Far from home: bat activity and diversity in row crop agriculture decreases with distance to potential roost habitat

Louis Hunninck[1], Kjirsten Coleman[1], Melissa Boman[1], and Joy O'Keefe[1]

[1]University of Illinois at Urbana-Champaign

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Abstract

As demand for food increases, agricultural production is poised to increase dramatically. Pesticides are commonly used to maintain high crop yield, though they have several drawbacks, including reduced efficacy over time and harmful effects to human and ecosystem health. Bats are highly effective predators of crop pests and have great potential to reduce crop damage resulting from insects. However, few studies have investigated how pest control by bats might change over large expanses of continuous row crop agriculture, which is common in the Midwest. Agricultural landscapes offer few roosting opportunities and could be difficult for bats to traverse, which might affect the degree of ecosystem services provided by bats. We hypothesized that with increasing distance into uninterrupted row crop agriculture 1) bat activity would decrease and 2) bat species richness would decrease, but that these effects would be buffered when insect pest abundance is high. We deployed 50 acoustic bat detectors over 10 transects in east-central Illinois from July to September 2021. In each transect, we placed detectors on crop field edges at increasing distance from a large riparian corridor assumed to be frequented by bats. Bat activity was high across the landscape but declined by 56% from the forest edge to 4000m into row crop agriculture, while bat diversity decreased by 34%. Pest abundance seemed to decrease overall bat activity but had no effect on bat diversity. These results indicate that bats, although able to have a large effect on crop pest reduction, might not be as efficient in suppressing crop pests in vast uninterrupted agricultural landscapes which offer scant roost availability. Our work will inform recommendations to landowners and private lands managers on ways to increase bat access to roosts and forest cover near agricultural areas, thereby enhancing the potential for bats to provide pest control services.

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Authors: Hunninck, Louis[1]; Coleman, Kjirsten[1]; Boman, Melissa[1,2]; O'Keefe, Joy[1]

Author affiliations:

[1] Department of Natural Resources and Environmental Sciences, University of Illinois Urbana-Champaign, Urbana, IL USA

[2] Minnesota Department of Natural Resources, Minnesota Biological Survey, Saint Paul, MN USA

Corresponding author:

Louis Hunninck, Ph.D.

University of Illinois Urbana-Champaign

Department of Natural Resources and Environmental Sciences

Urbana, IL 61801

+1 (217) 693-9290

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louishunninck@gmail.com

Highlights:

1. Bats are important for pest control in row-crop agriculture
2. Estimates of the economic value of bats generally assume homogenous activity
3. We measured bat activity and species diversity by distance to forested corridors
4. Activity and diversity declined significantly with distance into fields
5. Habitat heterogeneity is crucial to sustaining ecosystem services from bats

Abstract

As demand for food increases, agricultural production is poised to increase dramatically. Pesticides are commonly used to maintain high crop yield, though they have several drawbacks, including reduced efficacy over time and harmful effects to human and ecosystem health. Bats are highly effective predators of crop pests and have great potential to reduce crop damage resulting from insects. However, few studies have investigated how pest control by bats might change over large expanses of continuous row crop agriculture, which is common in the Midwest. Agricultural landscapes offer few roosting opportunities and could be difficult for bats to traverse, which might affect the degree of ecosystem services provided by bats. We hypothesized that with increasing distance into uninterrupted row crop agriculture 1) bat activity would decrease and 2) bat species richness would decrease, but that these effects would be buffered when insect pest abundance is high. We deployed 50 acoustic bat detectors over 10 transects in east-central Illinois from July to September 2021. In each transect, we placed detectors on crop field edges at increasing distance from a large riparian corridor assumed to be frequented by bats. Bat activity was high across the landscape but declined by 56% from the forest edge to 4000m into row crop agriculture, while bat diversity decreased by 34%. Pest abundance seemed to decrease overall bat activity but had no effect on bat diversity. These results indicate that bats, although able to have a large effect on crop pest reduction, might not be as efficient in suppressing crop pests in vast uninterrupted agricultural landscapes which offer scant roost availability. Our work will inform recommendations to landowners and private lands managers on ways to increase bat access to roosts and forest cover near agricultural areas, thereby enhancing the potential for bats to provide pest control services.

