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Agroecological farming practices promote bats

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ABSTRACT

Intensive agriculture is a major driver of biodiversity loss, and a critical part of creating sustainable food systems is finding ways to balance production and conservation. While practices characteristic of agricultural intensification tend to erode biodiversity, agroecological farming practices can potentially support biodiversity and enhance pest suppression services. Bats are important predators of agricultural pests, yet little is known about how prescriptive management practices can be used to support bats and their associated pest-suppression services. We investigate how bats use natural habitat and conventional and organic farms in an agricultural landscape, ask which on-farm management practices may benefit bats, and examine how these management practices influence bats by mediating changes in habitat quality. We conducted acoustic surveys at 54 sites in the California Central Coast Region, a productive region with high ecological and economic value. We found higher bat activity in natural habitat compared to farms for total bat activity and clutter-adapted, but not open space bats, and slightly higher bat diversity in natural habitat compared to conventional farms. We found no effect of habitat type on species richness and a weak effect of habitat type on bat diversity, although bat community composition differed significantly between natural habitat and farms. Crop diversification increased the activity of all bat species and clutter-adapted, but not open space bats, regardless of the amount of semi-natural habitat surrounding farms. Both crop diversification and less frequent pesticide applications increased prey biomass, and the activity of clutter-adapted bats was positively correlated with greater Lepidoptera biomass. We suggest that improving habitat quality (increasing abundance of insect prey) through vegetative diversification and/or less frequent pesticide applications offers flexible management options to growers by considering both bat ecology and the constraints of regional agricultural management practices.

1. Introduction

Intensive agriculture is a major driver of biodiversity loss, and predicted intensification of agriculture suggests major shifts in land use patterns and biodiversity (Foley et al., 2005; Loos et al., 2014; Sala et al., 2000). Agricultural intensification is characterized by increased chemical and mechanical inputs, limited noncrop vegetation, and lower levels of planned biodiversity (Loos et al., 2014; Philpott, 2013). Although intensive agricultural production tends to erode biodiversity, ecological communities provide substantial benefits to humans, such as suppression of crop pests (Tscharntke et al., 2012). In many agroecosystems, insectivorous bats facilitate crop production by suppressing economically important insect pests (Maas et al., 2013; Maine and Boyles, 2015; Wanger et al., 2014; Williams-Guillén et al., 2015). The negative consequences of intensive agricultural systems on biodiversity and ecosystem services have spurred the development of agroecological farming schemes that promote ecological interactions, lead to the

provisioning of ecosystem services, and support biodiversity (Gonthier et al., 2014; Hole et al., 2005; Ponisio et al., 2016).

Through the diversification of crops and habitats and the reduced use of pesticides, agroecological practices may improve habitat quality for insectivorous bats. These practices may increase bat dispersal across the landscape and provide more stable populations of insect prey, although bats in different functional guilds may have different responses to these practices. The addition of linear habitat - strips of perennial vegetation, such as treelines and hedgerows - can increase bat activity because many bat species utilize linear habitat as flyways for foraging and commuting (Frey-Ehrenbold et al., 2013; Verboom and Huitema, 1997). Linear habitats may reduce energy costs for commuting bats by providing shelter from wind and predators, increase foraging efficiency by concentrating insect prey, and serve as navigational aids (Verboom and Spoelstra, 1999). The positive effect of linear habitat is more pronounced for bat species with structure-bound ecologies (Frey-Ehrenbold et al., 2013; Verboom and Huitema, 1997). Open area bats

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are well-suited for crossing vast agricultural fields, whereas clutter-adapted bats are more strongly associated with forest and tend to stay closer to linear habitat (Schnitzler and Kalko, 2001). Lower levels of pesticide applications and increased plant diversity may also improve foraging habitat quality for bats by providing a more abundant insect prey base, although this mechanism has not yet been tested. Insect communities are more abundant in organic systems with lower pesticide use levels (Bengtsson et al., 2005; Hole et al., 2005; Wickramasinghe et al., 2004). Intercropping, crop diversification, and the maintenance of non-crop vegetation can all help to maintain insect populations by providing a variety of insect habitat niches, which is especially important in annual cropping systems with frequent disturbances (Letourneau and Goldstein, 2001; Letourneau et al., 2011; Nicholls and Altieri, 2013).

Many studies that investigate the impact of agricultural intensification on bats focus on categorical comparisons of management intensity (i.e. organic vs conventional). These studies show mixed responses (Williams-Guillén et al., 2015), perhaps because few studies consider both local farming practices and the effect of the surrounding landscape (e.g., Davy et al., 2007; Herrera et al., 2015; Lesinski et al., 2013; but see Froidevaux et al., 2017). Categorical comparisons are limited by the reality that farming practices likely vary within and may be shared among management intensity categories (Appendix Fig. S1), making it difficult to pinpoint which practices drive observed patterns in biodiversity.

