

Landscape connectivity, habitat structure and activity of bat guilds in farmland-dominated matrices

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Summary

1. Agricultural intensification has caused a decline in structural elements in European farmland, where natural habitats are increasingly fragmented. The loss of habitat structures has a detrimental effect on biodiversity and affects bat species that depend on vegetation structures for foraging and commuting.
2. We investigated the impact of connectivity and configuration of structural landscape elements on flight activity, species richness and diversity of insectivorous bats and distinguished three bat guilds according to species-specific bioacoustic characteristics. We tested whether bats with shorter-range echolocation were more sensitive to habitat fragmentation than bats with longer-range echolocation. We expected to find different connectivity thresholds for the three guilds and hypothesized that bats prefer linear over patchy landscape elements.
3. Bat activity was quantified using repeated acoustic monitoring in 225 locations at 15 study plots distributed across the Swiss Central Plateau, where connectivity and the shape of landscape elements were determined by spatial analysis (GIS). Spectrograms of bat calls were assigned to species with the software BATIT by means of image recognition and statistical classification algorithms.
4. Bat activity was significantly higher around landscape elements compared to open control areas. Short- and long-range echolocating bats were more active in well-connected landscapes, but optimal connectivity levels differed between the guilds. Species richness increased significantly with connectivity, while species diversity did not (Shannon's diversity index). Total bat activity was unaffected by the shape of landscape elements.
5. *Synthesis and applications.* This study highlights the importance of connectivity in farmland landscapes for bats, with shorter-range echolocating bats being particularly sensitive to habitat fragmentation. More structurally diverse landscape elements are likely to reduce population declines of bats and could improve conditions for other declining species, including birds. Activity was highest around optimal values of connectivity, which must be evaluated for the different guilds and spatially targeted for a region's habitat configuration. In a multi-species approach, we recommend the reintroduction of structural elements to increase habitat heterogeneity should become part of agri-environment schemes.

Key-words: acoustic monitoring, agricultural landscape, automated species recognition, conservation, echolocation, fragmentation, structural elements

Introduction

Intensively cultivated agricultural mosaic landscapes, interspersed with few semi-natural habitats, are common throughout Europe today (Robinson & Sutherland 2002; Bennett, Radford & Haslem 2006). After World War II,

increased mechanization and the subsidized intensification of agriculture led to a loss of semi-natural habitats such as unmown grass strips, hedgerows, groves and orchards (Robinson & Sutherland 2002). Intensively managed agricultural landscapes have since become increasingly monotonous.

However, patches and networks of natural elements (e.g. groves, hedgerows) are essential for increasing a

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landscape's connectivity (Bennett, Radford & Haslem 2006). Animals may effectively be isolated by large, monotonous agricultural areas because they hesitate to traverse extended unsuitable habitat, even when physically capable of crossing long distances (Saunders, Hobbs & Margules 1991). Structural connectivity facilitates access to resources and exchange between subpopulations, which helps to sustain populations and reduce the risk of population decline and local extinction (Matson *et al.* 1997; Debinski & Holt 2000; Bennett, Radford & Haslem 2006).

Structural connectivity is thus instrumental in maintaining biodiversity in agricultural landscapes. It influences the distribution and persistence of diverse taxa by providing them with corridors or stepping stones for daily movement or occasional dispersal (Gelling, Macdonald & Mathews 2007). In addition to connectivity, the heterogeneity and cover provided by landscape elements also foster species diversity (Benton, Vickery & Wilson 2003; Haslem & Bennett 2008). Several studies, also covering anthropogenic habitats (Bennett, Radford & Haslem 2006), showed a positive correlation between habitat heterogeneity and faunal diversity. Other characteristics of landscape elements, such as their height or the number of trees and the immediate surroundings, seem to influence bird species richness (Parish, Lakhani & Sparks 1994). Persistent agro-ecosystems with diverse vegetation structures may even sustain bird species that are normally confined to, or dependent on, undisturbed habitats (Matson *et al.* 1997).

Insectivorous bats have great potential as bioindicators as they react in parallel with many other taxa to a variety of stressors (Jones *et al.* 2009), including the loss of structural landscape elements, which impacts the abundance, distribution and activity of bats (e.g. Boughey *et al.* 2011). As certain bat species are reluctant to fly in open habitats (Walsh & Harris 1996; Stone, Jones & Harris 2009), linear landscape elements may be of prime importance. Bats can follow connecting treelines or hedgerows when commuting (Limpens & Kapteyn 1991; Schnitzler, Moss & Denzinger 2003). These structures also provide more protection against wind and more prey than open areas (Grüebler, Morand & Naef-Daenzer 2008).

Nevertheless, bat species differentially depend on landscape structures (Bernard & Fenton 2007). Wing morphology, echolocation call design and foraging behaviour of bat species have adapted to certain habitats (Neuweiler 1984; Aldridge & Rautenbach 1987). The loss of these essential habitats, or their connectivity, in human-controlled landscapes could be detrimental for species that depend on them. Hence, bats that specialize in foraging close to or within vegetation clutter generally tend to be more endangered than more flexible aerial hawkers (Jones, Purvis & Gittleman 2003; Safi & Kerth 2004). As their foraging habitat diminishes, they become more vulnerable and less able to recolonize abandoned areas (Safi & Kerth 2004; Bontadina *et al.* 2008).

