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Remnant trees increase bat activity and facilitate the use of vineyards by edge-space bats

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ABSTRACT

Conversion of natural habitats to vineyard monoculture is rapidly increasing both globally and on the California central coast. Although agricultural expansion typically decreases species diversity and abundance, landscape heterogeneity can maintain biodiversity, ecosystem function, and provide pest control services within agricultural systems. Large remnant oak trees are sometimes retained within vineyards, yet little is known about their value to biodiversity or the beneficial services to grape growers. While insectivorous bats (order: Chiroptera) are natural predators of agricultural pests and commonly utilize trees for foraging and roosting, no study has quantified the influence of remnant trees within vineyards on bat abundance and diversity. During 2014 and 2015, we recorded bat activity and species richness as well as insect abundance at isolated remnant trees and paired open areas within 14 vineyards in coastal central California. We used generalized linear mixed models to assess the influence of remnant trees on total and species-specific bat activity and insect abundance, and how these effects were influenced by individual tree and landscape-scale characteristics. We recorded 11,465 bat passes representing 11 bat species. Overall, bat activity rates were 1.5 times greater at trees compared to open areas. Activity levels of low-frequency echolocators adapted to open habitats did not differ between trees and open areas; however, activity levels of high frequency echolocators adapted to edge habitats were 2.4 times higher at trees than open areas. Bat activity at trees increased with larger tree size, closer neighboring remnant trees, and lower remnant tree density in the surrounding landscape. Our study indicates that remnant trees within vineyards provide important habitat value for bats at the landscape-scale by allowing edge-space adapted bat species access to vineyards. Retention of individual large trees can help to maintain biodiversity and ecological function in vineyard landscapes, a benefit for both conservation and agricultural production.

1. Introduction

Monocultures negatively impact biodiversity and ecosystem processes, frequently resulting in habitat loss, deforestation, and ecological degradation associated with chemical fertilizers and herbicides (Altieri, 2009; Rosset and Altieri, 1997). However, retaining ecological structures in converted landscapes can help maintain biodiversity and ecosystem services such as natural pest control (Fischer et al., 2010; Frey-Ehrenbold et al., 2013; Kelly et al., 2016; Lumsden and Bennett, 2005; Medina et al., 2007). Remnant trees are important ecological structures in many habitats. They maintain bird and insect diversity by providing nesting, roosting, and foraging habitat, and by promoting connectivity for movement of wildlife within agricultural landscapes (DeMars et al., 2010; Dunn, 2000; Kelly et al., 2016; Manning et al., 2006). Remnant oak trees provide direct ecological services such as enrichment of topsoil nutrients, attenuation of extreme temperatures, protection from erosion, and carbon sequestration (Marañón et al., 2016), in addition to aesthetic, cultural, political, and historical values (Blicharska and Mikusiński, 2014; Lindenmayer et al., 2014; Standiford et al., 1986).

Bats have been shown to provide important natural pest control services in a variety of agricultural systems, including maize (Maine and Boyles, 2015), cotton (Federico et al., 2008; Lee and McCracken, 2005; McCracken et al., 2012;), coffee (Williams-Guillén et al., 2008), walnuts (Long et al., 1996; Pollock, 2015), and pecans (Brown et al., 2015). The role of bats as natural insect pest regulators has been valued at $3.7 billion annually to the U.S. agricultural industry (Boyles et al., 2011; Cleveland et al., 2006; Kunz et al., 2011). Yet bat populations

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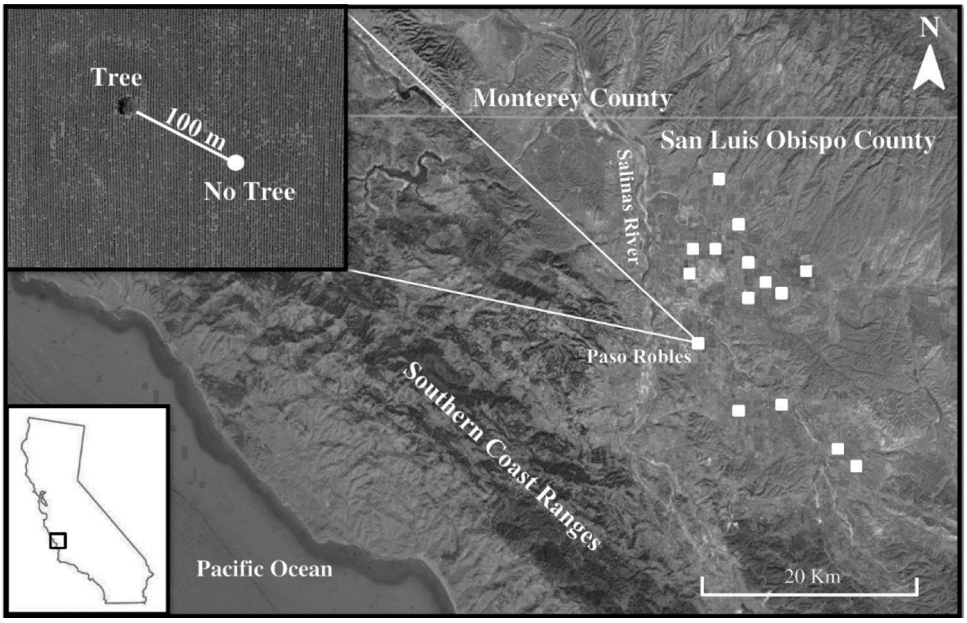

