixels filled partly with water and partly with another landcover type.
5. Edge: Land filled only partly with trees and partly with a different land cover type.
6. Field: Land with grass but no trees.
7. Forest: Pixels containing only trees.
8. Bare ground: Empty land without grass, trees, water, or rice, often roads.
9. Urban: Area with construction/houses, or roads. Although roads were often also classified as 'Bare ground'.

This list was later condensed by merging three pairs of classifications: dry rice and wet rice; and water and bank, and 'urban' and 'bare ground'. 'Dry rice' and 'wet rice', and 'water' and 'bank' were merged because these pairs were, from the perspective of a bat, nearly identical. 'Urban' and 'bare ground' were merged because roads were often classified as 'bare ground', and represented many of the negative features of urban land – artificial light, noise, and pollution.

The following types of landscape metrics were calculated for the analysis:

1. Area of all landscape types except water within the four buffers. Size of water bodies was not considered because at the scale of analysis we used, without access to characteristics such as water depth, and in a landscape with an abundance of water bodies, distance to the nearest water body was considered to be the most important water variable.
2. Distance of each site to nearest patch of every landscape. Defining a 'patch' as 10 or more pixels of a water (equivalent to 50m * 20m) or 30 or more pixels of the other landscape types (equivalent to 50m * 60m), the distance to the nearest patch within 3000m from the recorder was measured. This metric was not calculated for rice because all the recorders were placed in rice fields.

3. Landscape structure metrics. Shannon's Diversity Index (SDHI) for landscapes, calculated as $-\sum_{i=1}^m (P_i * \ln(P_i))$ (Shannon 1948). Where 'i' is the selected landscape and P_i is the proportion of landscape 'i' in the selected buffer.

Statistical analysis:

Part 1: Accounting for spatial autocorrelation

To maximise the use of the data, while acknowledging and accounting for non-independent datapoints, sites were grouped according to buffers that resulted in no significant spatial autocorrelation. All statistical analysis was performed in R version 3.63 (R Core Team 2020). A distance matrix of all the points was created and transformed into a hierarchical cluster tree. Points were then grouped based on a set of scales: 0.1km, 0.2km, 0.3km, 0.4km, 0.5km, 1km, 5km, 10km and 30km. At each scale, standardized bat activity was tested for spatial autocorrelation using the Moran's I test with the `moran.test()` function in the 'spdep' package (Bivand and Wong 2018). The smallest scale at which sites could be grouped with no spatial autocorrelation was chosen for each sonotype. This grouping was used as the random effect in the subsequent models.

Part 2: Choosing one variable of each landcover

Most landcover types had five datapoints per site. They were: area within buffers of 0.5km, 1km, 2km and 3km - and distance of the site to the nearest patch of said landcover. In the case of rice and Shannon Landscape Diversity Index (SDHI), distance to the nearest patch was not applicable.

For each landcover type, the most significant of the five (or four) variables was selected using a generalized linear mixed model (GLMM) implemented as below. Here bat activity was the response variable, sampling effort and one variable of the focal landcover were explanatory variables, and the previously selected grouping variable was the random effect. The models of every variable of a landcover type were compared to each other and to a null model using Akaike's Information Criteria corrected for sample size (AICc) to determine the most significant variable of a given landcover type (Bartoń 2020). If the null model performed best, then the landcover type in question was not taken forward, otherwise the variable that contributed to the best model was standardized and incorporated into the global GLMM.

Part 3: Global model

The global GLMM was built with nightly bat activity as the response variable and the previously selected variable of each landcover as the explanatory variables. Also included were the standardized variables of 'moonlight intensity' (obtained for the study from WorldWeatherOnline.com on 16 August 2021) and distance to water. The previously determined site groupings were used as the random effect. Prior to running the model, all of the variables were z-standardized to make the results comparable (Schielzeth 2010), and tested for correlation with the Pearson's r. The global model was built using the 'glmmTMB' package (Brooks et al. 2017), with a negative binomial distribution parameter to account for overdispersion (Lindén and Mäntyniemi 2011).

Part 4: Best model

The resulting global model (above) was run through the 'dredge' command in the MuMIn package (Bartoń 2020) to select, using AICc, the best-performing subset of variables that explained bat activity. If any variable correlated with another by over |0.7|, then a condition was placed on the dredge function to test models with only one of the correlated variables. Models within two AICc units of each other were considered equivalent, and the most parsimonious model with no obvious pattern in the residuals was considered the 'best' model. The residuals of the best models were tested again for spatial autocorrelation at the previously created scales using the moran.test() function. R² values – the coefficient of determination based on the likelihood ratio test – was calculated using the 'r.squaredLR' function from the MuMIn package (Bartoń 2020). In addition to creating models for each sonotype individually, models were also created for combined bat activity that used data from all sonotypes.

Results

A total of 13,263 calls belonging to seven sonotypes were isolated, identified, and analysed from 18 nights of recordings. These were divided into seven FM-QCF sonotypes, calling at 20kHz, 28kHz, 31kHz, 34kHz, 38kHz, 47kHz, and 65kHz, respectively (Table I). Henceforth, these sonotypes will be referred to using 'S' followed by their identifying frequency (e.g. S20). An additional FM-QCF sonotype calling at 18kHz was identified, but separating calls from insect noise proved challenging and the large number of false positives led to it being dropped from further analysis. Sonotype S20 did not reach the modelling stage because spatial autocorrelation was detected at a 10km scale during Part 1 of the statistical analysis. Grouping data points by a larger scale was deemed redundant and the sonotype was dropped. S65 was also dropped due to insufficient data for statistical analysis.

Table I *Number and percentage of total passes recorded of each bat sonotype. Bat activity data were extracted from 481 hours of recordings collected using Audiomoth 1.0.0 full spectrum recorders over 18 nights between 9 May and 8 June, 2019, from rice fields in the Nagaon district of Assam. S.A. scale indicates the smallest scale tested at which spatial autocorrelation was not significant.*

	Sonotype	Number of passes	Percentage of total (%)	S.A. scale
1	S38	4214	31.8	1km
2	S35	2709	20.4	5km
3	S32	1676	12.6	500m
4	S28	1630	12.3	1km
5	S20	1453	10.9	N.A
6	S47	1329	10	400m
7	S65	252	1.9	NA

Overall, variables indicative of the presence of trees were most prominent and significant in the final models (Fig. 2). Edge variables were present in the final models of S28 and S32. Forest variables were present in the final models of S28, S35, S38. SDHI was only found in the best model of one sonotype – S47. Urban landcover was present in the best model of two sonotypes, S28 and S38 (Fig. 2a, 2d). Sampling effort contributed to the best model of all sonotypes. Water, which had only been included in the global model as a distance variable, did not feature in the best model of any sonotype. Similarly rice, which had only been included in the global model as an area variable, also did not feature in the best model of any sonotype. There was also similarity in the type of variable of each landcover type that made it into the best model. Edge was only present in the form of distance to edge. Forest was present in the form of distance to forest and forest area within 1km. Urban was only present as area of urban landcover within 1km (Fig. 2). Full details of model results of individual sonotypes can be found in online resource 1 (Table SI).

