



Enhanced crop diversity but not smaller field size benefit bats in agricultural landscapes

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Abstract

Context Farmland biodiversity continues to decline due to the expansion and intensification of agriculture. Historically, efforts to conserve farmland biodiversity have focused on conserving habitats outside agricultural production areas. More recently, attention has turned to the conservation potential of the cropland matrix, where reducing field size and increasing crop diversity to promote crop heterogeneity can significantly benefit farmland biodiversity. Bats are one group of farmland species that have experienced dramatic declines over recent decades.

Objectives Here we investigated the effects of crop heterogeneity (crop diversity, field size) and landscape structural elements (e.g. length of linear

structures, distance to forest, proportion of semi-natural habitat) on the activity of bat functional groups.

Results Increasing crop diversity led to greater bat activity, especially for open space foraging bats. However, contrary expectations, bat activity was not affected by heterogeneity in crop configuration, i.e. field edge density. Furthermore, structural landscape elements, including hedgerows and distance to forest, were important predictors of bat activity, especially for species that hunt in highly cluttered spaces. While crop diversity clearly benefited bat activity, the lack of effect of crop configurational heterogeneity on bat foraging activity may suggest heterogeneity-area trade-offs and intensive pesticide use in small-scale vegetable production.

Conclusions Therefore, in addition to maintaining high levels of crop diversity, promoting hedgerows and tree lines between farmland and woodland may facilitate bat activity across the agricultural landscape matrix. The combination of high crop heterogeneity and structural elements provides favorable hunting grounds for bats and may promote their conservation in agricultural landscapes.

Collection: Effects of agricultural landscapes on biodiversity, ecosystem services, and yield

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Introduction

Farmland biodiversity is on a continued decline due to the expansion and intensification of agriculture (Tscharntke et al. 2005; Newbold et al. 2015). In many landscapes, agricultural intensification has led to homogenous landscapes with large, intensively managed fields, and low crop diversity. Historically, efforts to conserve farmland biodiversity have concentrated on preserving natural and semi-natural habitats outside of agricultural production areas, but ongoing biodiversity losses within and outside of protected areas indicate that these efforts have been insufficient to slow down or even reverse declines (Brooks et al. 2012; Hallmann et al. 2017; Seibold et al. 2019; Grass et al. 2021).

Recently, attention has turned to the conservation potential of the cropland matrix (Fahrig et al. 2011; Clough et al. 2020). Reducing field size and increasing crop diversity to promote crop heterogeneity can have significant benefits for farmland biodiversity (Fahrig et al. 2015; Batáry et al. 2017; Sirami et al. 2019).

This being said, our understanding of the potential benefits of cropland heterogeneity remains limited. Increasing heterogeneity generally positively affects biodiversity (Stein et al. 2014). However, as heterogeneity increases, the effective area available to individual species decreases. The resulting area-heterogeneity trade-off may create unimodal or even negative relationships between species richness and habitat heterogeneity (Kadmon and Allouche 2007; Allouche et al. 2012) but so far has received little attention in studies of agricultural landscapes. Potential trade-offs may arise from the inclusion of crops that are unsuitable for species in landscapes with high crop diversity (e.g., crops that do not provide resources to animals; (Hass et al. 2018)) or from a reduction in the effective area available for species in landscapes with highly fragmented and small fields (Kadmon and Allouche 2007; Allouche et al. 2012).

Bats are a group of farmland species that have seen dramatic declines in species diversity and populations over the past decades. In Europe, 40% of the 45 bat species are listed as threatened or near threatened on the Red List of endangered species and only 13 species show stable population trends (Barova and Streit 2018). These declines occur despite all European bat species being listed

on Annex IV of the Habitats Directive, requesting European Member States to avoid destruction of hibernation and roosting places, and to undertake positive conservation measurements to ensure their populations (Barova and Streit 2018). Bats are also important for agricultural pest control, with an economic value to the US agricultural industry estimated between \$3.7–\$53 billion/year (Boyles et al. 2011).