Fig. 1. Map of the study area, showing vineyard locations (small squares) and bat detector location at tree and open sites (large square inset) within each vineyard (Google Earth, 2017).

have declined due to disease, habitat loss and fragmentation, and pollution (Jones et al., 2009; Kunz et al., 2011; Weller et al., 2009). Agricultural development contributes to decreases in abundance and diversity of bat species, mainly by reducing roosting and foraging habitat (Park, 2015). It is therefore important to determine the conditions under which agricultural landscapes can benefit bats, and how bats may benefit agricultural enterprises.

Vineyard acreage has expanded rapidly in California over the past four decades (Merenlender, 2000; Volpe et al., 2010), with the highest rates of increase in the Northern and Central coasts of California (Heien and Martin, 2003). We conducted our study in San Luis Obispo County, on the central coast of California. From 2000 to 2015, wine grape area in San Luis Obispo County doubled from 9,300 to 19,800 ha (San Luis Obispo Department of Agriculture, 2016). Although some vineyards are planted in treeless areas or on former cropland (Merenlender, 2000), grape monoculture often replaces natural oak savanna (Grismer and Caitlin, 2012). Studies in other systems have shown that retaining a wide variety of ecological features (riparian buffers, hedgerows, forest edges, and other remnant vegetation) around agricultural areas results in increased bat activity (Boughey et al., 2011; Fuentes-Montemayor et al., 2013; Heim et al., 2015; Kelly et al., 2016; Lumsden and Bennett, 2005; Park, 2015). Individual trees, in particular, have been shown to provide habitat to bat species in other agricultural systems (Fischer et al., 2010; Frey-Ehrenbold et al., 2013; Heim et al., 2015; Lumsden and Bennett, 2005). However, no study has quantified the value of remnant trees within vineyards for bats.

Isolated trees benefit bats by providing protection from wind and predators, greater insect abundance, and landscape-level connectivity (Frey-Ehrenbold et al., 2013; Heim et al., 2015; Kelly et al., 2016). However, the value of landscape structures to bats can vary among species (Bernard and Fenton, 2007). Wing morphology, echolocation call and foraging behavior of bat species are adapted to certain habitats (Aldridge and Rautenbach, 1987; Denzinger and Schnitzler, 2013; Neuweiler, 1984; Schnitzler and Kalko, 2001; Schnitzler et al., 2003). Typically, smaller and more maneuverable bats forage close to vegetation or edge habitat using higher frequency echolocation calls (≥ 35 kHz). Their high frequency echolocation calls limit the range of prey detection, making foraging less effective in open areas (Heim et al., 2015). Herein we refer to these as edge-space bats. Larger, less maneuverable species typically forage in open spaces and emit low frequency calls (< 35 kHz). These we refer to as open-space bats. Bats that specialize in foraging close to or within vegetation have been found to have higher extinction risks than more flexible aerial hawkers (Jones et al., 2003; Safi and Kerth, 2004).

We investigated whether remnant isolated trees influence bat species activity and diversity, and insect abundance, in 14 vineyards in central-coastal California. We also assessed how characteristics of the surrounding landscape influenced the relationships between bats and remnant trees. We used generalized linear mixed models to compare bat activity, species-specific activity, and insect abundance at remnant trees to nearby open areas in a paired design. We hypothesized that activity of edge-space bat species would be higher around remnant trees in vineyards, and activity of open-space bats would be higher in vineyard areas away from trees. We tested whether prey availability could be driving differences in bat activity. We hypothesized that insect abundance would be higher at trees relative to open areas. We also hypothesized that bat activity would be higher with increasing insect abundance (Dunn, 2000; Ohsawa, 2007). Finally, we hypothesized that overall bat activity at trees would increase with larger tree size, closer proximity to neighboring remnant trees, and with a larger number of remnant trees within 500 m.

2. Study area and methods

2.1. Methods

Our study was conducted from 2014 to 2015 in central-coastal California, in northeastern San Luis Obispo County on a study area of approximately 352 km^2 (120°39′10.43″W - 120°30′1.76″W, 35°44′45.17″N - 35°31′36.95″N; Fig. 1). The climate is Mediterranean, with mild winters and hot, dry summers. Most rainfall occurs between October and May, varying annually and by microclimate from 200 to 1000 mm (National Oceanic and Atmospheric Administration, 2017). The natural vegetation community is oak woodland, which forms a matrix of grassland, chaparral, and woodland areas. Woodland consists of heavily treed areas of blue oak (*Quercus douglassii*) and coast live oak (*Q. agrifolia*) surrounded by oak savanna with scattered blue oak, coast live oak, and valley oak (*Q.lobata*) trees. Throughout the study area, livestock grazing and grape farming are the predominant land uses, accounting for 46% of the land within the county (San Luis Obispo

Department of Agriculture, 2016).