In creating a model for overall bat activity, spatial autocorrelation was detected at all relevant scales. Despite this, an exploratory set of models were built by grouping points at the 400m, 1km and 5km scales. In addition to sampling effort, distance to forest and area of rice within 2km were the most important variables in the final models, with one model having area of edge within 1km as a predictor (online resource Table SII). The similarity of the models, despite having points grouped at different spatial scales, would indicate a relatively low effect of spatial autocorrelation and suggest that these variables do influence bat activity in general.

In considering individual effects, Fig. 3 shows the relationship between bat activity and individual variables present in the final models of all sonotypes. Since the models we built were mixed models, they included random effects that cannot be represented in scatter plots. Nonetheless, these plots are useful for observing patterns in the raw data. Distance to edge and forest, area of urban land, and moonlight intensity, seen in Fig. 3a, 3c, 3e, 3f, and 3g, represent variables that were statistically significant in the best models of sonotypes S28, S35 and S38. Despite not accounting for the random effect, all of them show a clear negative correlation with bat activity, which is in line with the model estimates and with

what other similar studies would predict. Figure 3b and 3d represent forest area within 1km (S28) and distance to edge (S32). These are neither statistically significant in the final models (Fig. 2), nor do they show an obvious pattern in scatter plots (Fig. 3b and 3d). On the other hand Fig. 3h and 3i, which represent urban land and SDHI within 1km for sonotypes S38 and S47, respectively, show a clear pattern in the scatter plots, despite being not significant in the final models of these sonotypes. This pattern is also what one would expect based on other similar studies, showing bat activity decreases with an increase in urban land, but increases with an increase in landscape heterogeneity.

Discussion

This study examined bat activity levels in rice fields, with the aim of exploring why rice fields set in different landscapes see different levels of insectivorous bat activity. Our results showed that key landscape features, namely forest and edge cover, urban land, moonlight intensity and landscape heterogeneity influenced the activity of five sonotypes of insectivorous bats.

In warm and dry environments, bats lose water rapidly (Webb et al. 1995) and it must be replenished through their food and by drinking. While many species have evolved mechanisms to limit water loss (Reher and Dausmann 2021), the presence of water bodies still exert considerable influence on where bats choose to fly, particularly in arid environments (Razgour et al. 2010). Past studies have found distance to water to be a key factor in driving selection of roost sites and foraging grounds (Adams and Thibault 2006; Adams and Hayes 2008; Rainho and Palmeirim 2011). However, water bodies in these studies tend to be few and far apart, increasing their importance to foraging bats. Despite our study being conducted in the summer, when temperatures regularly exceeded 30°C, having been conducted in rice fields, our sites were all within 600m of a water body (defined here as areas of water of at least 1000sq meters, equivalent to a 50m by 20m plot), with an average distance of 204m. This distance being well within the foraging ranges of insectivorous bats, water was not found to be an influencing factor in the best model of any sonotype, suggesting that for the analysed species, the range at which water becomes a limiting factor is greater than bats in our landscapes were presented with.

Urban landscapes are not entirely uninhabitable, and many bat species have adapted to them. The use of urban land by bats is influenced by built infrastructure, light pollution, noise levels, tree cover, bat physiology, predation pressure, and prey availability (Moretto and Francis 2017; Moretto et al. 2019; Jung and Threlfall 2021). While light pollution in urban areas is harmful to insect populations on the large scale (Owens et al. 2020), the attraction provided by street lights can create local prey-dense zones (Firebaugh and Haynes 2019), which in turn can increase the activity of some bats (Rodríguez-Aguilar et al. 2017). Bat activity is higher when patches of forest, water, and/or agricultural landcover are nearby (Dixon 2012; Ancillotto et al. 2019), in part because of higher insect activity in such areas (Avila-Flores and Fenton 2005). Studies have found that the complementation of anthropogenic and natural landcover can result in high levels of bat activity, particularly of mobile generalist species (Johnson et al. 2008). More universally, canopy cover has been found to be a key determinant of bat activity in urban contexts (Bailey et al. 2019). Bats exhibit extremely species-specific responses to landscapes and while some

studies have found increased activity of bats in urban landscapes (Rodríguez-Aguilar et al. 2017), many studies have found even moderate urbanization to have negative impacts on bat activity (Ancillotto 2015; Jung and Threlfall 2016). While our sites were set in rice fields, urban landcover was present around the sites in two forms: dense urban landscapes seen in Nagaon city and scattered nodes in villages. One or both of these negatively affected the activity of S28 and S38. For the other sonotypes, it is possible that the farmland and associated buildings, trees, and water bodies satisfied the requirements of most bats at the local scale, thereby overriding any negative (or positive) effects of the city.

Forests and forest boundaries, including linear features such as rows of trees, are important habitats for bats (Heim et al. 2015). However, separating the often concurrent incentives for the use of such habitats, including as roosting sites, for safety against predators (Heim et al. 2018) and the wind (Verboom and Huitema 1997), landmarks for navigation, and improved foraging (Jantzen and Fenton 2013), can be a challenge. Some of these benefits change with time. For example, brighter nights allow predators to see better (Prugh and Golden 2014), increasing the importance of shelter. Similarly, prey abundance relative to the surrounding landscape varies with season, particularly in agricultural landscapes. Conversely, the provision of trees as roosting sites remains more consistent over time.