Because bats respond to factors at both local and landscape scales (Akasaka et al., 2010; Fuentes-Montemayor et al., 2013; Kelly et al., 2016), landscape context must be considered when evaluating the impact of local practices on bats. Farms with similar practices may be spatially aggregated (Gabriel et al., 2009; Teillard et al., 2012), making it difficult to disentangle the effects of local management practices from confounding landscape factors. A nested sampling design can be used to minimize variation in the surrounding landscape when evaluating the effect of local management intensity (Chamberlain et al., 2010; Letourneau and Goldstein, 2001). Accounting for specific on-farm practices and minimizing variation in the surrounding landscape between paired farms provides a more nuanced understanding of which on-farm management strategies or practices are likely to impact bat conservation outcomes.

Landscape-scale conservation efforts are important for bat conservation in agricultural landscapes (Frey-Ehrenbold et al., 2013; Froidevaux et al., 2017; Fuentes-Montemayor et al., 2013; Kelly et al., 2016), but may be challenging to coordinate among multiple private landowners (Mckenzie et al., 2013). In productive agricultural regions, such as California's Central Coast Region (CCR), the high cost of cropland encourages intensification, resulting in the conversion of perennial habitat to arable fields, the destruction of edge habitat, and simplified, homogenous landscapes (Tschardt et al., 2005). With little remaining natural habitat, few incentives for growers to restore habitat, and the challenges associated with coordinated grower participation, a focus on local management practices as conservation solutions may be a more effective approach than landscape-scale conservation efforts, although the efficacy of local practices may depend on the landscape surrounding the farm (Concepción et al., 2012, 2008; Winqvist et al., 2012).

We investigate how bats use farms compared to surrounding natural habitat, assess which local practices may benefit bats, and ask if the influence of local practices on bats depends on the surrounding land use. Specifically, we ask: 1) How do bat activity, species richness, diversity, and community composition differ among natural habitat, organic farms, and conventional farms? 2) Which on-farm management practices (i.e., linear habitat, vegetative diversity, and pesticide use) underlie any observed differences in bat activity, species richness, and diversity? 3) Which on-farm management practices influence insect abundance, and are these the same practices that influence bat activity? 4) Does the influence of on-farm management practices on bats depend

on the amount of semi-natural habitat in the surrounding landscape? For each question, we explore bat activity for all bat species and by functional guild.

We conducted acoustic surveys in the CCR and compared bat responses across site types (natural habitat, organic farms, and conventional farms) and in response to local practices by comparing paired organic and conventional farms that vary in their adoption of agroecological farming practices. We hypothesized that focusing on specific practices would better explain bat activity, diversity, and richness than categorical comparisons between organic and conventional farms.

2. Methods

2.1. Study area and sampling design

We conducted research in the CCR, an economically and ecologically valuable area. Farms in the CCR produce 13% of vegetables in the USA (USDA Census of Agriculture, 2009; USDA National Agricultural Statistics Service, 2012). To understand how bats respond to agricultural intensification at the farm scale, we worked on farms and nearby natural areas in Santa Cruz, Santa Clara, San Benito, and Monterey Counties, CA within a 60 km (N-S) by 70 km (E-W) region (Fig. 1a). We selected woodland patches (including riparian corridors) as natural habitat sites because remnant woodlands are important bat habitat in agricultural landscapes (Kniewski and Gehrt, 2014). Study sites in the CCR were selected to be representative of the range of farms and remnant woodland patches present in the study area using a combination of aerial imagery and based on the interest of private landowners and growers in participating in this research.

We used a nested design and selected three clustered sites (natural vegetation, organic farm, conventional farm) within a 1.5 km radius circle and repeated this design across the region (N = 18 clusters, N = 54 sites) (Fig. 1a,b). The sites exist along a landscape gradient of semi-natural habitat density (mean = 42%, range = 2–80%) and agricultural land use density (mean = 50%, range = 14–98%) within a 1.5 km radius. Organic farms sites were all certified organic (www.ccof.com) and used less intensive practices (organically-approved fertilizers such as compost and animal-based pellet fertilizers, multiple crop types, inclusion of habitat for beneficial organisms) than paired nearby conventional farms that used more intensive practices (use of synthetic fertilizers, pesticides, and herbicides; fewer crop types). Many farms grew a single crop variety, most commonly Brussel's sprouts, strawberry, broccoli, or lettuce. Farms with multiple crop varieties (mean = 2.7, range = 1–10, excluding one outlier farm described below) included a mix of vegetables (cucumber, cole crops, peppers, celery, peas, carrots, beets, lettuce), beans, squash, tomatoes, herbs, and strawberries. Within each farm pair, we chose monitoring sites in the center of fields planted in annual crops (vegetables or strawberries) with similar proximity to natural habitat. We used one detector for each site and placed detectors within fields (organic and conventional farms) and at the edge of woodland patches (natural sites) (Fig. 1c).