Keywords : Ecosystem services, Agricultural intensification, Pest suppression, Diversity, Forest management

Introduction

As the human population grows and the demand for food increases, there will be a greater need for more efficient agricultural land use (Godfray et al., 2010). Tilman et al. (2001) predicted that by 2050 one billion hectares of land would be converted to agriculture and anticipated a 2.4–2.7-fold increase in water eutrophication caused by the concomitant increase in fertilizer and pesticide use. Despite intensification via industrial monocropping, agricultural yields have not kept up with demand (Ray et al., 2013). This is in part due to an increase in crop pest abundance as a result of large-scale monocropping, which contributes to so-called yield gaps (Chaplin-Kramer et al., 2011). Harnessing the potential of natural predators to suppress crop pest populations is an efficient and cost-effective strategy to increase yields. Such a process of ecological intensification – increasing agricultural yield without also increasing anthropogenic inputs – would reduce our reliance on pesticides, which are less effective because many pests have developed resistance over time (Bommarco et al., 2013). Bats have been proposed as an important pest control species in agricultural landscapes, potentially worth 3 billion USD to the US agricultural industry alone (Boyles et al., 2011). In this study, we investigate how bat activity patterns change over agricultural landscapes in relation to distance from forested riparian corridors to better understand the spatial scope of crop pest control by bats.

Agricultural pests have pervasive impacts on various forms of agricultural production from animals to crops. Globally, an estimated 30% of crop loss is attributed to pests in both soybeans and corn, the two main crops

produced in the Midwest (Oerke, 2005). Protecting crops against animal pests remains difficult and costly, and relies heavily on synthetical chemicals (Oerke, 2005). Globally, the associated costs with controlling for these pests can surpass $10 billion yearly, with an additional $12 billion in external damages (Pimentel, 2009). These estimated costs could be inflated due to forecasted increases in agricultural pest abundance due to climate change (Diffenbaugh et al., 2008). Therefore, efforts to enhance natural pest control are imperative. Ecological intensification of agricultural landscapes reestablishes the ecosystem services derived from natural systems, thereby reducing costs of pest control while increasing crop yield (Bommarco et al., 2013). Using these biodiversity-based methods has been proven to sustainably increase crop yields (Maine and Boyles, 2015; Maslo et al., 2022; Tschumi et al., 2016).

All bats in the midwestern region of the USA are insectivores (Whitaker and Hamilton, 1998). These bats are voracious arthropod predators that can consume up to their body weight in arthropods over the course of a single night (Kunz et al., 1995). Bats may even exert a stronger top-down effect on insect abundance than do birds, as has been found in forest systems (Kalka et al., 2008). It is widely recognized that bats have significant impacts on crop pest species and therefore provide valuable ecosystem services (Boyles et al., 2011; Maslo et al., 2022; Whitaker, 1995). The diet of common species such as the big brown bat (*Eptesicus fuscus*) includes 160 known agricultural pest or disease vectors, including *Helicoverpa zea*, *Spodoptera frugiperda*, and *Chloridea virescens* (Hughes et al., 2021; Maslo et al., 2022). The effects of bats on pest control are multi-layered because by foraging on the adult stages of pests like moths, bats indirectly suppress egg production (McCracken et al., 2012). One study found that bats not only suppressed pest larval densities in corn, they furthermore contributed to the suppression of pest-associated mycotoxins and fungal growth (Maine and Boyles, 2015). These agricultural ecosystem services in the United States alone have been estimated to be worth between 3.7 and 53 billion dollars annually (Boyles et al, 2011). Ironically, bats are threatened by the very industry they help: agricultural intensification is considered a major contributor to pervasive bat declines in Europe and North America (Frick et al., 2020; Wickramasinghe et al., 2003). Bats are further threatened by rampant wind energy development (Davy et al., 2021; Friedenberg and Frick, 2021) and, in North America, white-nose syndrome (Frick et al., 2020; Hoyt et al., 2021). Urgent conservation action is needed to promote these species in agricultural landscapes if they are to continue their significant contribution to pest control.

Bats are not homogeneously distributed across the landscape. For example, bat activity increases with increasing landscape heterogeneity (Burgar et al., 2017; Chaplin-Kramer et al., 2011; Monck-Whipp et al., 2018). Woodland interfaces are important predictors of bat activity (Fill et al., 2022), and one study found that bat activity is 5 times higher in landscapes containing a double row of trees compared to standalone trees (Kalda et al., 2015). Bat species richness also varies with landscape structure. Due to species-specific characteristics, including wing aspect ratio and body size, some species prefer foraging in cluttered habitat (Aldridge and Rautenbach, 1987). Although bats are generalists, different species have specific diet preferences, and larger bats tend to consume larger prey such as agricultural pests (Hughes et al., 2021; Kunz et al., 2011). Because of their structural complexity, woodlands and wooded corridors offer habitat to bats with differing foraging behaviors and, therefore, often have higher bat diversity than uninterrupted row crop agricultural landscapes (Kalda et al., 2015). Indeed, bats prefer to forage along linear features in agricultural landscapes, such as natural vegetation remnants and farmland edges (Lentini et al., 2012). The sometimes surprisingly long distances between potential roost locations (i.e., large trees in forest patches) in the vast agricultural landscapes often found in the Midwest likely presents a formidable challenge to bats foraging over agricultural fields. Higher predation risk from raptors and owls in open landscapes could also decrease the likelihood of bats venturing out into agriculture (Lima and O'Keefe, 2013; Mikula et al., 2016; Murray and Kurta, 2004). To better understand how bats contribute to agricultural pest control, and how we can improve the efficacy, we require more nuanced information on bat activity in relation to landscape characteristics (Boyles et al., 2013).