Prey availability is a strong driver of bat activity and while it is difficult to compare the activity of different bats in different settings, studies have found that insectivorous bats do, in general, consider in-season rice fields to be prey-rich habitat (Sedlock et al. 2019; Toffoli and Rughetti 2020). Activity is increased by the presence of forest patches nearby (Heim et al. 2015; Bailey et al. 2019). Some studies have shown insectivorous bats to preferentially hunt over rice fields compared to forested areas (Puig-Montserrat et al. 2015; Kemp et al. 2019; Katunzi et al. 2021). Other studies report that while rice fields were attractive foraging grounds, nearby natural wetlands saw higher levels of foraging activity (Toffoli and Rughetti 2017).

While the edge variables calculated and tested for in this study included area of forest edge (within various buffers from the focal site), only distance to the nearest edge was retained in the best models of S28 and S32. The activity of sonotypes S35 and S38 was influenced by the distance to the nearest forest patch while S28 was influenced by the area of forest within 1km. Given that our landscapes were surrounded by forested area, rather than natural wetlands, we hypothesize that our rice fields were more attractive foraging sites than the surrounding forests or forest edges and therefore that the primary attraction of forests and forest edges was not prey availability but safety or the presence of roost sites. This is augmented by the fact that the bamboo houses and sheds in villages were known to be used as roost sites (IB, rigorous personal observation). These structures, being smaller than concrete buildings, more enclosed by trees, and bearing thatched roofs, were usually classified as 'edge' rather than 'urban' landcover. This adds to the argument that 'edges', as classified in this study, also represented roost sites to bats in the study area.

Area of rice was not present in the best models of any sonotype. The most likely reason being that since our sites were all in rice fields, set in rice-dominated landscapes, prey availability was high enough that

larger areas did not improve foraging success through reduced competition or increased prey availability.

Rice-dominated landscapes present a harsh matrix interspersed with patches of forest-urban-edge combinations that provide foraging grounds, roost sites, and relative safety. Harsher (more contrasting) matrices evoke stronger reactions to fragmented landscapes (Rodríguez-San Pedro and Simonetti 2015; Farneda et al. 2020) and unbroken rice fields provide little by way of shelter or roost sites. Greater landscape heterogeneity increases the proximity of different landcover types. This can result in larger bat populations and higher bat activity because bats that roost and forage in different landscapes now have easy access to both, reducing potentially commuting costs (Ethier and Fahrig 2011). An increase in landscape heterogeneity also correlates with availability of edges between natural and agricultural landcover. These interfaces are important for edge-space foragers that avoid open spaces either because they are more vulnerable to predators in open spaces, or because they have a higher foraging success at edges (Lentini et al. 2012; Frey-Ehrenbold et al. 2013). Greater heterogeneity also increases insect populations by providing spaces for them to breed and survive fallow seasons (Sigsgaard 2000; Fahrig et al. 2015; Bertrand et al. 2016; Chaperon et al. 2022). Sonotype S47 was influenced by landscape heterogeneity, most strongly at the scale of 1km (Fig. 2), supporting other studies that demonstrate the positive effect of landscape heterogeneity on bat activity (Frey-Ehrenbold et al. 2013; Monck-Whipp et al. 2018; Rodríguez-San Pedro et al. 2019).

Agricultural industries globally face an enormous challenge to reduce their reliance on environmentally unsustainable practices, such as the use of chemical pesticides, for both environmental and financial reasons. Pests are predicted to cause increasing losses to many major crops (Deutsch et al. 2018) and chemical methods of control, far from eliminating pests, have often prompted the emergence of more resistant strains (Normile 2013). The effective use of natural enemies as a sustainable alternative is only practised in pockets around the world (Lou et al. 2013; Puig-Montserrat et al. 2015), but holds great potential to alleviate the dual burdens of declining agricultural and ecological health. Realizing this potential requires both an understanding of the ecological relationships that underpin these ecosystem services and the ecology of the service providers to make agricultural landscapes more habitable to them.

Studies of bats in agricultural landscapes have shown the need for connectivity, heterogeneity, and the presence of natural landcover (Downs and Racey 2006; Frey-Ehrenbold et al. 2013; Finch et al. 2020). Few have considered the rice landscape, and none in India. This study demonstrated that in rice landscapes of Assam, while proximity to urban land decreased bat activity, the presence of forest patches and edges, and higher levels of landscape heterogeneity promoted bat activity, and likely by extension also increased the control of insect pests.

Declarations

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Competing interests

The authors have no relevant financial or non-financial interests to declare.

Author contribution

This manuscript is primarily the work of Iqbal Singh Bhalla, who contributed to the study conception and design, data collection, analysis and writing of the manuscript. Orly Razgour's contribution was in the form of advice on bat ecology and behaviour, as well as comments on the drafts of the manuscript. François Regal's contribution was in the form of statistical guidance, comments on the drafts of the manuscript, and small contributions to the code used for the statistical analysis. Robert Whittaker's contribution was in the form of guidance on project structure, fieldwork practicalities, comments on the drafts of the manuscript, and general scientific advice. All authors have read and approved the final manuscript.

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

References

1. Adams RA, Hayes MA (2008) Water availability and successful lactation by bats as related to climate change in arid regions of western North America. *J Anim Ecol* 77:1115–1121. <https://doi.org/10.1111/j.1365-2656.2008.01447.x>
2. Adams RA, Thibault KM (2006) Temporal resource partitioning by bats at water holes. *J Zool* 270:466–472. <https://doi.org/10.1111/j.1469-7998.2006.00152.x>
3. Ancillotto L (2015) Sensitivity of bats to urbanization: a review. *Mamm Biol* 80:205–212. <https://doi.org/10.1016/J.MAMBIO.2014.10.003>