We used Google Earth (2017) to identify vineyards with at least one isolated remnant mature oak tree (treatment) that was > 100 m from another tree, vineyard edge, or anthropogenic feature such as a vineyard road, open water, or building. We paired the treatment area with an open, treeless area (control) within the vineyard that met the same spatial criteria as the treatment area. Paired areas were always within the same vineyard. The distance of 100 m between treatment and control sites helped to ensure similar habitat, topography, soil conditions, ground vegetation, management practices, and microclimate, while being far enough apart to prevent simultaneous detection of an individual bat's echolocation calls in both locations (Frey-Ehrenbold et al., 2013). Of the 20 vineyards that met our study criteria, we received access to 14. For each selected tree, we measured height, diameter at breast height, and canopy radius. We defined canopy radius as the mean of four measurements taken from the trunk to the edge of the canopy in each cardinal direction.

2.2. Bat activity

We recorded echolocation calls of bats using Anabat II bat detectors (Titley Electronics Ballina, NSW, Australia). Detector microphones were attached to a metal pole and positioned 3 m above the ground. The effective range of detection of echolocation calls using this device varies with bat species, vegetation clutter, and atmospheric conditions, but a reasonable estimate is 2–50 m. Polycarbonate sound reflector plates on the microphone enclosures ('bat hats'; EME System, Berkeley, California) were positioned at a 45-degree angle to the ground, while microphones were directed straight down so that the angle of call reception was directed upward at 45 ° (Weller and Zabel, 2002; Fig. 2). The height and orientation of the microphones was selected to record echolocation calls of bats flying above the height of the grape vines. Microphones were connected via Canare LE5-C microphone cable to bat detectors and ANABAT storage Zero-Crossings Analysis Interface Modules (Z-CAIMs), which were stored in weather- and dust-proof containers. We powered detectors using 10 W solar panels. To maximize solar exposure, we attached the detection system to a vine post approximately 30 cm beyond the canopy on the south side of the tree, and oriented the microphone south. This orientation provided both maximum solar exposure during the daytime and unobstructed vertical exposure to bat passes above the vineyard. An identical echolocation recording system was deployed similarly at open areas.

Echolocation recorders were programmed to operate from sunset (18:51–20:22 Pacific Daylight Time or PDT) to sunrise (5:47–6:55 PDT). To control for night-to-night variation in bat activity resulting from factors such as weather or insect emergences, we deployed echolocation detection systems concurrently and for equal time at trees and open areas within a vineyard (Hayes, 1997). Sampling effort of bat activity differed between years, with 5 vineyards sampled from 14 July to 21 September in 2014, and 13 vineyards sampled from 5 May to 28 September in 2015. Four vineyards were sampled in both years. Detectors were deployed for a mean of 6 (SE = 0.254, range = 3–15) consecutive nights within each vineyard. To account for seasonal or stochastic changes in bat activity levels and species composition, we resurveyed each vineyard 2–5 times (median of 3), resulting in a range of 13–35 survey nights per vineyard (median of 20).

We viewed time-frequency sonogram recordings using AnalookW (version 4.1z, Titley Scientific 2016) with division ratio set to 8. Potential bat echolocation calls were separated from non-bat ultrasound via use of two filters. The first filter identified sounds with frequencies ≥ 20 kHz and durations > 2 ms. The second filter identified sounds ≥ 7 kHz and duration ≥ 5 ms (Weller and Baldwin, 2012). Each file that passed either filter was visually inspected to determine whether it was a bat pass. We defined a bat pass as either a series of ≥ 2 echolocation calls each with duration ≥ 2 ms or a single echolocation call with duration ≥ 5 ms. We then used a subsequent set of filters to assign each file (bat pass) to either a high frequency (≥ 35 kHz, hereafter HiF) or low frequency (< 35 kHz; LoF) category (Weller and Baldwin, 2012), which roughly distinguished edge-space from open-space species in our study area according to frequency groups defined by Denzinger and Schnitzler (2013).

Fig. 2. Echolocation recording device at a tree site. The Anabat II detector echolocation microphone with a polycarbonate sound reflector plate is mounted at the top of a 3m metal post. The detector and battery (charged by a 10 W solar panel) are contained within a weather-proof container that is connected to and hangs from the post. (Photo by S. Giordano).