In agricultural landscapes, bats need suitable habitats for roosting and foraging. Recent research has shown that bat activity and species richness are linked to structural landscape elements, including hedgerows and tree lines, as well as proximity to forest (Frey-Ehrenbold et al. 2013; Heim et al. 2015). Moreover, bats may benefit from increased crop heterogeneity (compositional as well as configurational), which increases the availability of prey insects (Monck-Whipp et al. 2018; Tortosa et al. 2023). However, the benefits of cropland heterogeneity are likely to differ between bat species that differ in foraging strategies and in particular their ability to forage in open, edge, and highly cluttered or narrow spaces (Schnitzler and Kalko 2001; Denzinger and Schnitzler 2013). While open space foraging bats are not strictly dependent on structural landscape elements for moving through the landscape, edge and narrow space foraging species frequently use forest edges and linear structures such as hedgerows for movement and foraging (Boughey et al. 2011). In addition, homeranges of narrow space foraging species are substantially smaller than those of open space foragers, whereby narrow space foragers are often reluctant to cross open fields and highly dependent on connecting structural elements (Browning et al. 2021). Whether and how a greater heterogeneity of the crop matrix in addition to linear structures and proximity to forests benefits bats in agricultural landscapes is still poorly understood.

Here we studied the effects of crop heterogeneity (crop diversity, field size) and landscape structural elements on activity of bat functional groups. We expected bat activity of edge and narrow space hunting bats to increase in landscapes characterized by smaller fields and high amount of linear elements. By contrast, we expected the activity of open space hunting bats to be mostly related to crop diversity of the agricultural landscape matrix and less dependent on structural landscape elements.

Methods

Study area

This study was conducted in the agricultural landscapes surrounding the city of Stuttgart in Southwestern Germany. We identified 32 study landscapes of (500 m × 500 m each (Fig. S1) with an average pairwise-distance of 37 km ± 18 km (min: 745 m, max: 81 km). These landscapes were composed of at least 67% (average 85%) agriculturally used area and differed in composition (number and identity) and configuration (fragment size and arrangement) of arable fields. We used the effective Shannon-diversity of crops as measure of crop composition and the edge length (as a proxy for field size) as a measure of crop configuration. Pre-selection of landscapes was based on a land-use map from 2020 provided by the Baden-Württemberg Ministry of Agriculture and aimed for independent gradients of crop composition and configuration. Crop identity was then reassessed by local inspection in June and July 2021, and the variables for landscape complexity were recalculated (Tables S1 and S2). The most dominant crop types in our study landscapes were winter soft wheat, winter barley, and silage maize (28.3%, 20.0%, and 19.1%, respectively).

Acoustic survey and analysis

We monitored bat activity with automated acoustic recorders (Audiomoth®, v1.1.0, Hill et al. 2018) on seven nights at each landscape in May and June 2021. Simultaneous recordings across two temporal blocks (18 and 14 landscapes, respectively) allowed us to minimize the effects of variations in temperature and cloud cover. The number of landscapes sampled simultaneously was determined by the available recording devices, ensuring that the gradient of crop heterogeneity was covered each time. Each Audiomoth was configured to record 30 s every 2 minutes from 20:30 pm to midnight, during the first peak in nightly foraging-activity of bats (Rydell et al. 1996; Hayes 1997), at a sample rate of 192 kHz, resulting in a total of 105 recordings per site and night.

We defined a “bat pass”, which was our measure for bat activity, as a 5 s recording of two or more pulses from a single bat species/sonotype (Torrent et al. 2018). Feeding buzzes or social calls were not included in our analysis. We edited all 30 s