2.2. Bat acoustic monitoring and call identification

We sampled bats at all sites with passive acoustic bat detectors (Wildlife Acoustics SM2BAT with SMX-US Ultrasonic Microphone, Concord, MA, USA) from mid-June to early September 2014. Bat detectors were mounted on t-posts and microphones were elevated on 3 m PVC poles attached to the t-posts. We monitored bat activity levels and species richness at all sites. We did not compare feeding buzzes due to high subjectivity in distinguishing between a bat inspecting research equipment, a novel structure in their environment, and pursuing insect prey (Weller et al., 1998). We sampled each site for 6–7 nights during one sampling period from sunset to sunrise to account for high variability of bat activity across nights; the three sites clustered within each landscape (natural site, organic farm, conventional farm) were sampled

sites: N=54

clusters: N=18

Fig. 1. Map of study region showing A) all sites, B) three sites arranged in a landscape cluster, and C) arrangement of clustered sites within farm fields and along the edge of a linear habitat. Each landscape cluster included one natural habitat site, one organic farm site, and one conventional farm site. Landscape clusters represented a gradient of landscape contexts, with some clusters surrounded by a mix of agriculture and natural habitat (top circle), and other clusters surrounded predominantly by agriculture (bottom circle).

simultaneously to reduce variability and increase sampling efficiency (Hayes, 1997).

Recorded calls were processed using Kaleidoscope V2.3.0 (Wildlife Acoustics, Concord, MA) to filter noise files and split files to a max duration of 5 s, which we defined as a bat pass and used in subsequent analyses. Files were automatically classified using Sonobat V3.1 West (Arcata, CA) and then manually vetted by a team of trained technicians. To account for potential bias among technicians, we worked as a team until our classification decisions were at least 90% in agreement and used a decision key to finalize call identifications. Identification of rare or hard to identify species was completed by one of us (EO) to minimize bias. Remaining calls that could not be positively identified to species (due to overlap in call repertoires and/or poor recording quality) were classified by characteristic frequency (frequency at lowest slope of call) into three phonic groups, with species that comprise each phonic group listed in parenthesis: 50 kHz (*Myotis yumanensis*, *Myotis californicus*), 40 kHz (*Myotis ciliolabrum*, *Myotis volans*), and 30 kHz (*Eptesicus fuscus*, *Lasionycteris noctivagans*, *Tadarida brasiliensis*, *Lasiurus cinereus*).

To account for differences in how bats perceive their environment, we grouped a subset of the species recorded in the study region based on their echolocation call structure, characteristic frequency, and foraging ecology into two functional guilds: clutter-adapted and open-space bats. Of the 12 species recorded in the study region, two were classified as clutter-adapted bats (*Myotis yumanensis*, *Myotis californicus*, and calls identified as 50 kHz) and four were classified as open-space bats (*Eptesicus fuscus*, *Lasionycteris noctivagans*, *Tadarida brasiliensis*, *Lasiurus cinereus*, and calls identified as 30 kHz). These groups include the most common species in the study region and represent 97% of recorded calls. We used guidelines described in Schnitzler and Kalko (2001) and Buchalski et al. (2013) and echolocation call parameters described by the Humboldt State Bat Lab (2011) to partition species into functional guilds. Species in the open-space guild have call characteristic frequencies < 30 kHz and > 6 ms in duration, which experience less environmental attenuation and are therefore suited for

foraging in uncluttered, open areas. Species in the clutter-adapted guild have calls with characteristic frequencies of > 45 kHz and duration < 6 ms. Bats in the clutter-adapted guild are able to forage in highly cluttered forest habitat by using short duration, high frequency calls to distinguish insect echoes from echoes produced by background clutter (Schnitzler and Kalko, 2001).

2.3. Nocturnal insect sampling

We designed bucket style light traps with 12 W black light bulbs and clear plastic vanes (BioQuip, Racho Dominguez, CA) and a brewer's funnel with a mesh collecting bag containing a 2cm² piece of pesticide strip (No-Pest Strip®, HotShot). Light traps were deployed simultaneously with acoustic detectors and were programmed to turn on at civil sunset for three hours during the first two nights that the detectors were deployed. Light traps were placed 10 m from bat detectors to prevent potential high-frequency interference from light traps from being recorded by bat detectors, either within fields or along linear habitat edges. Insects were later sorted and identified to order. We measured the length of each insect to estimate biomass using relationships described for terrestrial California insects in Sabo et al. (2002).

2.4. Farm management practices and characteristics

We surveyed local vegetation within concentric circles centered on acoustic monitoring sites. Within a 25 m radius, we measured the number of weed morphospecies and visually estimated the total number of flowers within the crop field. Within a 50 m radius, we measured the number of crop varieties, average crop height, and the percent of different ground cover types. For the percent of ground cover types, we focused on cover classes exceeding 5% of ground cover, and included bare ground, crops, non-crop herbaceous vegetation, and woody vegetation. Within both a 50 m and 100 m radius, we measured the

number of trees > 30 cm circumference (at 1 m height) and the number of tree species. For all farms, we estimated the percent of field margins in insectaries (flowering plants intentionally introduced or managed to provide resources for beneficial insects), the percent cover of insectaries in crop fields, and the percent of weedy field margins.