4. Ancillotto L, Bosso L, Salinas-Ramos VB, Russo D (2019) The importance of ponds for the conservation of bats in urban landscapes. *Landsc Urban Plan* 190:103607. <https://doi.org/10.1016/j.landurbplan.2019.103607>
5. Avila-Flores R, Fenton MB (2005) Use of spatial features by foraging insectivorous bats in a large urban landscape. *J Mammal* 86:1193–1204. <https://doi.org/10.1644/04-MAMM-A-085R1.1>
6. Bailey AM, Ober HK, Reichert BE, McCleery RA (2019) Canopy cover shapes bat diversity across an urban and agricultural landscape mosaic. *Environ Conserv* 46:193–200. DOI: 10.1017/S0376892919000109
7. Bartoń K (2020) MuMIn: Multi-Model Inference
8. Bertrand C, Burel F, Baudry J (2016) Spatial and temporal heterogeneity of the crop mosaic influences carabid beetles in agricultural landscapes. *Landsc Ecol* 31:451–466. <https://doi.org/10.1007/s10980-015-0259-4>
9. Bivand RS, Wong DWS (2018) Comparing implementations of global and local indicators of spatial association. *Test* 27:716–748. <https://doi.org/10.1007/s11749-018-0599-x>
10. Blažek J, Konečný A, Bartonička T (2021) Bat aggregational response to pest caterpillar emergence. *Sci Rep* 11:13634. <https://doi.org/10.1038/s41598-021-93104-z>
11. Brooks ME, Kristensen K, van Benthem KJ, et al (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J* 9:378–400. <https://doi.org/10.3929/ethz-b-000240890>
12. Cassano CR, Silva RM, Mariano-Neto E, et al (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. <https://doi.org/10.1016/j.agee.2016.08.013>
13. Chaperon PN, Rodríguez-San Pedro A, Beltrán CA, et al (2022) Effects of adjacent habitat on nocturnal flying insects in vineyards and implications for bat foraging. *Agric Ecosyst Environ* 326:107780. <https://doi.org/10.1016/j.agee.2021.107780>
14. Cohen Y, Bar-David S, Nielsen M, et al (2020) An appetite for pests: Synanthropic insectivorous bats exploit cotton pest irruptions and consume various deleterious arthropods. *Mol Ecol* 29:1185–1198. <https://doi.org/10.1111/mec.15393>
15. Denzinger A, Kalko EK V, Tschapka M, et al (2016) Guild Structure and Niche Differentiation in Echolocating Bats. In: Fenton MB, Grinnell AD, Popper AN, Fay RR (eds) *Bat Bioacoustics*. Springer New York, New York, NY, pp 141–166
16. Deutsch CA, Tewksbury JJ, Tigchelaar M, et al (2018) Increase in crop losses to insect pests in a warming climate. *Science* (80-) 361:916–919. <https://doi.org/10.1126/science.aat3466>
17. Directorate of Economics and Statistics (2019) *Agricultural statistics at a glance 2019*. Ministry of Agriculture, Government of India
18. Dixon MD (2012) Relationship between land cover and insectivorous bat activity in an urban landscape. *Urban Ecosyst* 15:683–695. <https://doi.org/10.1007/s11252-011-0219-y>

19. Downs NC, Racey PA (2006) The use by bats of habitat features in mixed farmland in Scotland. *Acta Chiropterologica* 8:169–185. [https://doi.org/10.3161/1733-5329\(2006\)8\[169:TUBBOH\]2.0.CO;2](https://doi.org/10.3161/1733-5329(2006)8[169:TUBBOH]2.0.CO;2)
20. Ethier K, Fahrig L (2011) Positive effects of forest fragmentation, independent of forest amount, on bat abundance in eastern Ontario, Canada. *Landsc Ecol* 26:865–876. <https://doi.org/10.1007/s10980-011-9614-2>
21. Fahrig L, Girard J, Duro D, et al (2015) Farmlands with smaller crop fields have higher within-field biodiversity. *Agric Ecosyst Environ* 200:219–234. <https://doi.org/10.1016/j.agee.2014.11.018>
22. Farneda FZ, Meyer CFJ, Grelle CE V (2020) Effects of land-use change on functional and taxonomic diversity of Neotropical bats. *Biotropica* 52:120–128. <https://doi.org/https://doi.org/10.1111/btp.12736>
23. Finch D, Schofield H, Mathews F (2020) Habitat associations of bats in an agricultural landscape: Linear features versus open habitats. *Animals* 10:1856. <https://doi.org/10.3390/ani10101856>
24. Firebaugh A, Haynes KJ (2019) Light pollution may create demographic traps for nocturnal insects. *Basic Appl Ecol* 34:118–125. <https://doi.org/10.1016/j.baae.2018.07.005>
25. Fischer J, Stott J, Law BS (2010) The disproportionate value of scattered trees. *Biol Conserv* 143:1564–1567. <https://doi.org/10.1016/j.biocon.2010.03.030>
26. Frey-Ehrenbold A, Bontadina F, Arlettaz R, Obrist MK (2013) Landscape connectivity, habitat structure and activity of bat guilds in farmland-dominated matrices. *J Appl Ecol* 50:252–261. <https://doi.org/10.1111/1365-2664.12034>
27. Gorelick N, Hancher M, Dixon M, et al (2017) Google Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote Sens Environ* 202:18–27. <https://doi.org/10.1016/j.rse.2017.06.031>
28. Harms K, Omondi E, Mukherjee A (2020) Investigating bat activity in various agricultural landscapes in northeastern United States. *Sustainability* 12:1959. <https://doi.org/10.3390/su12051959>
29. Heim O, Lenski J, Schulze J, et al (2018) The relevance of vegetation structures and small water bodies for bats foraging above farmland. *Basic Appl Ecol* 27:9–19. <https://doi.org/10.1016/j.baae.2017.12.001>
30. Heim O, Schröder A, Eccard J, et al (2016) Seasonal activity patterns of European bats above intensively used farmland. *Agric Ecosyst Environ* 233:130–139. <https://doi.org/10.1016/j.agee.2016.09.002>
31. Heim O, Treitler JT, Tschapka M, et al (2015) The importance of landscape elements for bat activity and species richness in agricultural areas. *PLoS One* 10:e0134443–e0134443. <https://doi.org/10.1371/journal.pone.0134443>
32. Hill AP, Prince P, Piña Covarrubias E, et al (2018) AudioMoth: Evaluation of a smart open acoustic device for monitoring biodiversity and the environment. *Methods Ecol Evol* 9:1199–1211. <https://doi.org/10.1111/2041-210X.12955>
33. Hinz R, Sulser TB, Huefner R, et al (2020) Agricultural development and land use change in India: A scenario analysis of trade-offs Between UN sustainable development goals (SDGs). *Earth's Futur* 8:e2019EF001287. <https://doi.org/10.1029/2019EF001287>