Echolocation call design of European bat species differ to varying degrees, allowing calls to be used for species identification. We employed synergetic pattern recognition to classify full spectrograms of acoustic signals automatically to species (Obrist, Boesch & Flückiger 2004). This proved to be a powerful and efficient tool for processing recordings that were automatically sampled on a large scale. Earlier ecological bat studies relied on subjective analyses of echolocation calls and of flight behaviour (Ahlén 1980; Fenton, Merriam & Holroyd 1983). Recent methods usually involve statistics (Zingg 1990; Vaughan, Jones & Harris 1997) or sophisticated techniques such as artificial neural networks (Parsons & Jones 2000; Russo & Jones 2002). The latter approaches depend on feature extraction from the original signal, which contrasts with our image recognition approach.

Here, we applied automated bioacoustic recording and novel synergetic methods to investigate the response of a diverse insectivorous bat community to varying degrees of landscape connectivity. Our aims were to (i) reveal bats' sensitivity to fragmentation depending on their behavioural repertoire, (ii) identify thresholds of interpatch distances that hinder or even prevent bats from accessing a habitat patch, (iii) test whether more diverse bat species occur around landscape elements with higher connectivity and (iv) determine habitat configurations that promote the presence of bats. Such information is essential for developing guidelines for the revitalization of bat-friendly habitat matrices within agricultural areas.

Material and methods

STUDY TAXON

We investigated the same community of 26 bat species studied previously by Obrist, Boesch & Flückiger (2004). To account for presumed differences in the bats' perceptual ranges, we grouped the different species according to their echolocation call designs and parameters into three foraging guilds, namely short-range echolocators (SRE), mid-range echolocators (MRE) and long-range echolocators (LRE) (Table 1). For the parameters describing echolocation calls, see Obrist, Boesch & Flückiger (2004).

Species in the LRE guild called with bandwidths <30 kHz and durations >9 ms, whereas those in the SRE guild had bandwidths >50 kHz and call durations ≤6 ms. All remaining species with intermediate bandwidths and call durations were assigned to MRE with two exceptions. The genus *Plecotus* is known to echolocate with faint calls restricting its perception range (Waters & Jones 1995). *Barbastella barbastellus* (Schreber 1774) has been observed foraging around edges and gaps in vegetation showing call intervals of ≈90 ms (Denzinger *et al.* 2001), and Goerlitz *et al.* (2010) indicate a prey detection distance of <5 m. These two taxa were correspondingly grouped into the SRE guild.

FIELD SITES

The 15 study plots on the Swiss Central Plateau were selected to be representative of the Swiss lowlands (Fig. 1), using digital aerial photographs (0.25 m resolution), topographic vector maps

Table 1. The three bat foraging guilds, grouped according to their echolocation call parameters and their echolocation call designs

Genus	Species	Duration	LFR	PFR	HFR	Bandwidth	Call type	Guild
<i>Myotis</i>	<i>blythii</i>	3.3	24.5	53.2	106.2	81.7	FM	SRE
<i>Myotis</i>	<i>daubentonii</i>	3.9	27.3	42.7	81.2	53.9	FM	SRE
<i>Myotis</i>	<i>emarginatus</i>	3.6	36.3	54.5	113.1	76.8	FM	SRE
<i>Myotis</i>	<i>myotis</i>	6.0	22.2	37.1	86.0	63.8	FM	SRE
<i>Myotis</i>	<i>mystacinus</i>	3.6	27.9	46.8	99.7	71.8	FM	SRE
<i>Myotis</i>	<i>nattereri</i>	4.1	14.0	40.4	108.6	94.6	FM	SRE
<i>Barbastella</i>	<i>barbastellus</i>	4.3	25.7	36.0	48.3	22.6	FM-CF	SRE
<i>Plecotus</i>	<i>auritus</i>	2.9	22.7	37.7	55.7	33.0	FM	SRE
<i>Plecotus</i>	<i>austriacus</i>	5.8	18.0	27.6	45.3	27.3	FM	SRE
<i>Hypsugo</i>	<i>savii</i>	7.3	28.8	34.9	48.3	19.5	FM-CF	MRE
<i>Pipistrellus</i>	<i>kuhlii</i>	6.3	33.6	39.5	63.6	30.0	FM-CF	MRE
<i>Pipistrellus</i>	<i>nathusii</i>	6.9	36.1	41.3	61.5	25.4	FM-CF	MRE
<i>Pipistrellus</i>	<i>pipistrellus</i>	6.3	42.6	47.4	73.8	31.2	FM-CF	MRE
<i>Pipistrellus</i>	<i>pygmaeus</i>	6.0	51.5	56.2	84.1	32.6	FM-CF	MRE
<i>Eptesicus</i>	<i>serotinus</i>	10.9	22.4	26.8	47.2	24.8	FM-CF	LRE
<i>Eptesicus</i>	<i>nilssonii</i>	10.7	24.6	29.8	48.2	23.6	FM-CF	LRE
<i>Vespertilio</i>	<i>murinus</i>	15.0	20.2	24.6	35.8	15.6	FM-CF	LRE
<i>Nyctalus</i>	<i>leisleri</i>	9.3	22.1	27.4	49.4	27.3	FM-CF	LRE
<i>Nyctalus</i>	<i>noctula</i>	14.4	17.7	22.1	33.8	16.1	FM-CF	LRE

For parameter values delimiting guilds, see the text.