We studied bat activity and diversity in central Illinois, USA in relation to expansive, uninterrupted agriculture. We hypothesized that both bat activity and bat diversity would decline with increasing distance from forested corridors, but that this effect would be buffered by insect pest abundance. With respect to

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overall bat activity, we hypothesized that activity would decline with increasing distance from large forested riparian corridors, which we assume to be favorable roosting and foraging areas. However, we suspected this effect would be buffered by pest insect species abundance, such that bats would be more active further away from riparian corridors when pest abundance is high than when pest abundance is low. Furthermore, we hypothesized that there would be variable responses from bat species, such that larger bats would be more active and persistent in areas further into uninterrupted agriculture, while smaller species would be restricted to areas around the riparian corridors, and that larger bat species would increase activity rates in response to high pest abundance more so than smaller bat species. With respect to bat diversity, we hypothesized that bat diversity would decline with increasing distance from riparian corridors, but that the magnitude of this effect would decrease with increasing pest abundance.

Methods

Study area

This study was conducted in east-central Illinois (40.0° N, 88.2° W), an area of approximately 13,100km^2 characterized by flat terrain (elevation range 45–93m) and expansive agriculture (85.1% of land cover, NLCD 2016, Fig. 1). Most crops grown in this region are soybeans and corn — the two most valuable crops in the USA, with Illinois being the second largest producer of corn nationally (USDA WASDE; USDA, NASS, Crop Production 2021 Summary). Several riparian corridors intersect the landscape (3.3% of land cover; Fig. 1).
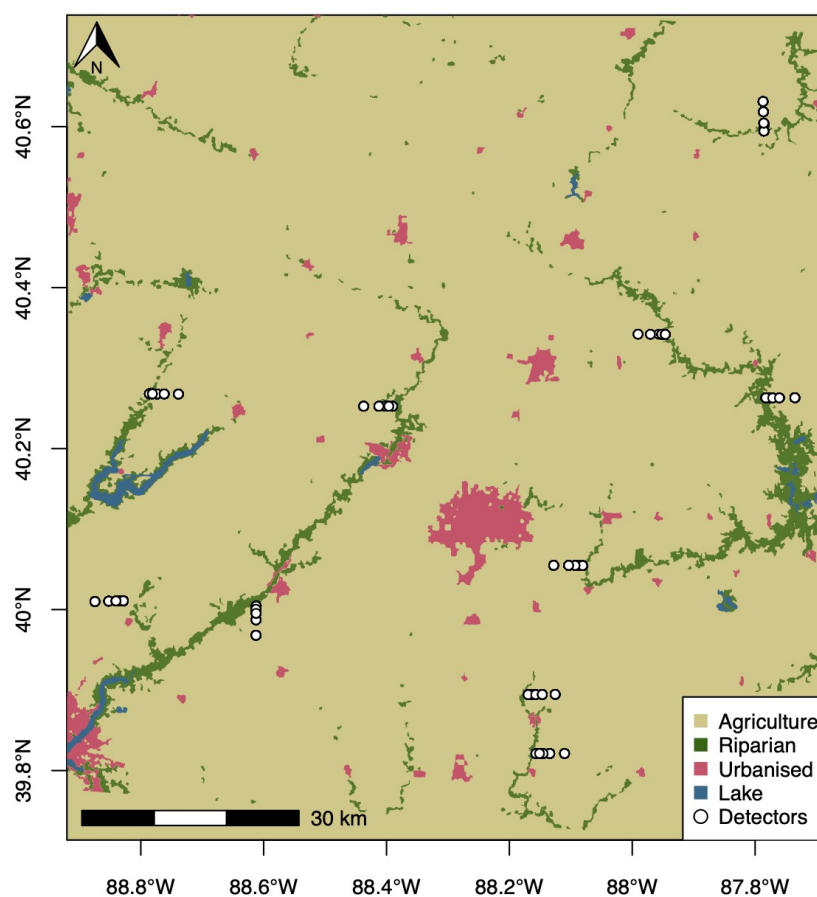

Figure 1. Map of study area, located in east-central Illinois, USA, indicating the location of the 50 bat

detectors (white circles) placed along 10 transects. Transects followed roads, starting at a forested area (green) and into uninterrupted row crop agriculture (brown) at 0m, 500m, 1000m, 2000m and 4000m from the forest edge.