34. Jantzen MK, Fenton MB (2013) The depth of edge influence among insectivorous bats at forest–field interfaces. *Can J Zool* 91:287–292. <https://doi.org/10.1139/cjz-2012-0282>
35. Johnson J, Gates J, Ford W (2008) Distribution and activity of bats at local and landscape scales within a rural–urban gradient. *Urban Ecosyst* 11:227–242. <https://doi.org/10.1007/s11252-008-0055-x>
36. Jones G, Jacobs DS, Kunz TH, et al (2009) Carpe noctem: the importance of bats as bioindicators. *Endanger Species Res* 8:93–115. <https://doi.org/10.3354/esr00182>
37. Jones PL, Page RA, Ratcliffe JM (2016) To Scream or to Listen? Prey Detection and Discrimination in Animal-Eating Bats BT. In: Fenton MB, Grinnell AD, Popper AN, Fay RR (eds) *Bat Bioacoustics*. Springer New York, New York, NY, pp 93–116
38. Jung K, Threlfall CG (2016) Urbanisation and its Effects on Bats—a Global Meta-Analysis. In: *Bats in the Anthropocene: Conservation of Bats in a Changing World*. Springer, Cham, pp 13–33
39. Jung K, Threlfall CG (2021) Trait-dependent tolerance of bats to urbanization: a global meta-analysis. *Proc R Soc B Biol Sci* 285:20181222. <https://doi.org/10.1098/rspb.2018.1222>
40. Kahnonitch I, Lubin Y, Korine C (2018) Insectivorous bats in semi-arid agroecosystems – effects on foraging activity and implications for insect pest control. *Agric Ecosyst Environ* 261:80–92. <https://doi.org/10.1016/j.agee.2017.11.003>
41. Kalda O, Kalda R, Liira J (2015) Multi-scale ecology of insectivorous bats in agricultural landscapes. *Agric Ecosyst Environ* 199:105–113. <https://doi.org/10.1016/j.agee.2014.08.028>
42. Katunzi T, Soisook P, Webala PW, et al (2021) Bat activity and species richness in different land-use types in and around Chome Nature Forest Reserve, Tanzania. *Afr J Ecol* 59:117–131. <https://doi.org/10.1111/aje.12783>
43. Kelly RM, Kitzes J, Wilson H, Merenlender A (2016) Habitat diversity promotes bat activity in a vineyard landscape. *Agric Ecosyst Environ* 223:175–181. <https://doi.org/10.1016/j.agee.2016.03.010>
44. Kelm DH, Lenski J, Kelm V, et al (2014) Seasonal bat activity in relation to distance to hedgerows in an agricultural landscape in Central Europe and implications for wind energy development. *Acta Chiropterologica* 16:65–73. <https://doi.org/10.3161/150811014X683273>
45. Kemp J, López-Baucells A, Rocha R, et al (2019) Bats as potential suppressors of multiple agricultural pests: A case study from Madagascar. *Agric Ecosyst Environ* 269:88–96. <https://doi.org/10.1016/j.agee.2018.09.027>
46. Kunz TH, Braun de Torrez E, Bauer D, et al (2011) Ecosystem services provided by bats. *Ann N Y Acad Sci* 1223:1–38. <https://doi.org/10.1111/j.1749-6632.2011.06004.x>
47. Kusuminda T, Mannakkara A, Gamage R, et al (2021) Roosting ecology of insectivorous bats in a tropical agricultural landscape. *Mammalia*. <https://doi.org/doi:10.1515/mammalia-2021-0056>
48. Lentini PE, Gibbons P, Fischer J, et al (2012) Bats in a farming landscape benefit from linear remnants and unimproved pastures. *PLoS One* 7:e48201. <https://doi.org/10.1371/journal.pone.0048201>

49. Lindén A, Mäntyniemi S (2011) Using negative binomial distribution to model overdispersion in ecological count data. *Ecology* 92:1414–1421. <https://doi.org/10.2307/23035094>
50. Lou Y-G, Zhang G-R, Zhang W-Q, et al (2013) Biological control of rice insect pests in China. *Biol Control* 67:8–20. <https://doi.org/10.1016/J.BIOCONTROL.2013.06.011>
51. Maine JJ, Boyles JG (2015) Bats initiate vital agroecological interactions in corn. *Proc Natl Acad Sci USA* 112:12438–12443. <https://doi.org/10.1073/pnas.1505413112>
52. Mas M, Flaquer C, Rebelo H, López-Baucells A (2021) Bats and wetlands: Synthesising gaps in current knowledge and future opportunities for conservation. *Mamm Rev* 51:369–384. <https://doi.org/10.1111/mam.12243>
53. Maslo B, Mau RL, Kerwin K, et al (2022) Bats provide a critical ecosystem service by consuming a large diversity of agricultural pest insects. *Agric Ecosyst Environ* 324:107722. <https://doi.org/https://doi.org/10.1016/j.agee.2021.107722>
54. Mayer RR, Scribner DA (2002) Extending the normalized difference vegetation index (NDVI) to short-wave infrared radiation (SWIR) (1- to 2.5- μ m). In: *Proc.SPIE*
55. McCracken GF, Westbrook JK, Brown VA, et al (2012) Bats track and exploit changes in insect pest populations. *PLoS One* 7:e43839–e43839. <https://doi.org/10.1371/journal.pone.0043839>
56. 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. <https://doi.org/10.1016/j.ecoleng.2014.11.050>
57. Monck-Whipp L, Martin AE, Francis CM, Fahrig L (2018) Farmland heterogeneity benefits bats in agricultural landscapes. *Agric Ecosyst Environ* 253:131–139. <https://doi.org/10.1016/j.agee.2017.11.001>
58. Moretto L, Fahrig L, Smith AC, Francis CM (2019) A small-scale response of urban bat activity to tree cover. *Urban Ecosyst* 22:795–805. <https://doi.org/10.1007/s11252-019-00846-w>
59. Moretto L, Francis CM (2017) What factors limit bat abundance and diversity in temperate, North American urban environments? *J Urban Ecol* 3:1. <https://doi.org/10.1093/jue/jux016>
60. Mtsetfwa F, McCleery RA, Monadjem A (2018) Changes in bat community composition and activity patterns across a conservation-agriculture boundary. *African Zool* 53:99–106. <https://doi.org/10.1080/15627020.2018.1531726>
61. Normile D (2013) Vietnam turns back a “tsunami of pesticides.” *Science* (80-) 341:737–738. <https://doi.org/10.1126/science.341.6147.737>
62. Owens ACS, Cochard P, Durrant J, et al (2020) Light pollution is a driver of insect declines. *Biol Conserv* 241:108259. <https://doi.org/10.1016/j.biocon.2019.108259>
63. Park KJ (2015) Mitigating the impacts of agriculture on biodiversity: bats and their potential role as bioindicators. *Mamm Biol* 80:191–204. <https://doi.org/10.1016/J.MAMBIO.2014.10.004>
64. Prugh LR, Golden CD (2014) Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. *J Anim Ecol* 83:504–514.