We gathered information about pesticide application on each farm (as reported by growers directly to EO). Most growers applied broad-spectrum insecticides and/or fungicides, although a few smaller, organic operations reported that they had not applied pesticides in years. Some of these pesticides (e.g. Spinosad) were widely used by organic and conventional growers; only conventional growers used organophosphates. For each farm, we categorized frequency of pesticide applications according to these categories: 1 = pesticides applied every 1–10 days; 2 = pesticides applied every 11–30 days; 3 = pesticides applied less than once a month; 4 = pesticides applied less than once a year.

We also gathered information about distance to habitat features that are important for bats, and that we could not standardize across the trio of clustered sites. We used Google Earth to calculate the shortest distance to water (Kniewski and Gehrt, 2014; Rainho and Palmeirim, 2011) and distance to the nearest linear habitat element, such as a treeline, hedgerow, or forest edge (Gehrt and Chelsvig, 2003; Kelm et al., 2014; Verboom and Huitema, 1997).

2.5. Landscape characterization

We created land cover maps from the National Agricultural Imagery Project 2014 (1 m² resolution data; available at <https://nationalmap.gov>) using manual likelihood classification in ArcMap V10.3.1 (Environmental Systems Research Institute, Redlands, CA). We categorized agriculture and semi-natural habitat, and smoothed and re-sampled maps to a resolution of 7 m² to reflect ground-truthed land cover classes. We then calculated the land use density of agriculture and semi-natural habitat within a 1.5 km radius, an ecologically relevant scale for bats and insects (Fuentes-Montemayor et al., 2011; Kniewski and Gehrt, 2014; Letourneau and Goldstein, 2001).

2.6. Statistical analysis

We used total bat activity, clutter-adapted bat activity, open-space bat activity, diversity, and species richness as response variables. Bat activity (average bat passes per night) is a measure of relative abundance calculated for each site over a minimum of six nights of sampling, and thus not true count data. Therefore, we opted to log transform the average number of bat passes per night to meet assumptions of normality with a Gaussian error distribution, instead of using the Poisson error distribution recommended for count data (O'Hara and Kotze, 2010). We used the Chao1 species richness estimator (Chao et al., 2005) to assess the completeness of species inventories and to compare species richness across site types (Appendix: Fig. S2). We calculated estimated species richness and diversity (Shannon index) using all calls identified to species and the 40k phonic group with the package “vegan” (Oksanen et al., 2016) in R software, version 3.3.1 (R Core Team, 2016).

To compare response variables (total bat activity, clutter-adapted bat activity, open-space bat activity, diversity, and species richness) between organic farms, conventional farms, and natural sites, we used a randomized block ANOVA, with sites blocked by landscape cluster, and conducted multiple comparison tests using Tukey contrasts as implemented in the “multcomp” package in R (Hothorn et al., 2008). We checked that assumptions of normality and homogeneity of variance were met using the Shapiro-Wilk test and the Brown-Forsyth test in the “HH” package in R (Heiberger, 2017). To compare community composition between organic farms, conventional farms, and natural sites, we used a one-way Analysis of Similarity (ANOSIM) test. We used the Bray-Curtis index to characterize species dissimilarity between habitat types using the “vegan” package in R (Oksanen et al., 2016).

We used linear mixed models (LMMs) to compare differences in responses (total bat activity, clutter-adapted bat activity, open-space bat activity, species richness, diversity) to local, on-farm management practices. We selected predictor variables that represent agroecological farming practices and/or practices characteristic of intensive agriculture that growers could potentially manipulate. We included the percent of weedy field margins, number of crop varieties (50 m), average height of herbaceous vegetation (25 m), distance from a linear element, and percent woody vegetation (50 m). We did not include the percent of field margins planted in insectaries or the percent of field planted in insectaries as covariates because many farms did not utilize either of these practices. Selected predictor variables were not strongly correlated (Pearson correlation coefficient < 0.6 and $p > 0.05$ used as threshold), although they were somewhat correlated with a number of other farm characteristics (Appendix: Table S1). In addition, we included distance to water as a fixed effect and landscape cluster as a random effect to account for variation in the surrounding landscape, and to avoid spatial autocorrelation problems. We used standardized model residuals obtained by the top model for total bat activity to create a variogram and verify spatial independence (Zuur et al., 2009).

We performed model selection using the *dredge* function in the package “MuMIn” (Bartoń, 2016) after testing for normality (Shapiro-Wilk test). We log-transformed total bat activity, clutter-adapted bat activity, and crop diversity, and used a square root transformation for open-space bat activity to meet assumptions of normality. We tested all possible combinations of explanatory variables (all candidate models contained a random effect of landscape cluster) and selected the top model if the corrected Akaike's Information Criterion (AICc) score was at least two points less than the next best model ($\Delta\text{AICc} < 2$) (Burnham and Anderson, 2002). When the top models had similar AICc scores ($\Delta\text{AICc} < 2$), we selected the top models within two points of the lowest AICc score and adopted a model averaging approach to obtain estimated coefficients and the relative importance of predictor variables from the top model set.