Illinois Bat Community

Illinois has 13 insectivorous bat species (Whitaker and Hamilton, 1998), of which four are known to forage in open habitats such as agricultural landscapes: big brown bats (*Eptesicus fuscus* , EPFU), silver-haired bats (*Lasionycteris noctivagans* , LANO), eastern red bats (*Lasiurus borealis* , LABO), and hoary bats (*Lasiurus cinereus* , LACI). These species have high wing aspect ratios or long and narrow wings, resulting in decreased maneuvering abilities, high flight speeds, and sustained flight endurance capabilities, all traits that facilitate foraging in open habitat (Loeb and O'Keefe, 2011). These larger-bodied bats have been documented to consume a range of agricultural pests such as June beetles (*Scarabidae*), cucumber beetles (*Chrysomelidae*), Asiatic oak weevil (*Curculionidae*), corn earworm moth (*Helicoverpa zea*), and stink bugs (*Pentatomidae* ; reviewed by (Kunz et al., 2011). While sustained flight endurance should facilitate foraging in open expanses of agricultural landscapes, all open-foraging species rely on trees as roosting habitat and, thus, forest availability is a factor that could limit bat presence and activity on the landscape. Eastern red bats and hoary bats are foliage-roosting species that roost in tree canopies, hanging from leaves, twigs, and branches (Mager and Nelson, 2001; Willis and Brigham, 2005). While big brown bats use tree cavities and crevices as roosts (Willis and Brigham, 2004), this species often roosts in buildings, including barns (Benedict et al., 2017). Small-bodied bats, consisting mainly of Myotis species, generally remain in or close to forested habitat (Beilke et al., 2021; Henderson and Broders, 2008). Although they consume fewer large agricultural pest species, small-bodied bats are extremely important in consuming defoliating arthropods in forests (Hughes et al., 2021; Kalka et al., 2008).

Study design

We selected 10 transects, with each beginning at a prominent riparian corridor and heading perpendicularly into agricultural landscapes devoid of any large (> 1ha in size) natural features such as patches of forest or prairie (Fig. 1). For each transect, we deployed 5 passive acoustic bat detectors placed between roads and crop field edges at positions approximately 0m, 500m, 1000m, 2000m, and 4000m from the riparian corridor assumed to be frequented by bats (Fig. 1). The bat detectors were placed at a height of 3m, adjacent to corn and soy fields and facing the field interior.

To determine our study design, we piloted detector placement to test whether detectors placed adjacent to fields would differ in the number of bat recordings from those placed deeper within fields. We placed 7 pairs of detectors on properties, one adjacent to the field and one 100 m into the field, perpendicular to the road, for a total of 41 days. There was no difference in bat activity between detectors adjacent and those placed 100m inside of a field ($z = 0.29$, df = 170, p = 0.772).

Acoustic data

Acoustic detectors were deployed from May 29th to September 29th 2021. We used OpenAcoustics' AudioMoth bat detectors (v1.1.0 and v1.2.0), deployed in sealed, waterproof cases (AudioMoth IPX7 Waterproof case). We recorded throughout the evening, from 6pm to 6am Central Daylight Time, sampling at a rate of 250kHz with medium gain in full-spectrum format. We used an amplitude threshold at 0.1% and a high-band filter at 40kHz – which reduces the amplitude of frequencies below 40kHz (AudioMoth operation manual, p14), and is recommended when monitoring a bat community where common low frequency calls are 16kHz or above. Settings were based on pilot trials in May, but this amplitude threshold was deemed far too low when analyzing data from July – resulting in more noise being recorded – however this threshold was kept to ensure consistent parameters across the study. Data were collected in 55s recordings with a sleep duration of 5s; these files were later split into segments of 15s or less (i.e., 4 parts or call files).

Acoustic data were analyzed with Kaleidoscope Pro (v.5.4.6; KPro) to allow for the use of automated identification (i.e., autoID). We followed the protocol proposed by the North American Bat Monitoring Program

(NABat; Loeb et al., 2015) to analyze the acoustic files, using a minimum of 3 pulses, a pulse length range of 0–50ms, and a call frequency range of 10–120kHz. We used the standard species list for Illinois, USA for this analysis; this list includes EPFU, LABO, LACI, LANO, *Myotis austroriparius* (MYAU), *Myotis grisescens*(MYGR), *Myotis lucifugus* (MYLU), *Myotis septentrionalis*(MYSE), *Myotis sodalis* (MYSO), *Nycticeius humeralis*(NYHU), and *Perimyotis subflavus* (PESU); two species that occur only in southern Illinois are not on this list.