WAV recordings generated by the Audiomoths into 5 s snippets using Kaleidoscope v5.3.9 (Wildlife Acoustics, USA). Using the same program, we then applied a pulse detection algorithm to select recordings containing at least two pulses (frequency range: 17–96 kHz, pulse length 2–500 ms). All automatically selected recordings were manually reviewed, and if more than one bat/sonotype was detected in a single recording, we counted each as a single bat pass. We identified bat species based on call structure and measurements, and comparing them with published data (Parsons and Jones 2000; Obrist et al. 2004; Marckmann and Pfeiffer 2020, 2022). In cases where the echolocation call parameters could not be assigned to a specific species, we formed groups of acoustically similar species. We clearly identified the echolocation sequences of *Pipistrellus pipistrellus*, *P. pygmaeus*, and the sonotype *P. nathusii/kuhlii*, as *P. kuhlii* has become more common in our study area and the call parameters of *P. nathusii* and *P. kuhlii* overlap almost completely (Marckmann and Pfeiffer 2020). In addition, we could confidently assign bat calls with a characteristic frequency below 21 kHz to *Nyctalus noctula*, while we grouped similarly structured calls above this threshold to the sonotype nyctaloid. Frequency-modulated calls typical of bats of the genus *Myotis* were all assigned to the *Myotis* sonotype. Finally, we assigned all bat passes to three ecologically and behaviorally distinct foraging guilds: open space forager (*N. noctula* and nyctaloid), edge space forager (*Pipistrellus* spp.) and narrow space forager (*Myotis* spp.) (Schnitzler and Kalko 2001; Denzinger and Schnitzler 2013).

Landscape variables

For each landscape, we calculated two measures of crop heterogeneity: composition (crop diversity) and configuration (field size). We estimated the total length of linear structures (rows of trees and hedge rows) and the amount of semi-natural habitat (e.g. fallow land, orchards) within a 500 m buffer around our audio recorder, as well as the distance to the nearest forest. The size of the buffer radius was selected to complement our crop heterogeneity variables and aligns with approaches commonly used in studies on bat activity and landscape features (Heim et al. 2015; Tortosa et al. 2023). Additionally, we included the length of continuous linear structures

accessible within a 50 m radius of our audiomoths (local linear structures) as a variable in our analysis. All structural landscape variables (Table S2) were calculated using QGIS (v3.22.7, QGIS Development Team (2023)) and satellite images from the year 2021 (Google Earth).

Statistical analysis

All statistical analyses were performed using the R software, version 4.2.2 (R Development Core Team (2023)). To identify the variables influencing the activity of bats, we used generalized mixed effect models with a negative binomial data distribution and corrected for zero-inflation, if necessary (function `glmmTMB()`, R package `glmmTMB`; Brooks et al. 2017). Due to pronounced ecological and physical differences, we also calculated a separate model for each foraging guild. We included *crop composition*, *crop configuration* and their interactions as well as the *total length of linear structures*, the *local length of linear structures*, the *amount of semi-natural habitat*, the *distance to the nearest forest*, and the *recording round* as explanatory variables in our models. We included the variable *recording round* as a fixed factor because there were insufficient levels to treat it as a random intercept, while still allowing us to account for variation between the two sampling events. Finally, we included the landscape identity as random intercept to address repeated sampling at the same locations. We log-transformed the variables *local length of linear structures* and *distance to nearest forest*, and scaled all continuous variables to account for differences in magnitude (function `scale()`, R package base). Model assumptions were confirmed by checking the homogeneity of variance and normality of residuals and all models were tested for multicollinearity of predictor variables (function `check_model()` and `check_collinearity()`, R package performance; Lüdecke et al. 2021). We further calculated Moran's I (function `Moran.I()`, R package ape; Paradis and Schliep 2019) to check model residuals for spatial autocorrelation of variance in the foraging activity of bats. For all models, we further calculated pseudo- R^2 values to estimate the variation explained by fixed and random effects

(function `r2()`, R package performance; Lüdecke et al. 2021).

Results

We recorded a total of 23,520 audio files, summing up to 196 h of audio recordings. From these, we identified a total of 3727 bat passes of which edge space hunting bats were the most commonly identified foraging guild (76.1%), followed by open space hunters (19.2%), and narrow space hunters (4.7%) (Table S3). Overall, the Common Pipistrelle (*P. pipistrellus*) was with 2817 passes the most commonly recorded bat species (Table S3). We further counted a total of 402 feeding attempts, which can be identified based on a typical change in the echolocation behavior (feeding buzz) (Schnitzler and Kalko 2001). The number of feeding buzzes was highly correlated with bat activity (Pearson $r=0.70$, $p<0.001$), suggesting that bat activity can be used as a measure of foraging habitat quality (Heim et al. 2015). Bat activity within landscapes ranged from 0.6 to 87.3 passes/night, with an average of 16.6 bat passes/night (Table S3).