LFR, lowest frequency; PFR, peak-frequency (frequency of highest energy); HFR, highest frequency. FM, frequency modulated; CF, constant frequency. SRE, short-range echolocators; MRE, mid-range echolocators; LRE, long-range echolocators.

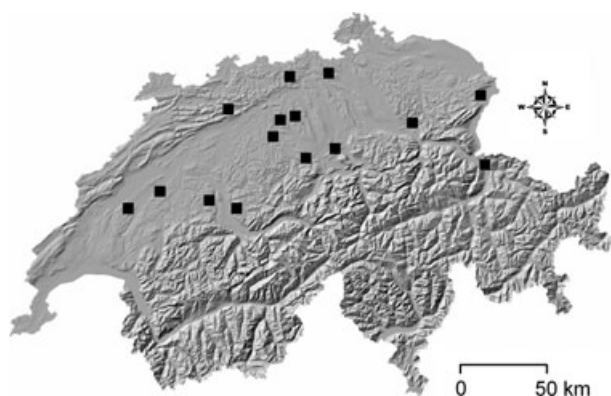


Fig. 1. Location of the 15 study plots on the Swiss Central Plateau.

and elevational LIDAR data (Light Detection and Ranging; 0.5-m resolution). Each plot consisted of a 2 × 2 km square covering a connectivity gradient, from open areas over poorly to tightly connected landscape elements. The resolution of 4 km² was chosen as it represents an area that still forms a contiguous landscape and contains the required elements as well as open areas. The home range of indigenous bat species can exceed the plot's range by up to an order of magnitude. Thus, in the present study, the connectivity of the landscape was investigated at a relatively small scale.

Landscape elements were defined as vegetational structures extending >1.5 m above-ground (e.g. single trees, tree groups, hedges, forests).

For each landscape element in the selected plots, in FRAGSTATS 3.3 (McGarigal *et al.* 2002), a shape index (function CIRCLE, related circumscribing circle), describing the linearity, and a connectivity index were calculated. The latter was calculated by summing up proximity indices (function PROX) with search radii

of 5, 10, 50 and 100 m (see detection distances, next paragraph), which were then weighted by multiplying by 100, 10, 2 and 1, respectively (see Fig. S1a,b,c in the Supporting Information). This resulted in a connectivity index emphasizing close landscape elements, thus taking into account bats' structure-bound ecology (Limpen & Kapteyn 1991). To select the recording locations, the hundreds of landscape elements per plot were classified into four categories of connectivity according to the quantiles of the connectivity index (isolated ≤ 16 < poorly connected ≤ 135 < connected ≤ 1931 < highly connected). Open areas with nearest landscape elements >100 m away were defined as control areas. These were used to compare bat activities around landscape elements with that in open fields. In each study plot, in a stratified random design, we selected three landscape elements in each of the four connectivity categories and the control areas. Recording locations were selected at the edge of each landscape element in a randomly selected cardinal direction (either N, E, S or W) relative to the element's barycentre. For each recording location and landscape element, 11 parameters were either calculated in ARCMAP GIS 9.3.1 (ESRI 2009) or recorded in the field (Table 2).

ACOUSTIC SAMPLING AND ANALYSIS

Bat vocalizations were recorded and georeferenced with autonomous ultrasound recorders (BATLOGGER; Elekon AG, Lucerne, Switzerland). Microphones were sensitive between 10 and 200 kHz (±5 dB), and signals were digitized at a rate of 312.5 kHz with 16 bit sampling depth. We expected approximate detection ranges of 100 m for LRE, 50 m for MRE and 10 m for SRE (except *Plecotus* <5 m). Sampling was performed twice between July and September 2009, with an interval of at least 3 weeks. Nights with rainfall, with mean temperatures <7 °C, and nights ± one night around full moon were not sampled. BATLOGGERS were mounted at ≈1 m above-ground, with the microphone directed tangentially to the structural element and ≈45° upwards. BATLOGGERS were programmed to record

Table 2. Characteristics of landscape elements and their surroundings recorded in the field (F) or with GIS (G)

Variable	Details
<i>Characteristics</i>	
Area (G)	Area (m ²) covered by the element
Orientation (G)	Deviance (degrees) from north-south axis
Forest (G)	Distance (m) from the next forest
Buildings (G)	Distance (m) from the next building
Settlements (G)	Distance (m) from the next settlement
Type (F)	Hedgerow, arboreal hedgerow, tree line, single tree, tree group (orchard), patch of bushes, forest-patch, grove
Character (F)	Homogenous (over whole area of same height and width), Heterogeneous (height and/or width vary over the area of the element)
Height (F)	Estimated average height (m) of the vegetation
Water (F)	Water/no water in a radius of 25 m
Altitude (G)	Meters above sea level
<i>Surroundings</i>	
Fraction of surroundings covered by (F)	Pasture, cropland, high vegetation, orchard, fertilized meadow, species-rich meadow or paved area (0%, 25%, 50%, 75%, 100%)

automatically for 2.5 h starting 0.5 h after sunset, and for another 2.5 h ending 0.5 h before sunrise, to focus on periods of foraging activity peaks. Cloudiness and wind were recorded, and temperatures measured 1 h after sunset and 1 h before sunrise.