We then identified bat passes to species using a multi-step process. First, we used a set of filters designed for use with the AnalookW software for identifying echolocation calls from the 19 species of bats identified in this region of California (Chris Corben in litt.). We then used the open-source software BatID (Kitzes and Merenlender, 2014) to cross-validate species identification. BatID was designed to identify California bat species from their echolocation call parameters as recorded using Anabat detectors. We set the maximum quality parameter in BatID to 0.5 and the minimum probability parameter to 0.75. When Anabat filters and BatID agreed on species identification, we accepted it after confirming species identity via manual vetting on a subset of files. For bat passes where the approaches were not in accordance, we generally assigned passes to frequency groups according to the characteristic frequency (frequency of the call at its lowest slope) determined by AnalookW. For less common species, those for which there were ≤ 20 passes by either species identification method, we visually inspected each file and assigned it to a species or frequency group. Passes identified to species were also assigned to the HiF and LoF frequency groups (Table 1).

2.3. Insect sampling

We sampled flying insects at tree and open areas with 15 × 30-cm

Table 1
Bat pass assignments to individual species within frequency categories HiF = minimum frequency ≥35 kHz; LoF < 35 kHz.

Species	Common Name	Characteristic Frequency Range (kHz)	Frequency Category	Passes (tree)	Passes (open)
Myotis yumanensis	Yuma myotis	47–53	HiF	3	2
Lasiurus blossevillii	Western red bat	40–55	HiF	1117	14
Parastrellus hesperus	Canyon bat	43–50	HiF	136	15
Myotis ciliolabrum	Western small footed bat	37–44	HiF	1	0
Antrozous pallidus	Pallid bat	28–34	LoF	5	16
Eptesicus fuscus	Big brown bat	24–34	LoF	3	7
Tadarida brasiliensis	Mexican free tailed bat	18–34	LoF	1161	851
Lasiurus cinereus	Hoary bat	16–32	LoF	56	38
Nyctinomops femorosaccus	Pocketed free tailed bat	14–19	LoF	3	0
Nyctinomops macrotis	Big free tailed bat	12–15	LoF	1	2
Eumops perotis	Western mastiff bat	6–12	LoF	2	1

Yellow Card Sticky Traps (Gempler's, Inc., Janesville, WI) attached to the top of a 5-m telescoping pole. The pole was attached to the same vineyard post that supported the echolocation detector microphone. Insect traps were deployed and collected on the same schedule as the echolocation recorders, and were available to capture insects both day and night. Placement of a trap for a full day (24 h) was designated as one trap-day. Sampling during the day introduced a confounding factor, as diurnal insects are not available to night-foraging bats.

We counted the total number of insects on each trap card with the aid of 2.5x and 16x magnifying lenses. We then overlaid each trap with an acetate sheet outlined with five circles of randomized variable diameter that comprised 40% of the trap card. We used a 5x–45x binocular scope to identify to order all insects within the 5 circles. We grouped insects into seven orders: Diptera, Coleoptera, Hymenoptera, Lepidoptera, Thysanoptera, Hemiptera, and the suborder Homoptera.

2.4. Landscape data

We collected landscape data using ArcGIS 10.1 (ESRI, Redlands, USA) following methods used in previous studies (Heim et al., 2015; Kelly et al., 2016) to determine distance, in meters, from each study tree to nearest remnant tree and forest patch. Forest patches were defined as a continuous block of trees with an area of 6000 m^2 or greater. Remnant trees were > 100 m from another tree, vineyard edge, or anthropogenic feature such as a vineyard road, open water, or building. We also counted the number of remnant trees within a 500 m radius of each study tree.

2.5. Statistical analyses

We used Generalized Linear Mixed Models (GLMMs) to determine the effect of trees on bat activity. Statistical analyses were conducted in R version 3.5.0 (R Development Core Team, 2017). We used bat passes per night as our primary response variable, a metric that is an index of bat activity but not abundance (Hayes, 1997). For our primary analysis, our main fixed effect was tree (tree or open area). Using R package lme4 (Bates et al., 2015), we ran models for total bat activity, HiF, LoF, and for the four most commonly-recorded species – Mexican free-tailed bat (*Tadarida brasiliensis*), canyon bat (*Parastrellus hesperus*), hoary bat (*Lasiurus cinereus*), and western red bat (*Lasiurus blossevillii*), which constituted 98.7% of all bat passes identified to species. We also ran models for total insect abundance and for the six separate insect orders and the suborder Homoptera, with insect count per survey session as the response variable.

To assess how individual tree and landscape characteristics affect bat activity at remnant trees within vineyards, we modeled bat passes per night at trees as the response variable. Predictor variables included tree size, number of remnant trees within a 500 m radius, distance to nearest remnant tree, and distance to nearest forest patch. Predictor variables were not highly correlated (variance inflation factor = 1.56). Using the global model with all explanatory predictors, we generated all possible candidate sets of models using the *dredge* command in the MuMIn package (Barton, 2009). In cases where there were many top-ranking models with no obvious best model (ΔAIC < 2), we used model-averaging to obtain coefficient estimates with 95% confidence intervals.