We visually inspected the relationships between predictors in top models and responses, and noted an outlier site for crop diversity and weed morphospecies, with most sites ranging from 1 to 10 crop varieties, and one site with 39 crop varieties. We decided to remove the outlier after exploring its leverage on LMMs and Pearson correlation coefficients. The effect of the outlier was minimal in most cases, but it changed the significance of the effect of crop diversity on open-space bat activity, and the strength and significance of the relationship between crop diversity and weed morphospecies within 25 m.

We asked if the same local management practices and farm characteristics that predicted bat activity would also predict the biomass of insect orders that are known to be consumed by bats and were commonly collected in light trap samples (Lepidoptera, Diptera, Coleoptera). We tested LMMs that contained the same set of predictors as bat models to assess if variables that predicted bat activity operated on bats via changes in abundance of insect prey. All models contained a random effect of landscape cluster. To meet assumptions of normality, we used a square root transformation for Diptera biomass, and a log transformation for Lepidoptera and Coleoptera biomass. We assessed Pearson correlations between bat activity and insect biomass for these common prey orders.

We used LMMs to test for an interaction between local practices that significantly predicted bat responses and semi-natural habitat density (1.5 km radius) using LMMs. We built a set of candidate models using the top model from model averaging and added an interaction with semi-natural habitat density (1.5 km), and compared models using AICc scores.

Table 1

Bat calls recorded per night (mean $\pm$ SE) in natural areas, organic farms, and conventional farms in the Central Coast Region, CA. We include the 40k phonic group because it represents at least one additional species (*M. ciliolabrum*, *M. volans*).

Species/group	Mean passes per night $\pm$ SE		
	Natural	Organic	Conventional
<i>Tadarida brasiliensis</i>	30.33 $\pm$ 18.89	18.84 $\pm$ 3.50	22.51 $\pm$ 7.13
<i>Myotis yumanensis</i>	31.16 $\pm$ 9.60	3.35 $\pm$ 0.98	2.03 $\pm$ 0.48
<i>Myotis californicus</i>	11.13 $\pm$ 5.01	1.58 $\pm$ 0.50	1.00 $\pm$ 0.37
<i>Eptesicus fuscus</i>	4.19 $\pm$ 2.43	0.98 $\pm$ 0.30	0.75 $\pm$ 0.25
<i>Lasiurus blossevellii</i>	1.80 $\pm$ 1.27	0.62 $\pm$ 0.16	0.66 $\pm$ 0.28
<i>Lasionycteris noctivagans</i>	0.17 $\pm$ 0.16	0.27 $\pm$ 0.15	0.18 $\pm$ 0.07
<i>Myotis thysanodes</i>	0.24 $\pm$ 0.24	0.09 $\pm$ 0.09	–
<i>Corynorhinus townsendii</i>	–	0.04 $\pm$ 0.03	0.06 $\pm$ 0.04
<i>Lasiurus cinereus</i>	0.02 $\pm$ 0.02	0.02 $\pm$ 0.01	0.02 $\pm$ 0.01
<i>Myotis evotis</i>	0.03 $\pm$ 0.02	0.01 $\pm$ 0.01	0.01 $\pm$ 0.01
<i>Antrozous pallidus</i>	–	0.03 $\pm$ 0.02	–
40k phonic group	26.57 $\pm$ 22.04	2.96 $\pm$ 1.04	1.71 $\pm$ 0.53
Clutter-adapted guild	147.37 $\pm$ 47.36	10.13 $\pm$ 2.42	4.03 $\pm$ 0.85
Open-space guild	60.49 $\pm$ 24.89	31.33 $\pm$ 6.21	33.08 $\pm$ 9.82
Total activity	236.49 $\pm$ 79.63	45.21 $\pm$ 7.95	39.54 $\pm$ 10.25

3. Results

3.1. Overview

Across 648 detector nights, we recorded 36,294 bat calls. Of these, we were able to confirm identification to species for 14,969 (41%) calls, and remaining calls were identified to phonic group. A total of 12 different species were recorded (Table 1), and of those, *Tadarida brasiliensis* (54% of identified calls) and *Myotis yumanensis* (28%) were the most common across all sites. Three recorded species are listed as species of special concern in California: *Lasiurus blossevellii* (344 calls), *Corynorhinus townsendii* (11 calls), and *Antrozous pallidus* (3 calls) (California Department of Fish and Wildlife, 2017). The species inventory appears to be complete for natural habitat, but not for farms, according to rarefaction analysis (Appendix: Fig. S2). We recorded fewer, high quality calls on farms compared to natural habitat. Bat calls recorded on farms had less noise interference (e.g., leaves rustling in the wind) than recordings from natural habitat, allowing us identify a greater number of species from fewer calls, resulting in steeper species accumulation curves that did not reach an asymptote.