We used *BATIT*, a custom written software (Obrist, Boesch & Flückiger 2004), to automatically identify echolocation calls to the most accurate taxonomic level possible. *BATIT* cut every sequence into single echolocation calls and processed them into spectrograms. These were then synergetically compared with five sets of prototype-spectrograms of every known species to classify the species. The five sets had been previously identified to best classify the 26 Swiss bat species (Obrist, Boesch & Flückiger 2004; Obrist *et al.* 2004), with an average correct classification rate of 86% (details: Obrist *et al.* 2004; Obrist, Boesch & Flückiger 2004). After automatic recognition procedures, all questionable sequences (e.g. multiple species and/or only few calls recognized) were visually screened for errors, manually measured and classified to the best taxonomic level possible (species group, genus, genus group). The spectral and temporal parameters were compared with published data (Zingg 1990; Obrist, Boesch & Flückiger 2004).

STATISTICAL ANALYSIS

Statistical analyses were performed using R 2.10.0 (R Development Core Team 2009). The statistical units were 450 repeated recordings from 15 locations in each of the 15 study plots. Connectivity was log-transformed to normalize the data. Explanatory variables were checked for correlation by calculating Pearson's correlation coefficients for continuous variables and ANOVAS for categorical and continuous variables. The independence of the categorical variables was tested using Pearson's chi-square tests. If pairs of variables correlated (Pearson's product-moment

correlation coefficient > 0.5, ANOVA: $P < 0.05$, Pearson's chi-square: $P < 0.05$), only the variable most closely related to the hypotheses was retained. Explanatory variables were standardized $((x - \mu)/\sigma)$, x being the observed value, μ the sample mean and σ its standard deviation).

Echolocation activity was, depending on analysis, either the overall activity or the species- or guild-specific activity, which always was standardized to 5-min intervals. It was used to test bats' responses to fragmentation, to compare their activity around linear and patchy elements and to find habitat configurations with more bat activity. To account for the fact that single bats may forage at a specific site for extended time, the activity of a given taxon was calculated by counting the number of 5-min intervals of its activity and then standardized to the total recording time. The resulting activity level (percentage) was transformed by arcsine-square root transformation ($\arcsin(\sqrt{x})$) to achieve normality (Zar 1984). Differences in the level of activity between control areas ($N = 90$, without connectivity index) and landscape elements ($N = 360$) were analysed using ANOVAS with the recording location nested in plot and season.

To test the interrelation of connectivity and activity, we ran basic linear mixed-effects models (LME) with connectivity as a fixed effect. In LMEs, we always used the same random structure containing recording locations nested within plots. Sensitivity to connectivity was investigated by conducting a LME, where the overall activity was related to the foraging guild, connectivity and their interaction, to differentiate linear trends. For each foraging guild, a moving window of average activity was plotted against connectivity (width = 100, beginning and end trimmed) to visually identify optima or threshold values.

The interrelation of connectivity with species richness and bat species diversity was also tested with LMEs, with connectivity as a fixed effect. To describe species diversity, Shannon's diversity index ($H = -\sum p_i \ln p_i$, $p_i = N_i/N$) was calculated for each recording location (Shannon & Weaver 1949). Finally, stepwise backward regressions were conducted using LMEs to find the environmental landscape variables (Table 2) that best explain the variations in activity. The full model contains all the explanatory variables remaining after the correlation analysis, including their two-way interactions and the quadratic term of connectivity. A P -value of 0.05 was used as the cut-off point for exclusion of a variable. The least significant terms were removed, starting with interactions and quadratic terms.

Results

A total of 26 139 bat passes were recorded at 225 locations over 2181 observation hours. Of these, 18 413 (75%) could be identified to species level, while 5557 (23%) were assigned to a single-genus complex and 439 (2%) to a multi-genus complex (Table 3). The vast majority of echolocation call sequences stemmed from *Pipistrellus pipistrellus* (Schreber 1774) (71%). Species in the genus *Myotis* contributed to 11% of the total activity. We registered 2947 SRE (12%), 20 742 MRE (85%) and 604 long-range echolocator (LRE, 3%) passes. The 116 bat detections that could not be assigned to one of the foraging guilds were excluded from further analyses. *P. pipistrellus* dominated the MRE guild and was thus analysed separately from the rest of the MRE guild. The number of bat

Table 3. Number of assignments of bat recordings to species- or genus-complex level and foraging guild at recording locations of different categories