Because our response variables were discrete count variables, we used a Poisson GLMM with a log link function to model the relationship between bat activity (or insect abundance) and predictor variables. Overdispersion was present in all models except for hoary bat activity. Therefore, we used the zero-inflated negative binomial distribution as a more suitable GLMM for all models (except for hoary bat activity) using the R package glmmADMB (Fournier et al., 2012). We extended our GLMM with a random effect for individual vineyards to account for repeated counts at vineyards over time, a fixed effect of treatment nested within random effect of vineyard to account for pairing of tree and open areas, a fixed effect of month within year to account for seasonal or monthly effects, and a fixed effect of year. We evaluated the significance of random effects in our models by using a parametric bootstrapping approach (1000 simulations). We considered coefficients with confidence intervals that did not overlap zero to be important predictors. To compare effect sizes among predictors, we standardized all continuous predictors to a mean of 0 and SD of 1.

3. Results

3.1. Total bat activity and frequency groups

During 40 recording sessions comprising 206 detector-nights, we recorded 11,465 bat passes, of which 39% were identified as HiF and 61% as LoF species. Total bat activity was 1.45 times higher at trees than open areas (Table 2; Fig. 3). HiF bat activity was 2.39 times higher

Table 2
Coefficient estimates for treatment predictor variable (tree or open area) from generalized linear mixed models of bat passes/night in central California coast vineyards. Full model formula is bat passes/night ~ Treatment + Year + (1|Vineyard) + (1|Vineyard:Treatment) + (1|Month). Estimates and 95% confidence intervals are provided for total bat passes/night, HiF and LoF bat passes/night, and the four most common species: the Western red bat (*Lasirurs blossevillii*), canyon bat (*Parastrellus hesperus*), Mexican free-tailed bat (*Tadarida brasiliensis*), and hoary bat (*Lasiurus cinereus*) passes/night. The coefficient estimate is the increase in the expected log count of bat passes relative to the reference level (Open area).

Model	β coefficient (Treatment)	95% CI
Total bat activity	0.37	(0.05, 0.68)
HiF bat activity	0.87	(0.42, 1.31)
LoF bat activity	−0.006	(−0.22, 0.21)
Lasiurus blossevillii	1.24	(0.29, 2.19)
Parastrellus hesperus	1.32	(0.34, 2.31)
Tadarida brasiliensis	−0.005	(−0.23, 0.22)
Lasiurus cinereus	−0.09	(−0.77, 0.58)

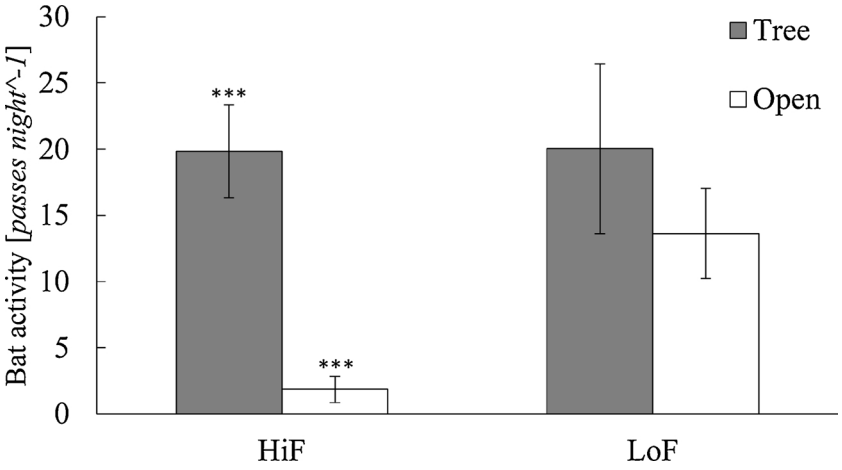

Fig. 3. Mean number of bat passes per night (mean ± 95% CI) of high frequency (HiF, ≥ 35 kHz), or edge-space bat species, and low frequency (LoF, < 35 kHz), or open-space bat species at tree and open sites within fourteen vineyards in San Luis Obispo County, California in 2014 and 2015. Differences in group-specific activity patterns were assessed by fitting generalized linear mixed effects models and are indicated by (***) at $P < 0.001$.

at trees (Table 2; Fig. 3). LoF bat activity did not significantly differ between tree and open areas (Table 2; Fig. 3). In models of total activity as well as activity of HiF and LoF species, random effect of vineyard, nested effect of treatment within vineyard, and nested effect of month within year were significant.

3.2. Bat species activity

Overall, we assigned 33% of passes to 11 species (Table 1), of which 4 were HiF species. Of these, western red bats comprised 87.8% and canyon bats comprised a further 11.7% of HiF bat passes. We identified 7 LoF species, with Mexican free-tailed bats comprising 94%, and hoary bats comprising 4% of the LoF passes identified to species. All 11 species were found at trees, while 9 species were found in open areas. Western red bat were 3.46 times and canyon bat activity levels were 3.74 times higher at trees than open areas (Table 2; Fig. 4). Activity rates of Mexican free-tailed and hoary bats did not differ between trees and open areas (Table 2; Fig. 4).