<https://doi.org/10.1111/1365-2656.12148>

65. Puig-Montserrat X, Torre I, López-Baucells A, et al (2015) Pest control service provided by bats in Mediterranean rice paddies: linking agroecosystems structure to ecological functions. *Mamm Biol* 80:237–245. <https://doi.org/10.1016/j.mambio.2015.03.008>
66. R Core Team (2020) R: A language and environment for statistical computing
67. Rainho A, Palmeirim JM (2011) The importance of distance to resources in the spatial modelling of bat foraging habitat. *PLoS One* 6:e19227. <https://doi.org/10.1371/journal.pone.0019227>
68. Razgour O, Korine C, Saltz D (2010) Pond characteristics as determinants of species diversity and community composition in desert bats. *Anim Conserv* 13:505–513. <https://doi.org/10.1111/j.1469-1795.2010.00371.x>
69. Razgour O, Persey M, Shamir U, Korine C (2018) The role of climate, water and biotic interactions in shaping biodiversity patterns in arid environments across spatial scales. *Divers Distrib* 24:1440–1452. <https://doi.org/10.1111/ddi.12773>
70. Reher S, Dausmann KH (2021) Tropical bats counter heat by combining torpor with adaptive hyperthermia. *Proc R Soc B Biol Sci* 288:20202059. <https://doi.org/10.1098/rspb.2020.2059>
71. Robinson RA, Sutherland WJ (2002) Post-war changes in arable farming and biodiversity in Great Britain. *J Appl Ecol* 39:157–176
72. Rodríguez-Aguilar G, Orozco-Lugo CL, Vleut I, Vazquez L-B (2017) Influence of urbanization on the occurrence and activity of aerial insectivorous bats. *Urban Ecosyst* 20:477–488. <https://doi.org/10.1007/s11252-016-0608-3>
73. Rodríguez-San Pedro A, Rodríguez-Herbach C, Allendes JL, et al (2019) Responses of aerial insectivorous bats to landscape composition and heterogeneity in organic vineyards. *Agric Ecosyst Environ* 277:74–82. <https://doi.org/10.1016/j.agee.2019.03.009>
74. Rodríguez-San Pedro A, Simonetti JA (2015) The relative influence of forest loss and fragmentation on insectivorous bats: does the type of matrix matter? *Landsc Ecol* 30:1561–1572. <https://doi.org/10.1007/s10980-015-0213-5>
75. Rossum V, Jr G and D, L F (1995) Python reference manual. Centrum voor Wiskunde en Informatica Amsterdam
76. Russ JM, Briffa M, Montgomery WI (2003) Seasonal patterns in activity and habitat use by bats (*Pipistrellus* spp. and *Nyctalus leisleri*) in Northern Ireland, determined using a driven transect. *J Zool* 259:289–299. <https://doi.org/10.1017/S0952836902003254>
77. Russo D, Salinas-Ramos VB, Cistrone L, et al (2021) Do we need to use bats as bioindicators? *Biology (Basel)* 10:693. <https://doi.org/10.3390/biology10080693>
78. Saikiam K, Saikia S, Medhi B (2020) Changing trends of landuse landcover in Nagaon district and its impact on agricultural and environmental sustainability. *Eur J Mol Clin Med* 7:1388–1410
79. Schielzeth H (2010) Simple means to improve the interpretability of regression coefficients. *Methods Ecol Evol* 1:103–113. <https://doi.org/10.1111/j.2041-210X.2010.00012.x>

80. Sedlock J, Stuart A, Horgan F, et al (2019) Local-scale bat guild activity differs with rice growth stage at ground level in the Philippines. *Diversity* 11:148. <https://doi.org/10.3390/d11090148>
81. Shannon CE (1948) A mathematical theory of communication. *Bell Syst Tech J* 27:379–423. <https://doi.org/10.1002/j.1538-7305.1948.tb01338.x>
82. Sigsgaard L (2000) Early season natural biological control of insect pests in rice by spiders-and some factors in the management of the cropping system that may affect this control. *Eur Arachnol* 2000:57–64
83. Simmons NB, Cirranello AL (2021) Bat Species of the World: A taxonomic and geographic database. <https://batnames.org/>. Accessed 16 Dec 2021
84. The MathWorks Inc. (2019) MATLAB and Statistics Toolbox Release 2019b. Natick, Massachusetts
85. Toffoli R, Rughetti M (2020) Effect of water management on bat activity in rice paddies. *Paddy Water Environ* 18:687–695. <https://doi.org/10.1007/s10333-020-00811-w>
86. Toffoli R, Rughetti M (2017) Bat activity in rice paddies: Organic and conventional farms compared to unmanaged habitat. *Agric Ecosyst Environ* 249:123–129. <https://doi.org/10.1016/j.agee.2017.08.022>
87. Tournayre O, Leuchtman M, Galan M, et al (2021) eDNA metabarcoding reveals a core and secondary diets of the greater horseshoe bat with strong spatio-temporal plasticity. *Environ DNA* 3:277–296. <https://doi.org/10.1002/edn3.167>
88. Verboom B, Huitema H (1997) The importance of linear landscape elements for the pipistrelle *Pipistrellus pipistrellus* and the serotine bat *Eptesicus serotinus*. *Landsc Ecol* 12:117–125. <https://doi.org/10.1007/BF02698211>
89. Wang J, Chen KZ, Gupta S Das, 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. <https://doi.org/10.1108/CAER-01-2015-0005>
90. Webb PI, Speakman JR, Racey PA (1995) Evaporative water loss in two sympatric species of vespertilionid bat, *Plecotus auritus* and *Myotis daubentoni*: relation to foraging mode and implications for roost site selection. *J Zool* 235:269–278. <https://doi.org/10.1111/j.1469-7998.1995.tb05143.x>
91. Wordley CFR, Foui EK, Mudappa D, et al (2014) Acoustic identification of bats in the Southern Western Ghats, India. *Acta Chiropterologica* 16:213–222. <https://doi.org/10.3161/150811014X683408>
92. Xue J, Su B (2017) Significant remote sensing vegetation indices: A review of developments and applications. *J Sensors* 2017:1353691. <https://doi.org/10.1155/2017/1353691>