All models fulfilled model presumptions to our satisfaction. Crop configuration and crop composition did not show any significant correlation (Pearson $r=0.26$, $p=0.15$) and variance inflation factors (VIF) for all variables in each model were very low (Table 1), indicating no collinearity issues (Lüdecke et al. 2021). There was further no indication for spatial autocorrelation in the variance in the activity of open space (Moran's I: -0.011 ; $p=0.49$), edge space (Moran's I: -0.002 ; $p=0.80$), and narrow space (Moran's I: -0.002 ; $p=0.75$) hunting bats. As we did not find any significant interaction between crop configuration and crop composition we dropped this interaction term in all models.

As expected, the importance of crop configuration, crop composition, and structural landscape elements for bat activity was foraging guild-specific. While the configurational heterogeneity did not affect bat activity at any level, crop composition had a significant effect on the activity of open space hunting bats, which increased by 405.7% with an increase from three to six crop species (Fig. 1). Although only marginally significant, also narrow space foraging bats showed this activity pattern ($p=0.08$; increase by 371.4%).

Table 1 Results from generalized linear mixed effects models for the activity of all three bat foraging guilds (edge hunting bats, open space hunting bats, and narrow space hunting bats)

Predictors	Edge space hunting bats				Open space hunting bats				Narrow space hunting bats			
	Estimate	Std. Error	p	VIF	Estimate	Std. Error	p	VIF	Estimate	Std. Error	p	VIF
(Intercept)	1.269	0.332	<0.001		-0.136	0.177	0.442		-1.081	0.403	<0.001	
Crop edge	-0.246	0.303	0.416	1.73	-0.107	0.160	0.506	1.69	0.215	0.267	0.419	1.32
Crop eff Shannon	0.064	0.283	0.820	1.46	0.504	0.141	<0.001	1.36	0.474	0.272	0.082	1.89
Log length struc in 50 m	0.459	0.261	0.078	1.26	0.586	0.132	<0.001	1.30	0.932	0.258	<0.001	1.47
Linear structures length	-0.145	0.275	0.598	1.39	-0.206	0.144	0.154	1.43	0.565	0.218	0.010	1.55
Seminatural 500 percent	0.292	0.305	0.339	1.76	0.3222	0.162	0.047	2.08	0.455	0.232	<0.001	1.85
Log distance forest	-0.052	0.314	0.868	1.83	0.469	0.156	0.003	2.08	-1.012	0.284	<0.001	1.73
Bat recording round [second]	0.691	0.538	0.199	1.34	1.362	0.270	<0.001	1.30	-0.697	0.524	0.183	1.81
Marginal R ² /Conditional R ²	0.12/0.41				0.47/0.50				0.40/0.44			

Significant results are printed in bold, marginal and conditional R²-values are reported estimates of model fits

Further, bat activity increased with the amount of linear structures within a 50 m radius of the recording devices (Fig. 2). With an increase of linear structures from 50 to 200 m, bat activity increased by 35.9%, and 61.1% for open, and narrow space hunting bats, respectively. The overall amount of linear structures in a landscape (i.e., in the 500 m buffer area), however, was only a significant predictor for the activity of narrow space hunting bats (75.0% higher activity with an increase from 100 to 1000 m) (Fig. 2).

Bat activity also increased with greater amount of semi-natural habitat for open space and narrow space hunting bats (64.2% and 53.3% higher activity with an increase of semi-natural habitat from 5 to 15%) (Fig. 2). The proximity to forest affected the bat groups in different ways: while the activity of open space hunting bats increased with forest distance (by 154.0% from 100 to 500 m distance), the activity of narrow space hunting bats decreased (by 86.4% with an increase from 100 to 500 m distance) (Fig. 2).