We further filtered the Kpro output to exclude any species-night-entries that had a maximum likelihood estimate of 1, as these are considered unlikely to be present based on the number of files identified as this species. Furthermore, because of a potentially high proportion of false-positive species identifications when using bat calls to ID bat species, we opted to analyze our data according to phonic groups of bat species, as described in Beilke et al. (2021). This commonly used classification technique is based on the characteristic frequency (F_c) of a bat species call: low frequency bats (F_c range: 18–30 kHz) include LACI, EPFU, and LANO; mid frequency bat species (F_c range: 23–43 kHz) include NYHU, PESU, and LABO; and high frequency bats (F_c range: 38–48 kHz) include all *Myotis* species. Bat activity was thus differentiated between three phonic groups: low, mid, and high frequency bats (Beilke et al., 2021).

Relative pest abundance

To estimate the relative abundance of crop pest species in our study area, we used a data set collected during our study period by the Crop Protection and Pest Management Program (Grant No. 2021-70006-35476) from the USDA National Institute of Food and Agriculture, in Champaign County, Illinois. The data was collected using pheromone lures to attract insects to metal Hartstack traps or nylon Heliothis traps around agricultural fields, targeting the main agricultural pest species (all large moths, wingspan range 24–45 mm; https://bugguide.net/) in the area: black cutworm (*Agrotis ipsilon*), corn earworm (*Helicoverpa zea*), European corn borer (*Ostrinia nubilalis*), and fall armyworm (*Spodoptera frugiperda*). Although these data were not specific for each of our study locations, we assume that the emergence timing of pest species is similar across the county. We applied a best-fitting curve to the data to predict pest abundance (number of individuals per trap night) for our data points based on date (Fig 2). We then standardized these data by dividing pest abundance by maximum pest abundance in the dataset, yielding a relative measure of pest abundance from 0 (no pest species present) to 1 (maximum pest abundance).

Covariates

Distance to forest was measured using remotely sensed images of the study area, through the GoogleEarth engine (images dated April 21st 2019 or later). Weather covariates were sourced from wunderground.com based on a weather station in Champaign, IL. We downloaded data for daily minimum and maximum temperature, mean and maximum daily windspeed, maximum daily humidity, and precipitation. Initial analyses revealed that only minimum daily temperature and precipitation were correlated with both bat activity and bat diversity, therefore only these two weather variables were retained in the statistical analyses.
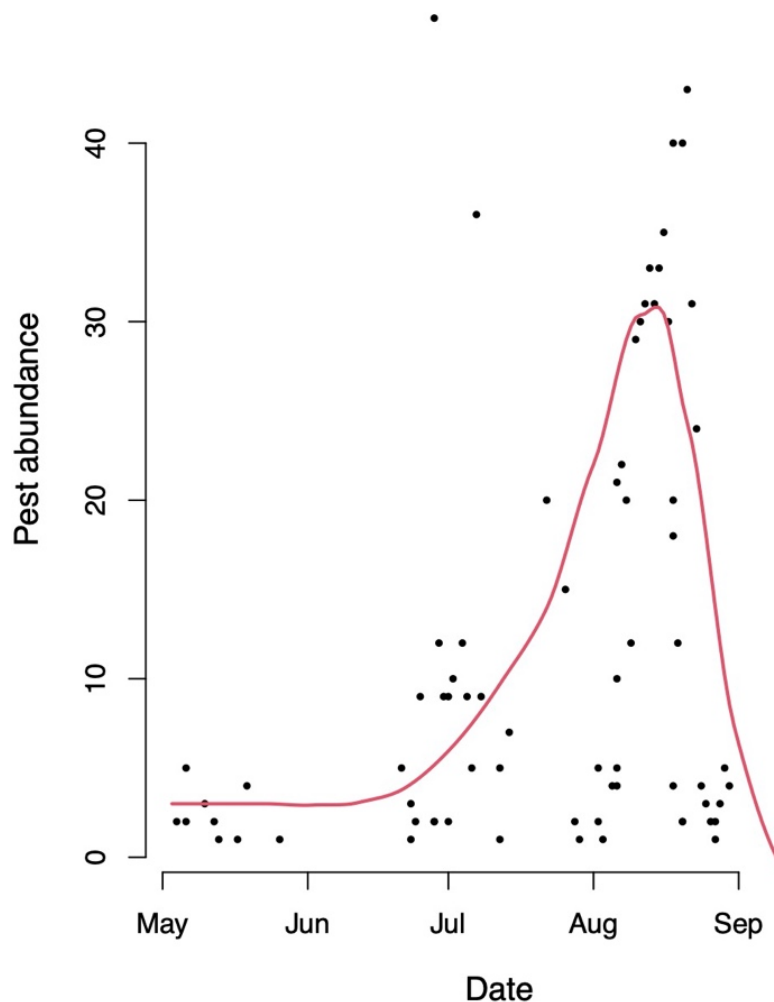
Figure 2. Pest abundance (total number of individuals per trap night) in relation to data collection date. Data were collected at agricultural fields in Champaign County, IL, in 2021. Red line represents a 'best-fitting-line'.