3.3. Tree and landscape characteristics

Among the focal trees in the 14 study vineyards, 10 were valley oaks and 4 blue oaks. Mean diameter at breast height (dbh) was 98.7 ± 19.6 cm (range: 68.6–142.2 cm); mean tree height was 18.0 ± 5.0 m (range: 11.0–31.1 m); and mean canopy radius was 8.7 ± 2.3 m (range: 6.4–15.9 m). Coefficients of variation were 0.20 for dbh, 0.28 for height, and 0.26 for canopy radius.

Tree height was correlated with canopy radius and tree dbh so we used a single allometric index called tree conicity (hereafter tree size) by taking the product of tree height and dbh. The two top-ranking models included tree size, remnant tree density, distance to nearest remnant tree, and distance to nearest forest patch (Table 3). The full model set is presented in Supporting Information (Table 1S). All model-averaged coefficient estimates were significant except for nearest forest patch, which was not significant (Table 4). Total bat activity was 2.1 times higher with every unit increase in tree size. As an example, a tree that is 11 m^2 in size was estimated to have 2.1 times more bat activity than one that is 10 m^2 in size. Higher total bat activity at trees was observed with decreasing distance to nearest remnant tree and with lower remnant tree density within a 500 m radius (Table 4).

3.4. Insects

Overall insect abundance was not different between trees and open areas during 204 insect trap-days. Of the seven insect groups, Thysanoptera and Hemiptera were found in larger numbers at open areas, whereas Hymenoptera, Homoptera and Diptera were found in larger numbers at trees (Table 5; Fig. 5). Abundance of Coleoptera and Lepidoptera did not differ between trees and open areas (Table 5). There was no relationship between insect counts and bat activity per insect survey session at trees or open areas.

4. Discussion

We found that bat activity at remnant isolated oak trees within central California vineyards was greater than at nearby treeless areas of these vineyards. This relationship was driven largely by activity of bats that echolocate at higher frequencies and are typically associated with vegetation edge habitats. In a close ecological analog to our study, a study in northern California found that total bat activity was 2.3 times

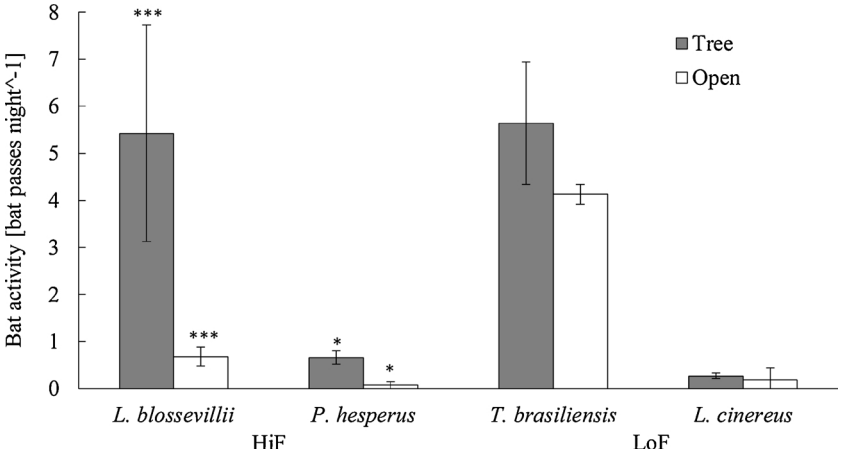

Fig. 4. Mean number of bat passes per night (mean ± 95% CI) for bat species comprising the majority of identifiable bat activity within fourteen vineyards of San Luis Obispo County, California in 2014 and 2015. Differences in species-specific activity patterns were assessed by fitting generalized linear mixed effects models and are indicated by (***) $P < 0.001$, (*) $P < 0.05$.

Table 3
List of top-ranking (ΔAIC < 2) generalized linear mixed model of total bat passes/night at trees in central California coast vineyards. The best fitting model for total bat passes/night at trees were negative binomial generalized linear models. Predictor variables included tree size, number of isolated trees within a 500 m radius, distance to nearest remnant tree, and distance to nearest forest patch.

Top models for total bat passes/night at trees	AIC	Delta AIC	Weight
nearest.forest + remnant.tree.density + tree.size	4913.2	0	0.225
nearest.forest + nearest.remnant.tree + remnant.tree.density + tree.size	4913.6	0.34	0.217

Table 4
Model-averaged coefficient estimates and 95% confidence intervals for significant predictors from the top-ranking (ΔAIC < 2) generalized linear mixed model of total bat passes/night at trees within central California coast vineyards.

Predictor	β Coefficient	95% CI
Tree size	0.74	(0.59, 0.89)
Nearest forest patch	−0.0008	(−0.14, 0.14)
Nearest remnant tree	−0.05	(−0.02, −0.08)
Remnant tree density	−0.25	(−0.40, −0.11)

Table 5
Coefficient estimates for treatment predictor variable (tree or open area) from generalized linear mixed models of insect counts per session in central California coast vineyards. Full model formula is insect counts/session ~ Treatment + (1|Vineyard) + (1|Vineyard:Treatment). Estimates and 95% confidence intervals are provided for total insect counts/session and the seven separate insect orders Coleoptera, Diptera, Hemiptera, Homoptera, Hymenoptera, Lepidoptera, and Thysanoptera. The coefficient estimate is the increase in the expected log count of insects relative to the reference level (Open area).