Figures

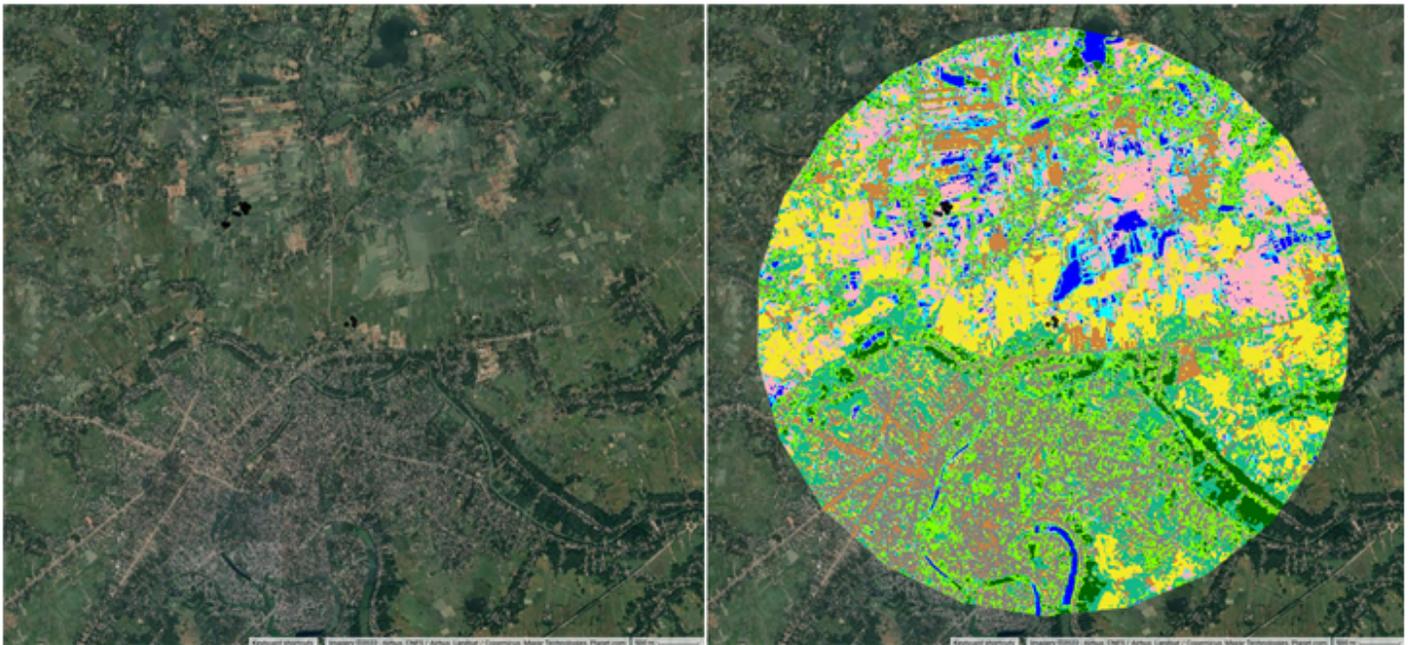


Fig. 1 An unclassified (left) and classified (right) map of the landscape around one set of sites in Nagaon, Assam. The landscape was classified within a radius of 4km around the centroid of one cluster of sites using a random forest supervised classifier in Google Earth Engine. The centroids are located at 92.61813539786188E, 26.353871760484573N. The landscape was classified into nine landcover types: Dry rice ■, wet rice ■, bare ground ■, water ■, bank ■, edge ■, field ■, forest (or algae) ■, and urban land ■. Black dots represent sampling sites. Maps for remaining sites can be found in online resource 1 (Fig. SI - SIII). Image source: Contains modified Copernicus Sentinel data (2022); Arbus, CNES/Airbus, Landsat/Copernicus, Maxar Technologies, Planet.com

Figure 1

See image above for figure legend.