3.2. Natural vs. organic vs. conventional

There were differences in overall and clutter-adapted bat activity, but not open-space bat activity, with habitat type. Total bat activity differed by habitat type (e.g. natural, organic, conventional) ($F_{2,34} = 10.05$, $p = 0.0004$) but not landscape cluster ($F_{17,34} = 1.67$, $p = 0.10$). Total bat activity in natural areas was ~ 5 times greater than on farms (organic: $p = 0.0046$, conventional: $p < 0.001$), and activity on organic and conventional farms did not differ ($p = 0.71$). Clutter-adapted bat activity also differed by habitat type ($F_{2,34} = 23.42$, $p < .0001$, Fig. 2a) but not landscape cluster ($F_{17,34} = 1.43$, $p = 0.18$). Clutter-adapted activity was greater in natural habitat than on farms (organic: $p < 0.0001$, conventional: $p < 0.0001$). Clutter-adapted activity on organic and conventional farms was not significantly different ($p = 0.445$), although it was ~ 2.5 times higher on organic compared to conventional farms. Open-space bat activity did not differ by habitat type ($F_{2,34} = 0.47$, $p = 0.63$, Fig. 2b) or landscape cluster ($F_{17,34} = 1.68$, $p = 0.096$).

Bat species richness was not affected by habitat type ($F_{2,34} = 1.63$, $p = 0.21$) or landscape cluster ($F_{17,34} = 1.64$, $p = 0.11$) (Fig. 2d). Bat diversity was marginally significantly different by habitat type ($F_{17,34} = 3.17$, $p = 0.054$) and landscape cluster ($F_{2,34} = 1.76$,

$p = 0.078$). Bat diversity in natural habitat was greater than on conventional farms ($p = 0.055$), although this difference was only marginally significant. Bat diversity did not differ between organic farms and natural or conventional farms (natural: $p = 0.66$; conventional: $p = 0.33$, Fig. 2c). Species composition (as assessed by the Bray-Curtis index) differed between the three habitat types ($r = 0.124$, $P = 0.001$). Significant statistical differences were found between natural habitat sites and farms ($r = 0.355$, $P = 0.001$), but not between organic and conventional farms ($r = -0.35$, $P = 0.95$).

3.3. On-farm management practices

Activity of all bat species and activity of clutter-adapted bats each responded to changes in local farm management and were both significantly positively correlated with the number of crop varieties within 50 m (Table 2). Activity of all bat species and activity of clutter-adapted bats ~ 1.5 and ~ 1.4 times higher, respectively, on the farm with the most crop varieties within 50 m (10) compared to a farm with one crop variety within 50 m (Fig. 3a,b). Open-space bat activity, bat diversity and bat species richness on farms were not predicted by any on-farm management practices and the null models were the top models.

3.4. Insect biomass

Top models for insect biomass included the number of crop varieties within 50 m and the frequency of pesticide applications (Table 2). Lepidoptera biomass was significantly positively correlated with crop diversity within 50 m ($p = 0.04$, Fig. 3d), and pesticide application frequency was not included in top models. Diptera biomass was significantly negatively correlated with the frequency of pesticide applications ($p = 0.05$, 0.20, 0.004 for pesticide use categories 1, 2, and 3, respectively), and was not correlated with crop diversity within 50 m ($p = 0.28$). Coleoptera biomass was not predicted by any farm management practices.

Activity of clutter-adapted bats was significantly, positively correlated with Lepidoptera biomass ($p = 0.02$, $R = 0.40$, Fig. 3c), but not with Coleoptera biomass ($p = 0.06$, $R = 0.32$) or Diptera biomass ($p = 0.53$, $R = -0.11$). Total bat activity and activity of open-space bats were not significantly correlated with any metrics of insect biomass ($p > 0.05$ and $R < 0.11$).

3.5. Interaction between local and landscape scales

The influence of crop diversity on activity of all bat species and clutter-adapted bats was not dependent on semi-natural habitat density (1.5 km radius) in the surrounding landscape. Bat activity models with crop diversity as a single predictor had lower AICc scores than models that included semi-natural habitat density (Table 3).

4. Discussion

4.1. Habitat type effects on bat activity, diversity, and species richness

Categorical comparisons of lower- and higher-intensity agricultural systems have documented mixed effects on bat activity, diversity and species richness, and provide limited insight on the effects of specific, agricultural management practices. We assessed differences between habitat types, as in previous studies, and did not detect consistent differences between organic and conventional farms; however, our analysis of the effects of specific farm practices on bats was much more informative (See Section 4.2). We documented significant overlap in practices between organic and conventional farms included in the study (Appendix: Fig. S1), which may explain why we did not detect strong differences between farm management types that mask the influence of local farm practices and characteristics on bats.

We found greater bat activity in natural areas compared to farms,

Fig. 2. Graphs showing A) clutter-adapted bat activity by management type, B) open space bat activity by management type, C) bat diversity by management type and D) species richness by management type. Activity of all bat species showed a similar pattern to clutter-adapted bats (figure not shown). Lines show median values, boxes show interquartile range, whiskers extend 1.5 times the interquartile range, and dots show outliers. Small letters show significant differences for bat activity ($P < 0.05$), and marginally significant differences ($P < 0.06$) for bat diversity.

Table 2

Top model or conditional model-averaged coefficient estimates $\pm$ SE for linear mixed-models. Predictors contained in full models that were not included in any top models (percent of weedy field margins, average height of herbaceous vegetation (25 m), distance from linear habitat, percent woody vegetation (50 m), distance to water) and the random effect of landscape cluster are not shown. Pesticide categories are defined by frequency of pesticide applications and pesticide category 4 (least frequent application) was used as the reference level in all models. Hyphens indicate that a predictor was not included in the top or averaged model. (***) $P < 0.001$, (**) $P < 0.01$, (*) $P < 0.05$.