Discussion

Here we studied how crop heterogeneity and structural elements affect bat activity in agricultural landscapes. We found that the compositional (i.e., crop diversity) heterogeneity of the crop matrix affected bat activity, whereas configurational heterogeneity (i.e., field size) had no effect. While this pattern was consistent for most foraging groups, only open space foraging bats showed a significantly higher activity with increasing crop diversity. Further, structural landscape elements were important predictors for bat activity, especially for bats that hunt in highly clustered spaces and rely heavily on those for orientation, but also open aerial hunting bats showed a strong response to landscape structures.

Effects of crop diversity and field size on bat activity

Bat activity in our study region was not affected by crop configuration, contrary to our expectation of a linear increase in bat activity with greater configurational heterogeneity (i.e., smaller field size) (Fig. 1). We found, however, the expected pattern for crop composition, with increasing bat activity in landscapes with increasing crop diversity. These effects

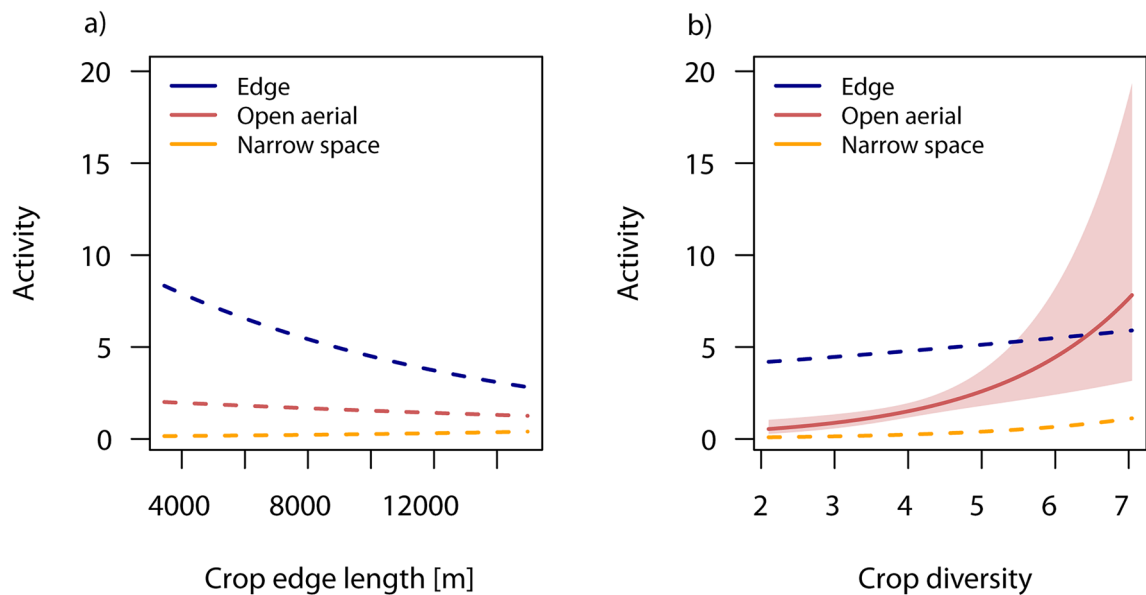


Fig. 1 Effects of (a) crop configuration (measured as crop edge length within 500×500 m landscapes) and (b) crop composition (crop diversity (exponent of Shannon diversity)) on

the activity of bats (measured as bat passes per night). Statistically significant effects ($p < 0.050$) are indicated with solid lines

were further moderated by differences in the bats' foraging behavior.

Several studies show a clear increase in insect biodiversity with increasing crop heterogeneity (Fahrig et al. 2015; Batáry et al. 2017). Bats, which predate in temperate zones predominantly on insects, follow this trend in Canada, Chile, and Germany (Heim et al. 2017; Monck-Whipp et al. 2018; Rodríguez-San Pedro et al. 2019). However, in our study we only found support for one of our measures of crop heterogeneity (i.e. crop diversity), while configurational heterogeneity had no effect on bat activity.

Possible reasons leading to this observed pattern could be an increasing amount of small-scale vegetable farming, which dominates small fields in our study region. Vegetable farming is known for high pesticide use and partly covering their crops, leading to reduced insect abundances and subsequently lower bat activity over these landscapes (Skórka et al. 2013). It might also be, that the most heterogeneous landscapes in our study were too small-scale, whereby the increase in heterogeneity (e.g., small fields of potentially unsuitable crops for bats) leads to a reduction in the effective area available for foraging, resulting in an area-heterogeneity trade-off (Allouche et al. 2012).