Level	Identification	Guild	Category					Total
			Control	iso	poc	con	hic	
Species	<i>Barbastella barbastellus</i>	SRE		16	7	19	48	90
	<i>Eptesicus nilssonii</i>	LRE			1			1
	<i>Eptesicus serotinus</i>	LRE				4	4	8
	<i>Hypsugo savii</i>	MRE	7	9	7	3	3	29
	<i>Nyctalus leisleri</i>	LRE		6	2	6	18	32
	<i>Nyctalus noctula</i>	LRE	34	39	16	43	34	166
	<i>Pipistrellus kuhlii</i>	MRE	14	73	31	54	54	226
	<i>Pipistrellus nathusii</i>	MRE	49	156	73	70	124	472
	<i>Pipistrellus pipistrellus</i>	MRE	864	4703	3740	2487	5469	17263
	<i>Pipistrellus pygmaeus</i>	MRE	9	36	5	23	47	120
	<i>Vespertilio murinus</i>	LRE	1	1		2	2	6
Single-genus complex	<i>Eptesicus spec.</i>	LRE	1	1	4	1	9	16
	<i>Myotis spec.</i>	SRE	74	514	762	340	987	2677
	<i>Nyctalus spec.</i>	LRE	6	3	7	6	69	91
	<i>Pipistrellus pipistrellus/nathusii</i>	MRE	117	675	341	164	451	1748
	<i>Pipistrellus nathusii/kuhlii</i>	MRE	53	263	129	150	215	810
	<i>Pipistrellus pygmaeus/pipistrellus</i>	MRE	1	7	2		6	16
	<i>Pipistrellus spec.</i>	MRE		4	6	2	7	19
Multi-genus complex	<i>Plecotus spec.</i>	SRE	32	30	49	28	41	180
	<i>Eptesicus/Nyctalus spec.</i>	LRE	3	8	17	9	10	47
	<i>Eptesicus/Vespertilio spec.</i>	LRE					2	2
	<i>Nyctalus/Vespertilio spec.</i>	LRE	9	8	12	8	21	58
	<i>Pipistrellus kuhlii/Hypsugo savii</i>	MRE	2	11	6	15	5	39
	<i>Eptesicus/Vespertilio/Nyctalus spec.</i>	LRE	18	30	41	35	53	177
	<i>P. pipistrellus/P. pygmaeus/Miniopterus schreibersi</i>	–	5	17	30	27	37	116
Total			1299	6610	5288	3496	7716	24409

iso, isolated elements; poc, poorly connected elements; con, connected elements; hic, highly connected elements; SRE, short-range echolocators; MRE, mid-range echolocators; LRE, long-range echolocators.

detections varied by up to tenfold between the study plots, despite standardized recording efforts, ranging from 448 in Villarepos to 4401 in Steffisburg (see Table S1 in Supporting Information).

ACTIVITY

Bat activity around landscape elements was significantly higher than in control areas for all three foraging guilds (ANOVA, SRE: $F = 37.9$, $P < 0.001$, MRE: $F = 8.7$, $P = 0.003$, LRE: $F = 4.9$, $P = 0.028$; all d.f. = 1), as well as for the dominant species *P. pipistrellus* ($F = 39.8$, d.f. = 1, $P < 0.001$). The largest difference was found for SRE species, which had a mean relative activity of 15.1% around landscape elements and 5.4% in control areas, but the differences were smaller with the other guilds (MRE 15.6% vs. 10.9%; LRE 4.9% vs. 3.5%) (Fig. 2). *P. pipistrellus* showed a mean relative activity of 40.0% around landscape elements and 24.5% in control areas.

SENSITIVITY TO FRAGMENTATION

The activity of SRE and LRE increased significantly with increasing connectivity of the linear mixed-effects model (effect size (with S.E.) 163 d.f.: SRE: 0.025 (0.010), $t = 2.50$, $P = 0.014$; LRE: 0.017 (0.006), $t = 3.06$,

$P = 0.003$). However, for MRE, no significant trend was evident (-0.008 (0.009), $t = -0.86$, $P = 0.392$; Fig. 3). In the linear mixed-effects model, the interaction between the foraging guild and connectivity was not significant between SRE and LRE (interaction term (\pm SE): SRE-LRE: 0.008 (0.010), $P = 0.436$), indicating that there was no significant difference in linear trends of sensitivity to fragmentation between these two foraging guilds. But linear trends differed between MRE and the other foraging guilds (value of the interaction (with S.E.): SRE-MRE: 0.032 (0.012), $P = 0.007$, MRE-LRE: -0.024 (0.010), $P = 0.021$).

With SRE and MRE, we found peak and threshold values of activity at different levels of connectivity, but not with LRE (Fig. 4). With SRE, the activity remained rather constant at high levels of connectivity, but dropped at more isolated landscape elements (connectivity (\log) ≈ 1.2 ; Fig. 4), which suggests there is a connectivity threshold. Interestingly, the activity of MRE increased with decreasing connectivity, but dropped again before elements became very isolated, indicating an optimum value (connectivity (\log) ≈ 0.5 ; Fig. 4). The relative activity of LRE increased linearly with increasing connectivity without a detectable threshold. Correlations of the connectivity index with distance from the nearest forest and with mean area of neighbouring structural objects are given in Fig. 5.

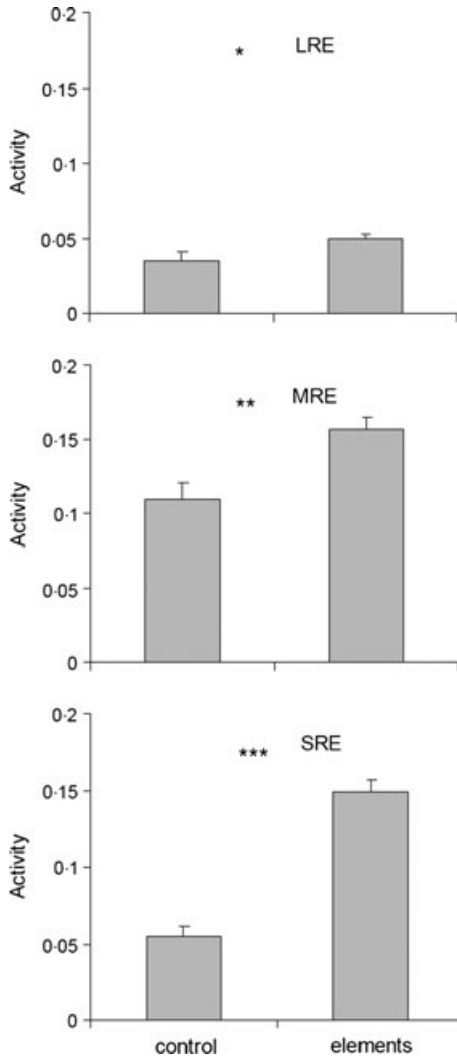


Fig. 2. Mean relative activity (proportion of time, \pm standard error) of the three foraging guilds around landscape elements and in control areas (significance of difference P : * \leq 0.05, ** \leq 0.01, *** \leq 0.001). SRE, short-range echolocators; MRE, mid-range echolocators; LRE, long-range echolocators.