Response	Intercept	No. crop varieties (50 m)	Pesticide 1	Pesticide 2	Pesticide 3
Bats					
Total bat activity	3.20 $\pm$ 0.24***	0.29 $\pm$ 0.11**	–	–	–
Clutter-adapted bat activity	1.22 $\pm$ 0.52*	0.46 $\pm$ 0.22*	–1.07 $\pm$ 0.69	–1.01 $\pm$ 0.65	–0.33 $\pm$ 0.69
Open-space bat activity	5.06 $\pm$ 0.93***	0.62 $\pm$ 0.38	–1.61 $\pm$ 1.19	–1.03 $\pm$ 1.11	–1.61 $\pm$ 1.20
Bat diversity	0.90 $\pm$ 0.07	–	–	–	–
Bat species richness	5.83 $\pm$ 0.34	–	–	–	–
Insects					
Lepidoptera biomass	2.47 $\pm$ 0.60***	0.81 $\pm$ 0.38*	–	–	–
Diptera biomass	8.07 $\pm$ 1.80***	–0.76 $\pm$ 0.68	–4.00 $\pm$ 1.94*	–2.49 $\pm$ 1.87	–5.54 $\pm$ 1.84**
Coleoptera biomass	1.10 $\pm$ 1.86	0.98 $\pm$ 0.77	–1.76 $\pm$ 2.36	–1.53 $\pm$ 2.24	–0.82 $\pm$ 2.26

highlighting the importance of conservation of natural habitat patches within intensive agricultural landscapes. This finding is consistent with previous studies in mixed annual cropping systems in the US (Davidai et al., 2015) and vineyards in North America (Kelly et al., 2016; Rambaldini and Brigham, 2011). Our finding that diversity was marginally significantly higher in natural habitat than on conventional farms may be explained by differences in local habitat features. Conventional farms had the least variation within site types, with large

monocultures of annual crops and little non-crop vegetation, creating open habitat dominated by *T. brasiliensis*. Natural vegetation sites comprised a range of vegetation forms spanning mixed riparian vegetation to oak woodlands, offering habitat niches for more diverse species. We found no evidence of differences in species richness (regardless of species identity) between site types, as the same species were usually documented across clustered sites. However, we did find that bat community composition differed between natural habitat and farms,

Fig. 3. Graphs showing relationships between A) all species bat activity as a function of the number of crop varieties within 50 m of bat detectors, B) clutter-adapted bat activity as a function of the number of crop varieties within 50 m of bat detectors, C) clutter-adapted bat activity and Lepidoptera biomass, and D) Lepidoptera biomass and the number of crop varieties within 50 m of bat detectors. All graphs show simple linear relationships between variables.

Table 3
Comparison of bat activity models to test for an interaction between local practices that significantly predicted bat responses and semi-natural habitat density (1.5 km radius).

Response	Model	AICc	ΔAICc
Total bat activity	No. crop varieties	85.2	0
	Semi-natural	91.4	6.2
	No. crop varieties + Semi-natural	93.5	8.4
Clutter-adapted bat activity	No. crop varieties * Semi-natural	105.0	19.8
	No. crop varieties	117.4	0
	Semi-natural	124.5	7.0
	No. crop varieties + Semi-natural	126.3	8.9
	No. crop varieties * Semi-natural	135.2	17.8

but not between organic and conventional farms.

4.2. Specific management feature effects on activity and diversity

Our finding that farms with more crop varieties had greater activity of all bat species and clutter-adapted bats is the first evidence that bats respond to herbaceous plant diversity on farms. The effect of crop diversity on bats has not been previously tested, and we are not aware of other studies that have documented effects of on-farm herbaceous plant diversity. Most similarly, a study comparing bat activity between farm

field margins planted in mixed grasses and conventionally managed field margins did not find a significant effect on bat activity (Fuentes-Montemayor et al., 2011).

In contrast to previous studies, we found no evidence that bat activity was positively correlated with proximity to linear habitat (Kelm et al., 2014; Verboom and Huitema, 1997). However, difference in the extent and configuration of linear habitat in European farmlands (where these studies were conducted) compared to the CCR may explain why our findings conflict with previous literature. Differences in woody vegetation that would impact environmental clutter did not predict clutter-adapted bat activity. If proximity to linear habitat influenced bat activity, it may have been necessary to monitor at a linear edge and at increasing distance into a crop field.

To link our findings of the relationship between crop diversification, bat activity, and insect biomass, we focus on clutter-adapted bats. Our finding that crop diversity was significantly correlated with higher clutter-adapted bat activity and greater biomass of Lepidoptera, and that greater biomass of this important insect prey order was significantly positively correlated with higher bat activity, suggests that crop diversification impacts bats via changes in populations of insect prey (Table 2). Farms with higher crop diversity also tended to have more noncrop herbaceous cover (e.g., weeds and insectaries) and weedy field margins (Appendix: Table S1) as farms often employed a suite of diversified practices. On-farm vegetative diversity can provide critical insect food and habitat resources that are not found in simple monocultures, increasing insect abundance (Andow, 1991; Wenninger

and Inouye, 2008), and improving foraging habitat for bats.