In addition, crop fields in our study region (0.9 ± 0.6 ha; min=0.3 ha, max=3.0 ha) were rather small compared to similar studies addressing the effect of landscape complexity on biodiversity (11.7 ± 12.1 ha, Batáry et al. 2017; 112.7 ± 17.5 ha, Monck-Whipp et al. 2018; 3.0 ± 2.0 ha, Sirami et al. 2019). This suggests that our study landscapes are at the lower end of the field size gradient in European farmland, and may explain why our highly mobile focus organisms, bats, are not as strongly affected by variation in field size in our study. Other studies could show clear crop configuration effects on bats (Fuller et al. 2005; Monck-Whipp et al. 2018) (average field sizes: 7.3 ± 0.5 ha and 10.7 ± 0.9 ha, as well as 112.7 ± 17.5 ha, respectively), indicating that there might even be a certain field size threshold above which an effect on the hunting activity of bats can be observed. This being said, the mechanistic linkages between crop heterogeneity, insect resources, and bat foraging activity still need further investigation.

Different bat guilds also responded slightly different to changes in crop heterogeneity in our study. The guilds distinguished here (open space, edge space, and narrow space) differ mainly in their foraging strategy (Denzinger and Schnitzler 2013) and

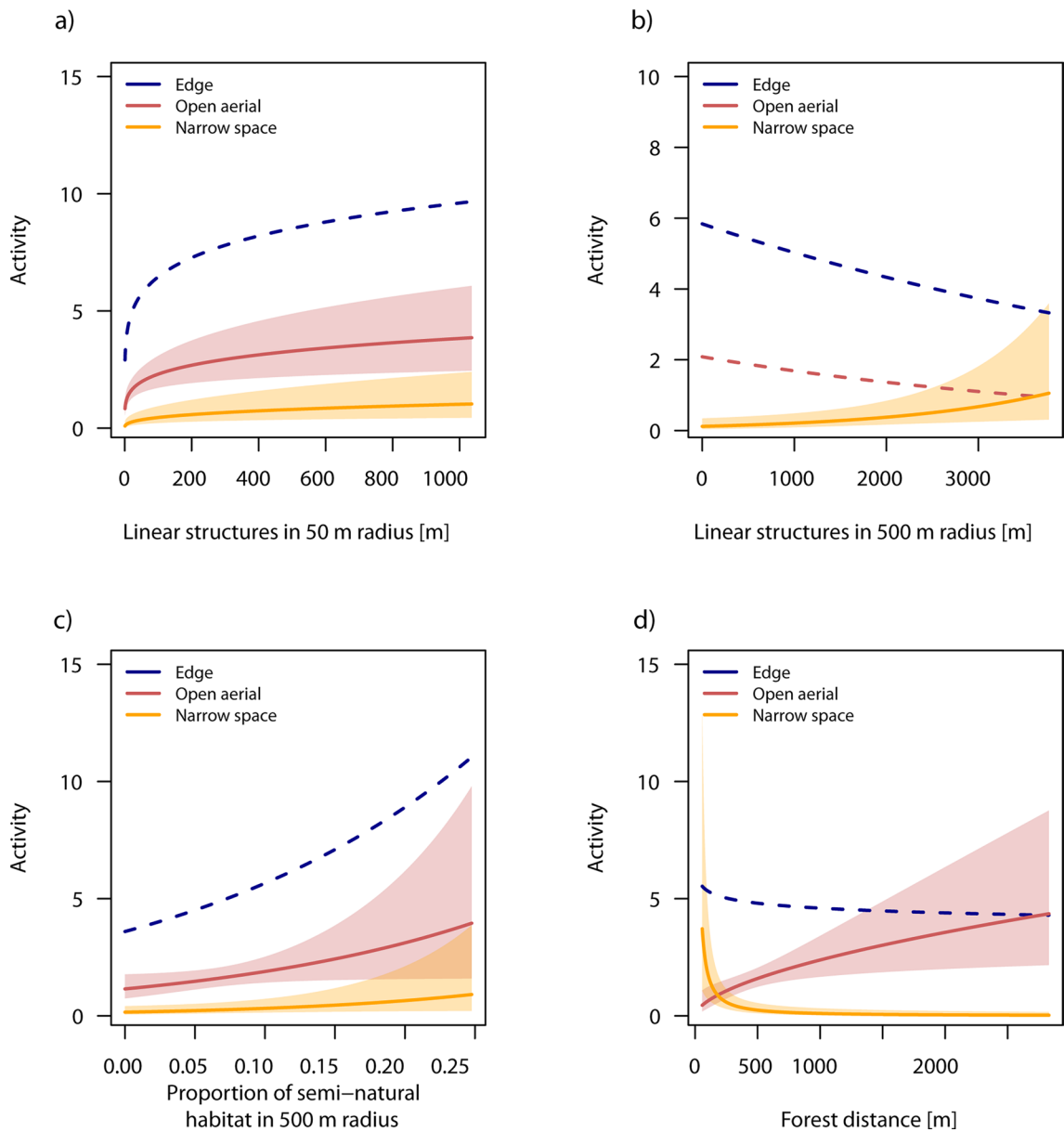


Fig. 2 Effects of (a) the length of local linear structures, (b) linear structures, (c) proportion of semi-natural habitat, and (d) the distance to forest on bat foraging activity (measured as bat

passes per night). Statistically significant effects ($p < 0.050$) are indicated with solid lines

subsequently how they make use of and maneuver throughout agricultural landscapes.

Edge hunting bats did not show a difference in activity with changes in crop composition or configuration. As mentioned above, edge hunting bats, and here especially the Common Pipistrelle (*P. pipistrellus*), were the most commonly recorded bat guild in

this study. Several studies assign them an intermediate mobility with home ranges of 2–3 km and quite flexible roosting, including in buildings (Davidson-Watts and Jones 2006). This suggests that the small home ranges of edge-hunting bats, combined with an abundance of potential roosting sites and their high hunting flexibility, may outweigh the influence