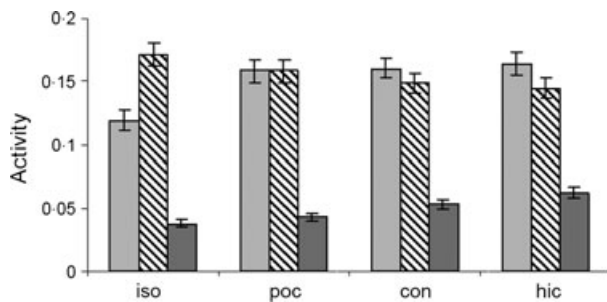


Fig. 3. Histogram of mean relative activity (proportion of time \pm standard error) of the three foraging guilds around landscape elements with increasing connectivity. Light grey, SRE; hatched, MRE (*P. pipistrellus* excluded); dark grey, LRE. iso, isolated elements; poc, poorly connected elements; con, connected elements; hic, highly connected elements.

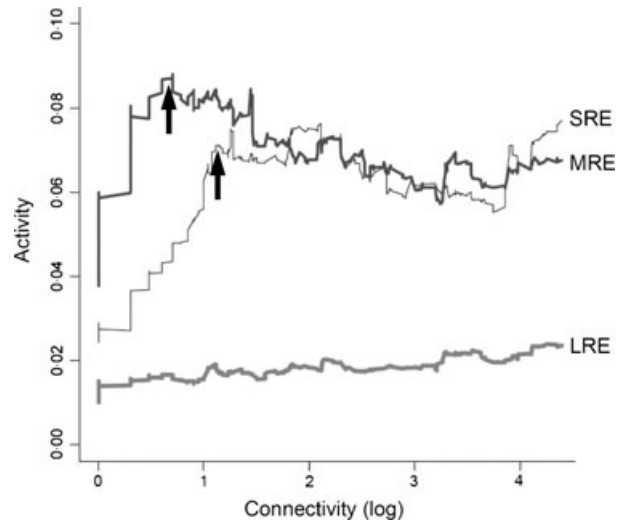


Fig. 4. Moving mean of activities of the three foraging guilds plotted against the connectivity (logtransformed). Optima or thresholds (black arrows) are shown for SRE and MRE. A linear positive trend is detectable for LRE. SRE, short-range echolocators; MRE, mid-range echolocators; LRE, long-range echolocators.

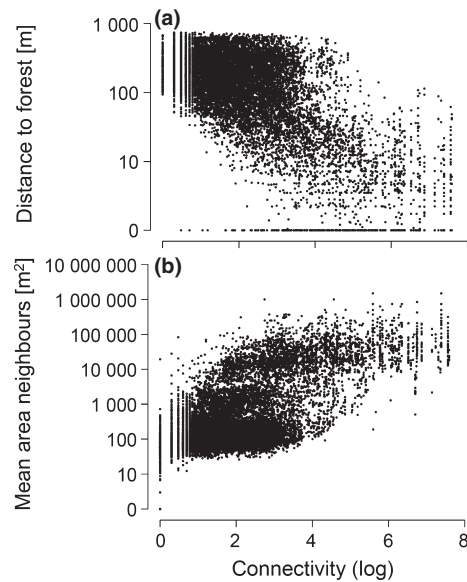


Fig. 5. Our connectivity index (see Material and methods) of landscape elements increases with: (a) decreasing distance from the nearest forest and (b) increasing average area of its surrounding neighbours within 100 m distance. All landscape elements available on the 15 sites are shown.

SPECIES RICHNESS AND DIVERSITY

Total species richness per recording location varied between two and ten and increased significantly with increasing connectivity (estimate = 0.144, SE = 0.072, P = 0.048). This effect was driven by species numbers of LRE (estimate = 0.109, SE = 0.036, P = 0.003) and SRE (estimate = 0.090, SE = 0.038, P = 0.021), both increasing with connectivity.

Shannon's diversity index ranged from 0.080 to 1.586, but did not increase with increasing connectivity (estimate = -0.019, SE = 0.013, $P = 0.152$; Appendix Figs S2a,b).

HABITAT CONFIGURATIONS

After testing for correlations and the independence of explanatory variables (Table S2), 11 variables were retained for further statistical analyses, namely vegetation height, presence of pastures, cropland, orchards, species-rich meadows, paved area, as well as altitude, area of structural elements, distance to the nearest building, distance to the nearest settlement, shape and connectivity. However, only a few variables appeared to have significant effects on the activity of bats (Table 4). Among the positive effects, the area of the structural elements appears to be most important for the SRE and MRE guilds, but not for LRE bats. With LRE and *P. pipistrellus*, the amount of paved areas had a positive effect on their activity. The amount of pastureland surrounding a landscape element had a significant negative effect on the activity of the SRE bat guild.