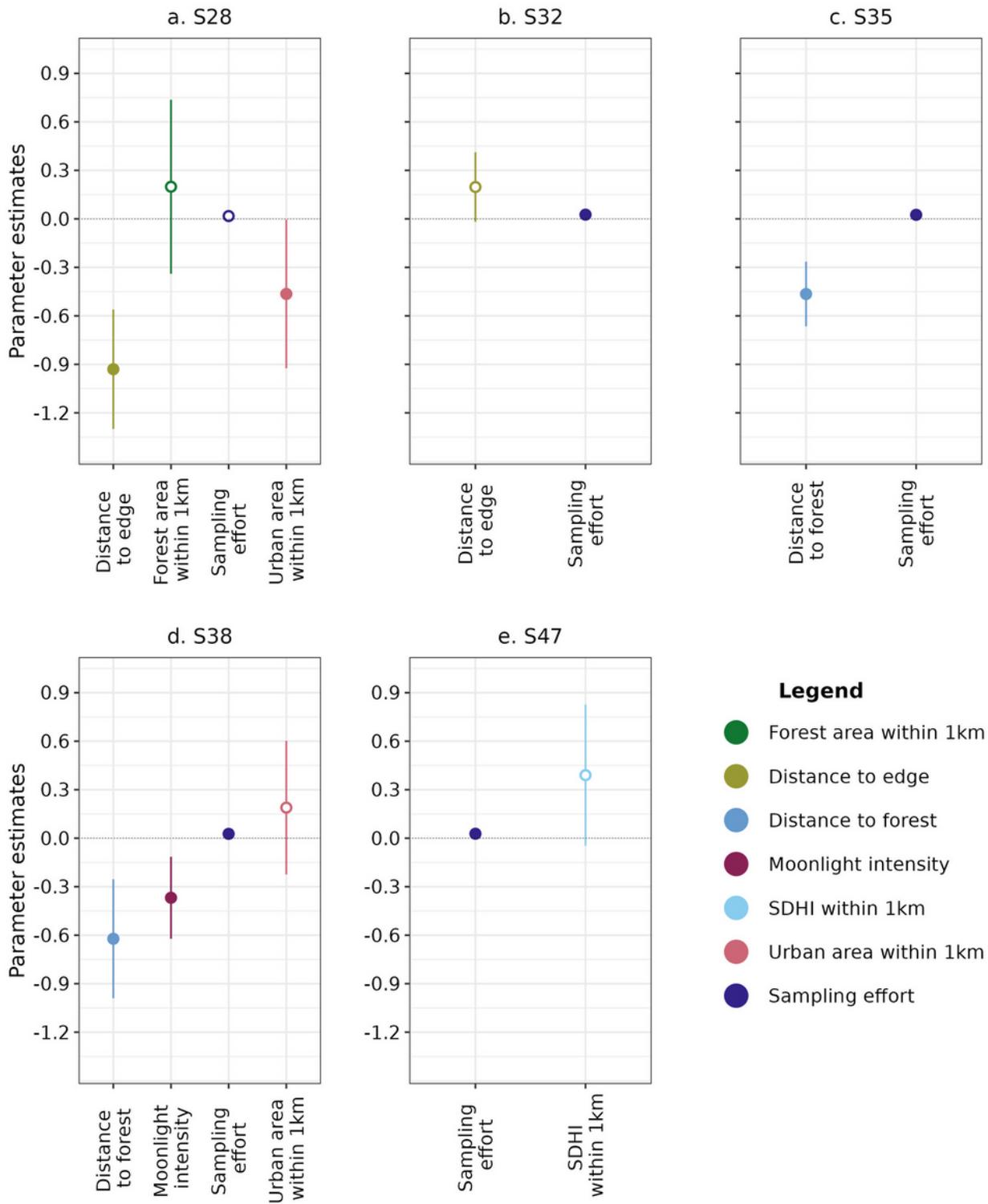


Figure 2

Effect of landscape variables on each sonotype. Generalized linear mixed models of five bat sonotypes built on data collected over 18 nights of recording between 9 May and 8 June 2019. Recordings were made using Audiomoth passive acoustic recorders in rice fields across the district of Nagaon, Assam. Variables were chosen from a global model based on their contribution to significant decrease in AICc values. Dots represents the estimate, solid dots indicate a p-value < 0.05 and hollow dots indicate a p-

value > 0.05. Error bars represent the 95% confidence interval. The confidence interval around 'Sampling effort' is not zero, but is too small for wings to extend beyond the perimeter of the solid dot

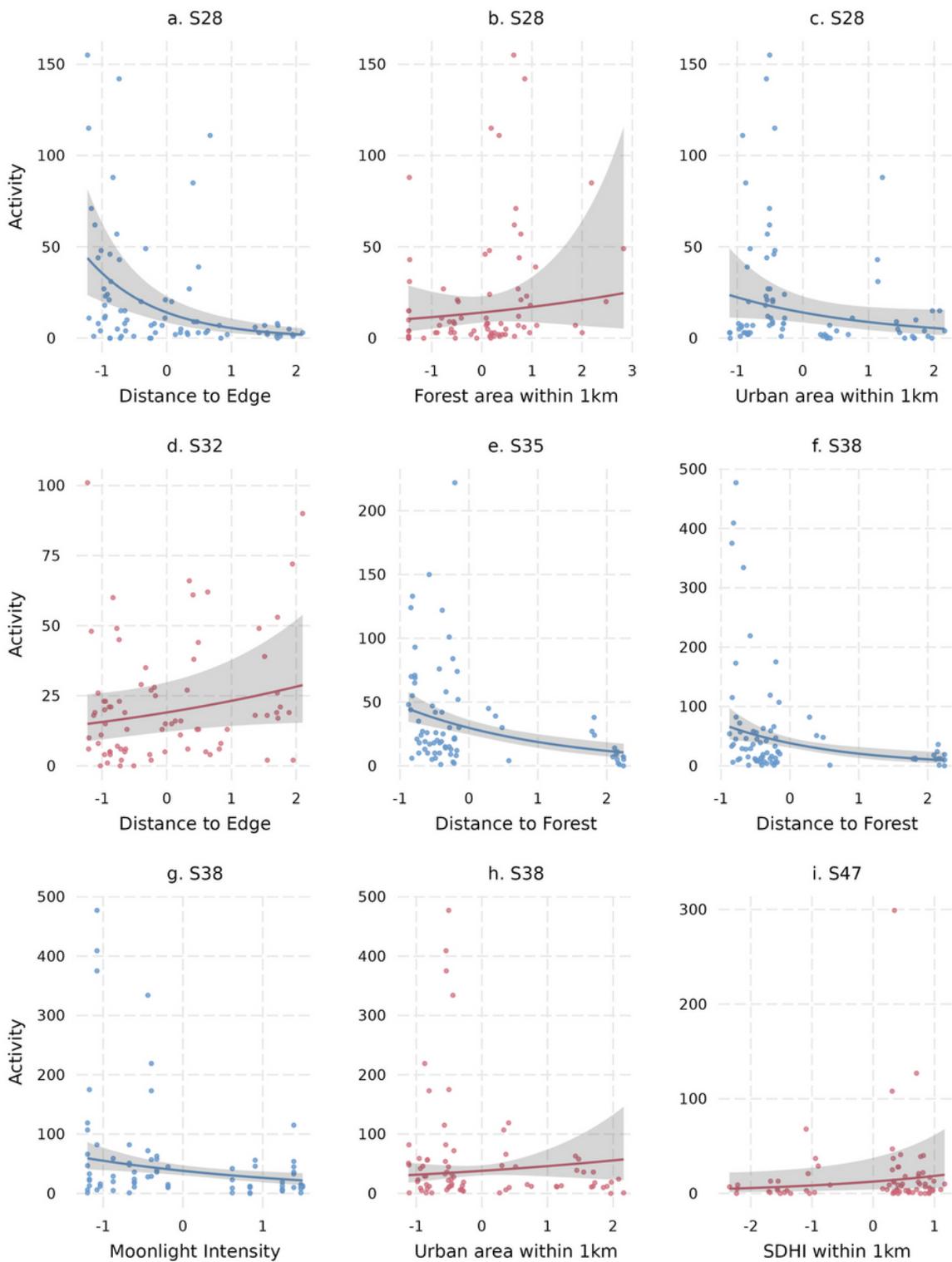


Figure 3

Scatter plots of bat activity over all standardized variables present in the final models of each sonotype (except sampling effort). Blue dots indicate a p-value < 0.05, salmon dots indicate a p-value > 0.05. These

points are raw data, and do not accurately represent the effect of variables in the final models. This is because mixed effect models used in this study included random effects that couldn't be accounted for in the above scatter plots. Lines and 95% confidence intervals represent the predicted values extracted from the relevant best models

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [BhallaetalESM1.doc](#)