The frequency of pesticide use decreased the biomass of Diptera, and Coleoptera, which account for 20–40% of the summer diet of *M. yumanensis* and *T. brasiliensis*, in California (Long et al., 1996), the two most common species in the study region. Higher application rates of pesticides and use of synthetic agrochemicals in conventional systems has been suggested as the mechanism driving increased insect abundance and bat activity on organic farms (Wickramasinghe et al., 2004, 2003).

Because bat activity increased with crop diversity and activity of clutter-adapted bats increased with Lepidoptera biomass, we suggest that both vegetative diversity and pesticide applications drive changes in insect populations and bat activity. Previous studies also demonstrate a positive correlation between bat activity and insect biomass in pastures, linear habitat, and crop fields in agricultural landscapes (Lentini et al., 2012; Wickramasinghe et al., 2004) and show that bats track and feed on populations of insect pests (McCracken et al., 2012). Of course, the correlation between bat activity and insect biomass is a two-way relationship. Bats may be attracted to higher quality on-farm foraging areas with greater insect biomass, in turn consuming more insects and suppressing insect population levels on these farms, which may explain why we did not see a correlation between open-space bats and insect biomass. Despite this two-way relationship between bats and insects, our findings provide evidence that crop diversification and less frequent pesticide use increase insect prey and bat activity on farms.

The influence of crop diversification on bat activity does not depend on the amount of semi-natural habitat surrounding the farm. Although a few studies in tropical agroforestry systems have confirmed an interaction between local and landscape scale agricultural intensification (e.g., Faria et al., 2006; Numa et al., 2005), Froidevaux et al. (2017) found that the effects of local vineyard management were not dependent on landscape complexity. Moreover, we found that crop diversity is a better predictor of bat activity on farms than semi-natural habitat density. Similarly, Kelly et al. (2016) did not find strong effects of semi-natural habitat density on bat activity on farms. Bat activity in remnant semi-natural habitat is higher in agricultural landscapes with more semi-natural habitat (Fuentes-Montemayor et al., 2013), but the effects of landscape-scale factors on bat ecology have not been extensively studied in temperate, annual cropping systems (Williams-Guillén et al., 2015).

4.3. Management implications

Hedgerows, woodland patches, and scattered trees can support bat conservation in agricultural landscapes (Boughhey et al., 2011; Fuentes-Montemayor et al., 2013; Lentini et al., 2012). A focus on the importance of structural, woody vegetation to bat conservation reflects species' specific roosting requirements that are not provided by farms, and the potential for structural vegetation to increase habitat connectivity for species with structure-bound ecologies. The conservation of woody vegetation is undoubtedly important to the long-term conservation of bats in agricultural landscapes. However, because the addition of woody, perennial vegetation is often not a feasible management strategy for growers in intensive agricultural systems, we suggest that including a complementary focus on improving the quality of bat foraging habitat offers additional management options in agricultural landscapes. Intensive agricultural systems provide inconsistent food resources to bats, whereas the maintenance of natural habitats can help to ensure stable food resources (Davidai et al., 2015). Similarly, diverse on-farm and within-field vegetation can help to ensure consistent food resources for bats without negatively affecting production practices or increasing pest problems. The addition of herbaceous plant diversity (e.g., insectaries to promote beneficial insects, plants to repel or trap insect pests) can be designed through species selection and timing of planting to support desired insect communities (Gareau et al., 2013). On-farm plant diversity can improve pest suppression, enhance

populations of beneficial insects, reduce crop damage, and increase crop yields (Iverson et al., 2014; Letourneau et al., 2011).

5. Conclusion

We used acoustic sampling to characterize bat activity, diversity, and species richness of bats in different habitat types in the CCR, an economically important agricultural region. Greater bat activity in natural habitat argues for the conservation of remnant natural habitat in agricultural landscapes. Although we did not find differences in bat activity using categorical comparisons of organic and conventional farms, we identified crop diversity as a management practice that drives bat activity and further determined that both crop diversity and less frequent pesticide use enhance insect prey populations for bats. These observed changes in bat activity and insect biomass with changes in crop diversity and frequency of pesticide use provide evidence that small changes in farm management practices can benefit biodiversity conservation. As such, our study provides a more nuanced understanding of which on-farm management strategies or practices are likely to impact conservation outcomes, even when the addition of hedgerows or treelines is not a feasible management option.

Especially important to note is that crop diversification may be a feasible option for many growers because it does not require organic certification or other transformative, system-wide changes that are unlikely to occur in intensive agricultural regions. The long-term conservation of bats in agricultural landscapes ensures that growers continue to benefit from bat-mediated pest-suppression services.

Competing interests

The authors have declared that no competing interests exist.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agee.2018.06.008>.

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