Linearity of landscape elements and the vegetation height significantly correlated with increasing activity of the dominant species *P. pipistrellus*.

Discussion

EFFECT OF CONNECTIVITY ON BAT ACTIVITY

Activity was 1.4–2.8 times higher around landscape elements compared to open, unstructured control areas in all three foraging guilds. This indicates that bats prefer landscape elements over open habitat, which corroborates previous findings that open habitats seem to be least attractive to bats for foraging (Walsh & Harris 1996; Lumsden & Bennett 2005). Many explanations for this preference exist: landscape elements help bats to navigate (Jensen, Moss & Surlykke 2005), they provide good foraging

Table 4. Statistical significances of habitat variables influencing the activity of the three foraging guilds and *P. pipistrellus*

Model	Habitat variables	Effect	SE	d.f.	<i>t</i>	<i>P</i>
SRE	Connectivity	0.024	0.010	161	2.43	0.016
	Pasture	-0.022	0.009	161	-2.35	0.020
	Area	0.049	0.009	161	5.64	<0.001
MRE	Area	0.024	0.008	163	2.88	0.005
LRE	Connectivity	0.016	0.006	162	2.91	0.004
	Paved	0.011	0.005	162	2.05	0.042
<i>Pipistrellus pipistrellus</i>	Shape	0.028	0.012	160	2.36	0.019
	Height	0.036	0.012	160	3.03	0.003
	Paved	0.035	0.012	160	3.02	0.003
	Area	0.039	0.012	160	3.28	0.001

SRE, short-range echolocators; MRE, mid-range echolocators; LRE, long-range echolocators.

habitat with high prey densities (Grüebler, Morand & Naef-Daenzer 2008), and they provide shelter from wind (Limpens & Kapteyn 1991) and predation (Verboom & Spoelstra 1999). The latter appears to be most pronounced in species with low flight speeds, generally SRE, as these species could be especially vulnerable to predation when flying in open areas (Jones & Rydell 1994; Weinberger, Bontadina & Arlettaz 2009). SRE bats are much more active around landscape elements than in control areas, which exemplifies the consequences of these observations at the landscape scale.

As SRE bats have a limited detection range, we expected this guild to be most sensitive to fragmentation. Surprisingly, decreasing connectivity was also correlated with lower activity in LRE bats. For these bats, we did not predict an effect of connectivity because they mostly forage at relatively high altitudes or clearly above the canopy. However, they still might be attracted to areas with more structural elements like trees as a resource for insect prey (Verboom & Spoelstra 1999; Grüebler, Morand & Naef-Daenzer 2008). However, LRE bats did not avoid open habitats to the same extent as SRE bats. Their activity merely decreased with decreasing connectivity, without the pronounced drop exhibited by SRE bats around poorly connected elements (Figs 3 and 4). This drop could be indicative of a boundary loss effect in SRE bats. SRE prefer foraging close to ecotones (e.g. boundaries between hedgerows and fields), which was also demonstrated by Pocock & Jennings (2008), who suggested there is such an effect with the majority of bats except the larger species (mostly LRE). MRE bat's activity decreased with increasing connectivity. However, as LME only calculates overall linear trends, it may be that thresholds are disguised by nonlinear interaction effects.

The highest activity of MRE bats was found around isolated elements. This guild might more readily cross open areas than SRE bats. Furthermore, if MRE bats feed on the same resources as SRE bats, this could theoretically lead to a competitive exclusion of the two guilds, which in turn forces the MRE bats to shift their foraging habitat towards more isolated elements (Arlettaz, Godat & Meyer 2000).

ACTIVITY AROUND LINEAR AND PATCHY ELEMENTS

Only *P. pipistrellus* appeared to differ in activity between linear and patchy elements. This confirms previous findings (e.g. Limpens & Kapteyn 1991; Walsh & Harris 1996), although most of these studies did not distinguish shape of structural elements. To our knowledge, this is the first study to directly compare the effects of linear and patchy elements and simultaneously disentangle connectivity and shape effects. Our findings suggest that the shape of landscape elements (linear vs. patchy) is much less crucial for bats than the area covered by vegetation structure, and whether the elements are sufficiently connected to allow access to a broad range of species to exploit the resources.

SPECIES RICHNESS AND DIVERSITY

Our results suggest that a matrix of interconnected farmland provides habitats that harbour bat communities of high species richness, which is a common measure of biodiversity (Lande 1996). However, Lande (1996) pointed out that this metric is bound by sampling bias, as it does not allow for rare species that are often lacking even in large samples. Shannon's diversity index is less biased as it reflects the variance of species composition within a community. In our study, Shannon's diversity index was not influenced by connectivity, even when the dominant *P. pipistrellus* was excluded from the analysis.

HABITAT CONFIGURATIONS

SRE, MRE and *P. pipistrellus* become more active the larger the area covered by landscape elements. Large landscape elements in agricultural areas consist mostly of wooded patches that provide a foraging habitat for typical forest species. The negative effect of pasture on SRE activity is surprising because the concentration of dung on pastures means that coprophagous arthropods tend to provide abundant food for aerial-hawking insectivorous birds and bats (Rydell 1992; Gruebler, Morand & Naef-Daenzer 2008). However, as most lowland pastures in Switzerland are only temporarily grazed in spring and autumn, they may offer lower food supplies in summer than other nearby cultivated or fallow land. The positive effect of landscape elements' vegetation height for *P. pipistrellus* is probably linked to the elements acting as wind-breaks as well as providing more food (Verboom & Spoelstra 1999; Wickramasinghe *et al.* 2003).