Statistical analysis

Bat activity

Bat activity (i.e., number of bat calls per detector per night per phonic group, N = 2471, mean ± SD = 17 ± 37, range = 1 – 470) is a count variable and, as such, we used a negative binomial generalized linear mixed effects model with quadratic parameterization (glmmTMB) to analyze the data (Brooks et al., 2017; Hardin and Hilbe, 2007). We included a two-way interaction between distance to forest and relative pest abundance, a two-way interaction between distance to forest and phonic group, and a two-way interaction between phonic group and relative pest abundance as main predictor variables. We also included daily minimum temperature (Tmin) and daily precipitation (Precip) as fixed covariates as these environmental factors have been shown to significantly affect bat activity (Gorman et al., 2021). Lastly, we included a quadratic effect of date as a fixed effect, as we expected bat activity to increase as pups become volant, until mid-August, and decline towards late-September, as bats migrate to hibernation sites. We included detector (N = 50) nested within transect line ID (N = 10) as random effects to control for potential spatial and temporal autocorrelation

biases. Statistical tests with a p-value lower than 0.05 were considered statistically significant. We report means and standard errors where appropriate.

Bat species diversity

We recognized several species within our dataset. Bat diversity was defined as the number of species detected per detector per night. However, in our study area *Myotis* species – apart from MYLU – were generally rarely identified through automated ID algorithms, so we combined all *Myotis* species with the exception of MYLU into one category '*Myotis* spp.' Consequently, bat species diversity in our dataset ranged from 1 to 8 (i.e., EPFU, LANO, LACI, LANO, NYHU, PESU, MYLU, and *Myotis spp*).

We used a similar negative binomial generalized linear mixed effects model with a quadratic parameterization to analyze bat diversity (N = 1698 detector-nights). We included a two-way interaction between distance to forest and relative pest abundance as main predictor variables. We also included the same covariates in this model: daily minimum temperature (Tmin), daily precipitation (Precip), and a quadratic effect of date as a fixed effect. The random effects were detector (N = 50) nested within transect line ID (N = 10).

Results

Bat Activity

Bat activity or bat calls per detector-night (calls/night) decreased significantly with increasing distance from forest (χ^2 = 16.37, df = 1, p < 0.001), such that bat activity decreased 56% from the forest edge (11.4 $\pm$ 1.8 calls/night) to 4000m away from the forest edge (5.0 $\pm$ 1.0 calls/night; Fig. 3A). Bat activity decreased less with increasing distance to forest when relative pest abundance was high (i.e., 1), compared to when relative pest abundance was low (i.e., 0; χ^2 = 10.04, df = 1, p = 0.002; Fig. 3A). The relation between bat activity and distance to forest was not affected by phonic group (χ^2 = 5.21, df = 2, p = 0.074; Fig. 3B). However, bat activity varied among phonic groups (χ^2 = 2167.74, df = 2, p < 0.001) such that, on average, low-frequency bats were most active (20.7 $\pm$ 2.8 calls/night), mid-frequency bats had less activity (4.2 $\pm$ 0.6 calls/night), and high-frequency bats had the least activity (1.2 $\pm$ 0.2 calls/night) throughout the study. Bat activity decreased significantly with increasing relative pest abundance (χ^2 = 14.22, df = 1, p < 0.001), but this effect varied by phonic group (χ^2 = 28.07, df = 2, p < 0.001); while activity of low-frequency bats decreased with increasing relative pest abundance, activity of med- and low-frequency bats did not vary with increased relative pest abundance (Fig. 3C).

Lastly, bat activity increased with increasing daily minimum temperatures (χ^2 = 137.67, df = 1, p < 0.001) and decreased with increasing daily precipitation (χ^2 = 4.26, df = 1, p = 0.039). Modeled bat activity was also highest in the beginning of July (χ^2 = 136.44, df = 2, p < 0.001).
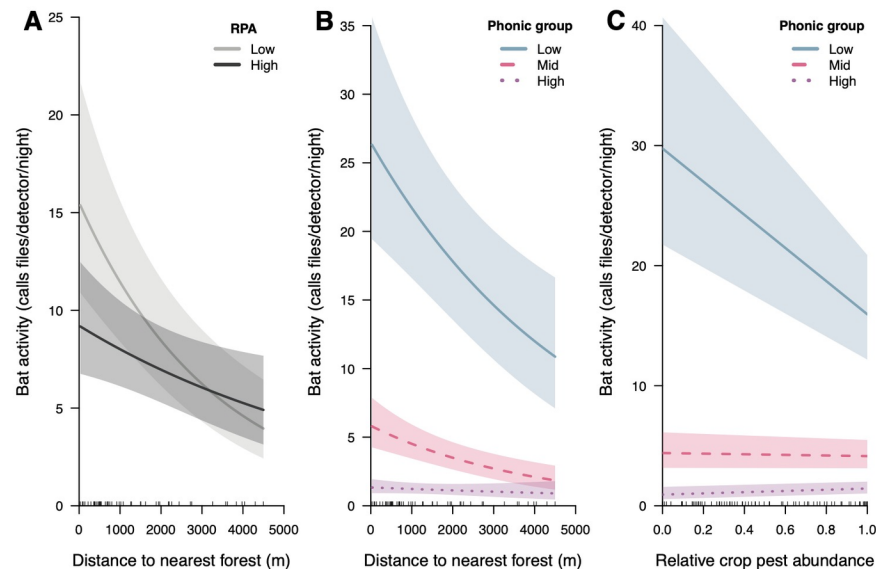
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Figure 3. The relationships between bat activity (number of call files per detector per night) and A) distance to nearest forest (in meters) with high relative pest abundance (RPA; dark grey) and low RPA (light grey); B) distance to nearest forest for high-frequency bats (dotted purple line), mid-frequency bats (dashed red line), and low-frequency bats (solid blue line); and C) RPA for high-, mid-, and low-frequency bats. Ticks on the x-axis indicate spread of data points on the x-axis. Lines indicate predicted mean; shaded areas represent 95%confidence intervals.