of crop composition and configuration on their foraging activity. By contrast, the more mobile hunting guilds (e.g. open aerial *Nyctalus noctula* with an average evening flight distance of around 26 km (Roeleke et al. 2016) and also narrow space hunters like *Myotis myotis* with flight distances to their hunting habitat exceeding 9 km (Audet 1990) showed a clear preference for landscapes with highly diverse cropping. This is consistent with several studies linking heterogeneity in crop composition to higher insect (=prey) abundance and diversity (Sirami et al. 2019). The high mobility of open space and, if certain structural landscape elements are present (see down), also narrow space hunting bats allows them to move through agricultural landscapes and access these areas. This makes these bats efficient pest control agents in the case of potential insect pest outbreaks. However, open-space hunters may be less effective in homogeneous landscapes, as they tend to respond negatively to reduced crop diversity.

Effects of structural elements and semi-natural habitats on bat activity

Structural landscape elements, such as hedge rows and tree lines, generally promote bat activity on farmland (Heim et al. 2018; Fill et al. 2022). We found that bat activity increased with local amount of linear structures, such as the length of hedgerows within a 50 m radius of bat recording stations. Linear structures like hedgerows or tree lines not only offer bats orientation and flight paths, but also act as a wind-breaks and thereby can promote the occurrence and abundance of flying insects, promoting bat foraging activity (Pasek 1988; Coulthard et al. 2016; Treitler et al. 2016). The effects of linear structures on bat activity in our study were scale-specific: increasing the amount of linear structures at the landscape scale (500 m buffer) correlated positively with the activity of narrow space hunting bats, which predominantly are forest specialists and depend on large amounts of linear structures. In contrast, the activity of open-space bats, which depend less on linear elements, and, unexpectedly, edge-space hunting bats, was not affected (Boughey et al. 2011; Toffoli 2016). However, when only locally-available structures (50 m radius from bat recording device) were considered, not only clutter space hunting bats, but all bats were promoted. While the elevated activity of clutter space

hunting bats is in concordance with their dependency on structural landscape elements, the higher foraging activity of open space hunting bats may result from their attraction to promising foraging areas (e.g., hedgerows; Pasek 1988; Fuentes-Montemayor et al. 2017; Fill et al. 2022).