Predictor (insect abundance)	β coefficient (Treatment)	95% CI
Total	0.16	(−0.17, 0.49)
Coleoptera	0.40	(−0.30, 1.07)
Diptera	1.24	(0.68, 1.81)
Hemiptera	−1.25	(−1.88, −0.64)
Homoptera	0.57	(0.03, 1.10)
Hymenoptera	1.13	(0.70, 1.56)
Lepidoptera	1.79	(−1.15, 4.73)
Thysanoptera	−0.91	(−1.53, −0.29)

higher near blocks of remnant vegetation along vineyard edges as compared to within the vineyards (Kelly et al., 2016). Thus, our study extends the conclusions of Kelly et al. (2016) by showing that in addition to habitat patches, individual large trees can help retain bat diversity in vineyard landscapes.

As we predicted, HiF bat species activity was greater at remnant trees than open areas within our study vineyards, while LoF bat species had similar levels of activity at remnant trees and open areas. HiF bats in our study area are typically edge-space adapted bat species that are more maneuverable than LoF bats. These bats tend to forage close to vegetation or edge habitat as their high frequency echolocation calls limit the range of prey detection, which makes foraging less effective in open areas (Heim et al., 2015). Our results suggest that large remnant trees in vineyards provide HiF bat species with habitat they otherwise may not use in agricultural landscapes.

We detected a similar number of bat species at trees (11 species) compared to open areas (9 species). However, the two most common HiF species, western red bat and canyon bat, had significantly higher bat activity at trees, with 99% of western red bat and 90% of canyon bat passes recorded at trees. This suggests that remnant trees allowed these species to make greater use of vineyard interiors. Similar results have been found in two agricultural landscapes in Australia. In the first, although all species were detected in treeless areas within cropland and pastures, activity levels for 8 of the 10 species around trees accounted for 93% of their total activity (Lumsden and Bennett, 2005). In the other, bat species richness more than doubled and bat activity increased by as much as 10 times in a livestock grazing landscape when 1–2 trees were present compared to areas without trees (Fischer et al., 2010). Thus, although differences in species richness between agricultural habitats with and without remnant trees may be modest, the presence of even a single remnant tree can lead to significantly greater activity levels by some bat species (Frey-Ehrenbold et al., 2013; Fuentes-Montemayor et al., 2013). Our results confirm that individual trees within vineyards function similarly and provide value in the maintenance of biodiversity (Fischer et al., 2010; Manning et al., 2006).

Contrary to our predictions, insect abundance did not differ between trees and open areas and did not predict activity of insectivorous bats. Similarly, studies in woodland remnants of Scotland (Fuentes-Montemayor et al., 2013) and farmlands of Australia (Lumsden and Bennett, 2005) found no relationship between insect abundance and bat activity. This suggests that the resource value provided by trees is more than simply a source of prey for bats. However, our results may have differed had we sampled only nocturnal insects. Because we did not evaluate bat diet nor identify insects to species, we do not know which of the insects we trapped in our central California vineyards were included in the bats' diet. We captured significantly more insects from the order Hemiptera, containing common vineyard pests such as planthoppers, mealybugs, and the western grape leafhopper (*Erythroneura*

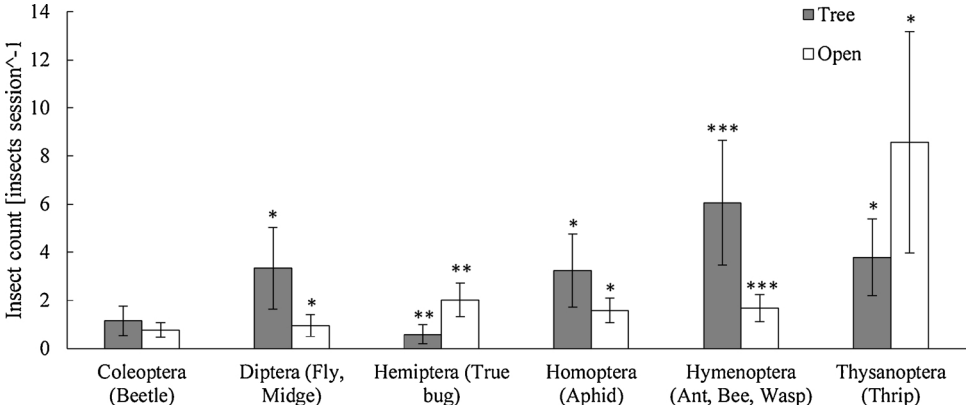

Fig. 5. Total number of insects, by order, captured at tree sites and open sites within fourteen vineyards in San Luis Obispo County, California during May to September in 2014 and 2015. Differences in group-specific insect activity patterns were assessed by fitting generalized linear mixed effects models and are indicated by (***) P < 0.001, (**) P < 0.05, (*) P < 0.01. Note that results for Lepidoptera are not presented due to low abundance. (***) P < 0.0001, (**) P < 0.01, (*) P < 0.05.