Bat diversity

Bat diversity (i.e., number of species per detector-night) declined significantly with increasing distance from forests ($\chi^2 = 29.80$, df = 1, p < 0.001), such that bat diversity declined by 1.4 species from the forest edge (4.1 ± 0.2 species/night) to 4000m away from the forest edge (2.7 ± 0.2 species/night; Fig. 4). Bat diversity was not affected by relative pest abundance ($\chi^2 = 0.16$, df = 1, p = 0.692) and the distance to forest effect did not vary with relative pest abundance ($\chi^2 = 2.05$, df = 1, p = 0.152). Modelled bat diversity increased through the summer season, peaking on 25 July ($\chi^2 = 70.64$, df = 2, p < 0.001). Bat diversity declined with increasing precipitation ($\chi^2 = 8.89$, df = 1, p = 0.003) , but was not affected by minimum daily temperature ($\chi^2 = 0.05$, df = 1, p = 0.831).
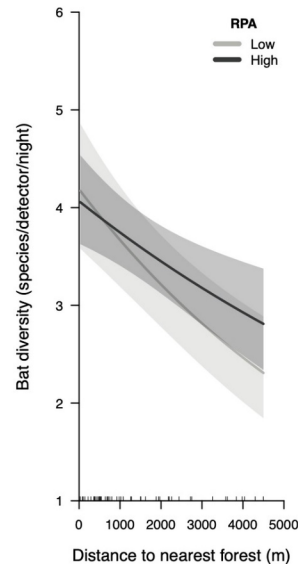
Figure 4 . The relationships between bat species diversity (number of species/groups per detector per night) and distance to nearest forest (in meters) with high relative pest abundance (RPA; dark grey) and low RPA (light grey). Lines indicated predicted mean; shaded areas represent 95% confidence intervals.

Discussion

We studied bat activity and bat species diversity in relation to distance from forested riparian corridors in a landscape dominated by row-crop agriculture and assessed how both activity and diversity might be affected by crop pest species abundance. Our results show that while bat activity and diversity decline with increasing distance from riparian corridors, increasing crop pest abundance does not increase activity or diversity. We also show that bat activity in agricultural landscapes is nuanced and that bats may require forest corridors in relatively close proximity if they are to provide valuable ecosystem services to agriculture.

Overall, bat activity declined with increasing distance from riparian corridors (Fig. 3A). This result supports our hypothesis and corroborated findings from previous studies, indicating bat activity to be higher in agricultural landscapes when forested corridors are present (Boughey et al., 2011; Davidai et al., 2015; Kalda et al., 2015) and when habitat heterogeneity is higher in general (Frey-Ehrenbold et al., 2013; Monck-Whipp et al., 2018; Russo et al., 2018). On organic farms, greater bat activity was attributed to higher landscape heterogeneity and improved water quality when compared to conventional farms (Wickramasinghe et al., 2003). Because bats provide considerable ecosystem services to agriculture (Boyles et al., 2011), in part by suppressing pest species, our results stress the importance of increasing habitat heterogeneity in agricultural landscape to ensure producers maintain or increase the pest control benefit provided by bats.

We found that a change in pest abundance altered the distribution of bats across the landscape (Fig. 3A). Our results indicate that when pest abundance is low, bats aggregate at the forest edge, resulting in much higher activity close to forests. However, when pest abundance is high, bats are more equally distributed across the landscape, resulting in lower activity at the forest edge and a smaller decline in activity further over uninterrupted agriculture. Importantly, overall bat activity was still lower farther from the forest edge, indicating that although bats may exploit increased foraging opportunities when pest abundance is high, their contribution to crop pest control still decreases with increasing distance from forest cover. This corroborates previous studies which have found that, crop pests make up a significant proportion of bats' diets in agricultural areas (Hughes et al., 2021; Kolkert et al., 2020a). Indeed, bats have been shown to track the changes in pest species abundance, exploiting the inflated prey availability (McCracken et al., 2012).