SPECIES COMPOSITION

The majority of call sequences in this study (71%) came from *P. pipistrellus*, as was expected (Sattler *et al.* 2007), given it is a generalist species (Davidson-Watts, Walls & Jones 2006). Our field surveys did not identify any rare, specialized species such as horseshoe bats. These species emit low-intensity calls very directionally and at high frequencies, but can regularly be detected when present. Considering the large sampling effort, we believe these species do not occur in the study plots (Duelli 1994; Bonatadina, Hotz & Märki 2006).

The small proportion (2%) of LRE sequences in our data set was at first sight surprising, especially given that low-frequency echolocation calls have wide detection ranges (Holderied & von Helversen 2003). But other acoustic monitoring studies have found similar low proportions of LRE (Walsh & Harris 1996; Wickramasinghe *et al.* 2003). This may be linked to their wide-ranging foraging for abundant insect swarms, especially along streams or illuminated streets, both of which we deliberately excluded from our sampling to reduce confounding factors. However, by using ground-level detectors, we

may have missed some of these high-flying LRE bats (Collins & Jones 2009).

BIOACOUSTIC MONITORING

Acoustic monitoring has recently become a common technique for identifying and surveying bats (Vaughan, Jones & Harris 1997; Parsons & Jones 2000; Russo & Jones 2002; Obrist, Boesch & Flückiger 2004), progressively replacing conventional capture methods (O'Farrell & Gannon 1999). Although it is a very cost-effective monitoring method, it does not necessarily provide a comprehensive, unbiased inventory of bat fauna (O'Farrell & Gannon 1999; MacSwiney, Clarke & Racey 2008). Acoustic recordings are invariably biased towards high-intensity echolocating bats (O'Farrell & Gannon 1999; Obrist, Boesch & Flückiger 2004). Moreover, the echolocation call designs of *Myotis* species vary greatly within species and less between species, which makes their identification especially challenging (Obrist, Boesch & Flückiger 2004). Automatic identification of bat echolocation calls is mostly superior to identification by humans, but it cannot detect patterns that are difficult to quantify (Jennings, Parsons & Pocock 2008). We thus double-checked automated identifications with experts.

Despite its drawbacks, bioacoustics still provides a powerful approach for investigating the habitat use of bats at a landscape scale. Furthermore, it allows a balanced sampling design that ensures a comparable treatment of all sites.

CONSERVATION IMPLICATIONS

Our findings demonstrate the importance of connectivity for bat communities in farmland-dominated landscapes and support Weller, Cryan & Shea's (2009) claim that fragmentation is a major threat to bat populations. Higher bat activity around structural elements suggests that the presence of a single isolated tree to a highly connected hedgerow or forest stand may benefit bats. Better connected elements are, however, clearly more valuable than single isolated elements for SRE bats, which include some of the most threatened species (Duelli 1994; Safi & Kerth 2004). To sustain bat communities, existing structural elements must be conserved and where possible, new elements must be reinstalled to promote habitat connectivity. A matrix of elements with varied connectivity counteracts the isolation that is so detrimental to bats. In restored matrices, linear and patchy elements equally provide valuable foraging habitats and stepping stones for bats. When considering the reintroduction of structural elements into the landscape matrix, their future connectedness has to be taken into account. Our connectivity index for particular elements increased with proximity to forest and with increasing average area of their surrounding neighbours (Fig. 5a,b). We thus recommend taking two simple measurements into account. First, new

landscape elements should be placed close to other, preferably large elements. Second, reintroduction of structural elements should be planned in the framework of agri-environment schemes (AES), which compensate farmers for loss of income due to measures they take to improve the environment or biodiversity. AES are implemented in the European Union and Switzerland to alleviate degradation of biodiversity that followed the course of intensified agriculture. In Switzerland, there was recently introduced a special subsidy which supports the connectivity of AES. The effectiveness of AES has been controversially discussed (e.g. Kleijn *et al.* 2001; Kleijn & Sutherland 2003; Whittingham 2006), which led to improvements that aim not only at increasing size but also quality of compensation areas. Measures differ in their effectiveness between organismal groups (Pocock, Evans & Memmott 2012) and can even be detrimental to specialist species (Batary *et al.* 2011). Nevertheless, in intensely managed farmlands, increasing heterogeneity and connectivity of structural elements (Benton, Vickery & Wilson 2003) seems to foster species that depend on these structures as some arthropod groups (Albrecht *et al.* 2010), birds (BirdLife International 2012) or, in the case presented here, bats. We therefore advocate that in future improved AES (Scherr & McNeely 2008), restorations or installation of such compensational structures as hedges or tree groups are additionally targeted spatially in accordance with the environmental service and the landscape in focus (Donald & Evans 2006; Uthes *et al.* 2010). Finally, we recommend that also the spatial position of structural elements should be part of a wider strategy that includes monitoring their effectiveness in the future (FOEN 2012).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Example of an agricultural landscape with mapped representation, aerial image and identification of the corresponding landscape characteristics (isolated to highly connected).

Fig. S2. Scatterplot of species richness and diversity against connectivity.

Table S1. Number of assignments of bat detections in each study plot.

Table S2. Correlations and dependencies of explanatory variables.