elegantula), at open areas. Bats consume insects from the orders Hemiptera and Lepidoptera within other agricultural landscapes (Williams-Guillén et al., 2016). Although ecosystem services provided by bats in vineyards have yet to be quantified, it is likely that higher activity by a greater breadth of bat species will result in a larger number and wider variety of nocturnal insects predated by bats. Hence, in addition to enhancing biodiversity in vineyards, remnant trees may facilitate ecosystem services provided by bats (Boyles et al., 2011; Kunz et al., 2011).

All remnant trees in our study were relatively large, and we found significant positive associations between tree size and overall levels of bat activity at trees. Taller trees with wider canopies are more conspicuous on the landscape and bats may explore these trees as sentinel locations where they can expect to find improved foraging conditions, interactions with other bats (Cryan and Brown, 2007), or roosting opportunities. Improved foraging conditions may result from greater protection from wind, cover from predators (Galindo-González and Vinicio, 2003; Rydell et al., 1996; Verboom and Spoelstra, 1999) or, although not the case in our study, a richer source of insect prey (Merckx et al., 2010). Bats adapted to narrow spaces or habitat edges are typically smaller and have less powerful flight than open-space bats, and thus may seek the leeward side of trees with wide canopies for a windbreak when foraging or crossing large open spaces (Boughey et al., 2011; Verboom and Spoelstra, 1999). Hence, bats may also use these trees as stepping stones of habitat or navigational reference points within the agricultural matrix to provide connectivity between important resources (e.g., roosts, water, foraging areas; Frey-Ehrenbold et al., 2013; Lindenmayer, 1999; Williams-Guillén and Perfecto, 2010). As such, remnant trees may represent connecting habitat elements that facilitate use by bats of open areas that they may otherwise avoid (Heim et al., 2015).

We found that the role of remnant trees for bats may differ according to surrounding landscape features. The influence of remnant trees was greater with closer proximity to neighboring remnant trees, indicating that nearby trees provide local connectivity for bat species and suggesting that a minimum level of local habitat integrity may be necessary for positive impacts of remnant trees on bat activity and diversity to be realized. This result is supported by other studies that indicate that retaining natural vegetation and remnant habitat around agricultural areas (e.g. hedgerows, riparian buffers) results in increased bat activity (Boughey et al., 2011; Fuentes-Montemayor et al., 2013; Heim et al., 2015; Lumsden and Bennett, 2005; Park, 2015). However, the influence of remnant trees was greater with lower density of remnant trees, indicating that these trees hold an especially high value for bats when the surrounding landscape is sparse and has few trees. In other systems, the marginal value of individual remnant trees to bats was also larger when density of remnant trees was lower (DeMars et al., 2010; Fischer et al., 2010; Lumsden and Bennett, 2005; Mazurek and Zielinski, 2004). Distance to nearest forest patch did not significantly affect bat activity at trees within vineyards. A possible reason for this could be because our study was in a highly agriculturally developed area, where distance to nearest forest patch was generally large.

Our study adds California vineyards to the list of agricultural landscapes where the presence of even a single large tree can help ameliorate the effects of habitat fragmentation on biodiversity loss (Lumsden and Bennett, 2005; Fischer et al., 2010; Kalda et al., 2015). Large trees provide historic, cultural, and aesthetic value to the landscapes they inhabit (Blicharska and Mikusiński, 2014) and our study demonstrates that they also provide habitat value to multiple bat species and allow a more diverse and potentially vulnerable group of bat species to use the interior of vineyards for foraging and perhaps other habitat requirements. Although we found that remnant trees in vineyards benefit bat biodiversity and provide habitat value to bats, we caution that this finding may not be universal and retention of individual trees may represent a minimum contribution to provision of wildlife habitat in agricultural landscapes (Fischer et al., 2010; Frey-Ehrenbold et al., 2013; Heim et al., 2015; Kalda et al., 2015). Specifically, although we found higher levels of the HiF group at remnant trees, we only identified two species, western red bat and canyon bat, that had greater species-level activity at trees. Up to five other HiF species could be present in the vicinity of our study, but we either recorded them occasionally or not at all. Additionally, activity of LoF species was not higher around remnant trees.

As conversion of natural habitats to agricultural production continues to increase, it is important to find ways to retain some of the biological integrity of these lands. Retention of some of the species and structures that help maintain ecological function is likely to result in agroecosystems that concomitantly benefit wildlife and the agricultural producer. An important step in this process is communicating to land owners and regulators the value of natural landscape elements for ecosystem function and how their retention can provide benefits in terms of aesthetic values, biodiversity conservation, landscape-level connectivity, and potential natural pest control services.

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Conflicts of interest

None.

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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.2019.05.008.

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