Unfortunately, we only have data on the temporal variation in pest abundance and lack information on

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any spatial or species patterns. If pest species abundance accumulated closer to forest edges, for example, or was higher further away from roads and into crop fields, our bat detectors would not necessarily detect the increased activity if bats did exploit the increase in pest abundance. However, there is evidence that pest abundance does not correlate with landscape complexity, suggesting that pest abundance might be more homogenous across the landscape than bat activity (Chaplin-Kramer et al., 2011). Furthermore, bats prefer to forage along linear features, such as hedges or grassy waysides (Lentini et al., 2012), suggesting that the majority of the bat activity in agricultural landscapes would be along linear features, and not over uninterrupted agricultural fields (Boughey et al., 2011).

We found that low-frequency bats, which are larger in size, were more active at greater distances into uninterrupted agriculture compared to smaller, high-frequency bats, supporting our hypothesis (Fig. 3B). Larger bat species typically have higher wing loading and higher wing aspect ratios, allowing them to travel further and faster over open space such as agricultural fields (Kalda et al., 2015). Foraging bats generally stay close to vegetated corridors, possibly to avoid predation (Lima and O'Keefe, 2013), but the faster flight speeds of larger bats could lessen the potential risks of venturing away from corridors and out into open fields. Our results corroborate previous findings that smaller bats are more sensitive to habitat fragmentation (Frey-Ehrenbold et al., 2013; Murray and Kurta, 2004), and are less likely to forage in open habitats (Ford et al., 2005; Henderson and Broders, 2008).

We also predicted that larger bats would benefit more from high pest abundance than smaller bat species, as larger bats prefer larger prey, and agricultural pest species are often large in size (Hughes et al., 2021). While bat activity of low-frequency bats declined with increasing pest abundance, activity of mid- and low-frequency bats was generally very low and unaffected by pest abundance (Fig. 3C). This corroborates findings that smaller bats are generally absent from large-scale agricultural landscapes and rarely forage on agricultural pest species (Ford et al., 2005; Heim et al., 2016).

Lastly, we found that bat species diversity declined with increasing distance into uninterrupted row crop agriculture (Fig. 4). This supports our hypothesis and corroborates previous studies that show that habitat heterogeneity in agricultural landscapes correlates with bat species diversity (Kolkert et al., 2020b; Monck-Whipp et al., 2018).

We also predicted that the decline in bat diversity further from riparian corridors would be buffered by pest abundance such that, with high pest abundance, bat diversity would be higher further away from riparian corridors. Lentini et al. (2012) found that bat species diversity increases with increased dry pest species biomass, and bats have been shown to seasonally expand and retract their range over cultivated landscapes in response to fluctuations in prey availability (Smith et al., 2021). However, our analysis found no effect of pest abundance on bat diversity (Fig. 4). Thus, the observed higher bat activity further from riparian corridors when pest abundance is high (Fig. 3A,B) is likely due to greater activity by a few larger species. Though bat dietary niches overlap to some degree (Cravens et al., 2018), species-specific prey preferences mean that increased bat species diversity could amplify their pest regulation ecosystem services (Maslo et al., 2022).

Conclusion

This study showed that both bat activity and species diversity in agricultural landscapes decrease with increasing distance from forest corridors. Habitat heterogeneity was most important for bats, regardless of crop pest abundance – an important food source for bats, as bat activity still declined from the forest edge even when pest abundance was high. Increasing habitat heterogeneity and natural features is important to promote bat activity in agricultural landscapes (Davidai et al., 2015; Kalda et al., 2015), and has also been shown to strongly increase biodiversity, including pollinators and birds (Cerezo et al., 2011; Eeraerts et al., 2019). As agricultural systems are increasingly expected to meet the growing demand for food production globally, it becomes pertinent to employ strategies that maximize output while limiting environmental damage. Bats benefit agricultural systems through intensive insect consumption, thereby decreasing the damage to crops caused by pests, while minimizing the need for pesticides (Kunz et al., 2011). We argue that agricul-

tural landscapes lacking habitat heterogeneity do not currently optimally benefit from natural pest control by bats due to the lack of foraging and roosting habitat that would facilitate bat presence, and emphasize the importance of increasing habitat heterogeneity for natural pest suppression strategies. Additional work is needed to further explore the relationship between bats and landscape features that promote foraging activity, and methods of increasing bat occupancy and activity within agricultural landscapes should be further investigated.

Acknowledgments

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