Finally, the amount of semi-natural habitats, which in our study region mainly includes orchards and grasslands, had a positive effect on the activity of open and narrow space hunting bats, highlighting the importance of structurally-rich orchards and extensively used grasslands for bat conservation (Ewert et al. 2023). The dependency on structural landscape elements is especially crucial for bats adapted to hunting in narrow spaces, which show significantly lower activity the farther away from forest fragments. Although quite mobile, these bats are disproportionately more threatened than bats of other hunting guilds (Jones et al. 2003) and rely on structural elements and semi-natural habitats to move through agricultural landscapes.

Possible implications on agricultural yield

The effectiveness of bats as pest control agents is well-established, as demonstrated through analysis of their feeding habits and experimental settings that exclude foraging bats from crops affected by herbivorous pests (Maas et al. 2013, 2016; Russo et al. 2018; Baroja et al. 2021; Hughes et al. 2021; Scholz and Voigt 2022). Although the focus in these studies is often on tropical regions (Ramírez-Francel et al. 2022), several studies on rice (Tuneu-Corral et al. 2024), wine (Rodríguez-San Pedro et al. 2020), or corn (Maine and Boyles 2015) also highlight the importance of bats as pest controllers in Mediterranean and temperate climates. In the U.S. alone, the value of bats to the cotton agricultural industry has been estimated at around US\$22.9 billion per year (Boyles et al. 2011). In Spain, the economic benefit of bat-provided pest control for rice farming is valued at 56€/ha (Tuneu-Corral et al. 2024), while in Chile, it ranges between US\$188-\$248/ha/year for wine production (Rodríguez-San Pedro et al. 2020). Although detailed studies in temperate zones on typical crops such as cereals or oil seed rape are still lacking, it has been clearly shown that bats reduce defoliation in forest ecosystems (Böhm et al. 2011; Beilke and

O’Keefe 2022), suggesting they offer significant pest control potential also for agriculture.

However, for agriculture to fully benefit from these services, landscapes must be designed to be bat-friendly. It is also crucial to minimize bat exposure to high pesticide levels when transitioning conventional agricultural land to more structurally rich and bat friendly environments (Russo et al. 2024).

Therefore, while further detailed studies in standardized systems are necessary to better understand these complex interactions, current evidence suggests that long, narrow fields, such as those found in strip-cropping systems, could be a promising solution for biodiversity-friendly agriculture. These systems create small yet manageable fields that are easier for bats to navigate and promote their movement between fields. In addition, strip-cropping often results in higher crop diversity per area than conventional agriculture, which promotes biodiversity, enhances ecosystem services, and contributes to high yields, all while keeping management costs relatively low (Clough et al. 2020; Alarcón-Segura et al. 2022).

Conclusions

The homogenization of landscapes due to agricultural intensification is a major driver of farmland biodiversity decline, including threatened bat species. Our study provides important insights for the conservation of bats in agricultural landscapes. We showed how European bat species respond to changes in the composition and configuration of the agricultural landscape matrix, as well as to local structural elements by altering their foraging activity. Increasing crop compositional heterogeneity led to significantly higher bat activity (open space foraging bats), whereas crop configuration had no effect on bat activity. The effects of crop heterogeneity on bat activity were dependent on bat hunting guild, reflecting behavioral and morphological adaptations to foraging. We also found a high, but variable, importance of structural elements in agricultural landscapes for all hunting guilds and at different spatial scales. Promoting hedgerows, tree lines, and semi-natural habitats such as orchards can facilitate bat activity across the agricultural landscape matrix. The combination of a high crop diversity and structural elements provides

favorable hunting grounds for bats and can promote their conservation in agricultural landscapes.

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Author contributions I.G. and T.H. conceived the ideas and designed methodology; F.G. and T.H. collected the data and conducted statistical analyses; T.H. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability Data is provided within the manuscript or supplementary information files.

Declarations

Conflict of interest The authors declare no competing interests.

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