Effects of fine-scale foraging habitat selection on bat community structure and diversity in a temperate low mountain range forest

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A b s t r a c t . The evolution of different foraging strategies, corresponding echolocation signals and adaptations of wing morphologies allowed niche differentiation and sympatric foraging habitat use of bat species. We investigated how different habitat selection transferred into sympatric species groups ("bat communities"). The occurrence of bat species at different transects and landscape structures of five sites of a low mountain range forest in the south west of Germany was determined. Species were present at transects in the following descending order: *Pipistrellus pipistrellus > Myotis myotis > Nyctalus leisleri > N. noctula > Myotis daubentonii > Eptesicus serotinus > Plecotus austriacus.* We analyzed patterns of habitat use and evaluated differences in community structure. Landscape structures (patch types) influenced more than geographical location of sites within the landscape the bat community structure. Bat communities at individual forest sites disaggregated into different smaller species groups of one to at least eight species at different landscape structures. The results confirm previously proposed models of foraging habitat use of bats. Species groups clustered in correlation with the landscape structures "open area" (clearance or grassland), "closed or open canopy forest", and "still water". The highest bat diversity foraged predominantly at open canopy forest, which may fulfil best the requirements of several distinct functional groups (guilds) of bats.

Key words: bat ecology, biosphere reserve, guild, patch type, Palatinate Forest, vegetation structure

Introduction

Different mechanisms may control patterns of diversity at different scales. Variations in regional factors such as climate, evolution and migration, play major roles in explaining variations in species richness at landscape scales. Biotic processes such as competition, predation, colonization, disturbance and dispersal, or abiotic conditions are important regulators at small scales (L e g e n d r e 1993, R i c k l e f s & S c h l u t e r 1993, H u s t o n 1999, L y o n s & W i l l i g 1999, W e i h e r 1999, S c h e i n e r et al. 2000, H i l l e b r a n d & B l e n c k n e r 2002). Trade-offs concerning locally applicable adaptations of species provide a strong influence on community structure and dynamics, and may explain patterns of species diversity. Interspecific trade-offs are invoked to avert that one species (a "super-species") dominates a community. Trade-offs within this community context represent niche differentiation among species. Interspecific trade-offs are typically thought to be a requirement for the coexistence of closely related species in communities at small spatial scales (K n e i t e l & C h a s e 2004). At which spatial scale coexistence of species occurs should depend on the taxonomic group that is considered.

Structurally complex habitats may provide more niches and diverse ways of exploiting the environmental resources and thus increase species diversity (B a z z a z 1975). In most habitats, plant communities determine the physical structure of the environment, and

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therefore, have a considerable influence on the distributions and interactions of animal species (L a w t o n 1983, T e w s et al. 2004). Positive relationships between vegetation-shaped habitat heterogeneity and animal species diversity are well documented on both local and regional scales (D a v i d o w i t z & R o s e n z w e i g 1998). Depending on the taxonomic group, structural parameters of the vegetation, and the spatial scale, species diversity may also decrease with increase in habitat heterogeneity (e.g. R a l p h 1985, S u l l i v a n & S u l l i v a n 2001, T e w s et al. 2004). Even for winged animals inside a limited landscape, spatially constrained processes can determine their distribution and the species diversity (e.g., N e k o l a & K r a f t 2002, K u s c h et al. 2005). Different species groups are closely linked to "keystone structures" that determine animal species diversity by their presence (T e w s et al. 2004). For bat species such keystone structures may be linear vegetation elements, e.g. forest edges that promote orientation by echolocation (K u s c h et al. 2004).

In bat species, niche separation evolved by, e.g. divergent modes of foraging and orientation, wing morphology, or choice of roost types (P a t t e r s o n et al. 2003, K u n z & F e n t o n 2003). Distinct adaptations in wing morphology and the structure of echolocation signals coincide with the preferred habitat and foraging behaviour (A l d r i d g e & R a u t e n b a c h 1987, S c h n i t z l e r et al. 2003, S i e m e r s & S c h n i t z l e r 2004). Bats experience a trade-off concerning several habitat characteristics that may influence the foraging suitability. Spatial heterogeneity of the habitat, besides prey availability, influence bat activities (K u s c h et al. 2004). Spatial orientation marks at a landscape level seem to help finding suitable foraging sites. Bat activity in different patches depended on the complexity of vegetation structures that may represent "land marks" and serve as orientation helps (E s t r a d a et al. 1993, B r i g h a m et al. 1997, J u n g et al.1999, V e r b o o m et al. 1999). Structural features of the vegetation may influence the abilities of bats to forage at a patch by echolocation (B r i g h a m et al.1997, J u n g et al.1999, E r i c k s o n & W e s t 2003). Spatial complexity of patches, e.g. high tree density negatively affects foraging activity by bats (K u s c h et al. 2004). Insectivorous bats were divided into three functional sub-groups ("bat guilds"; ensembles according to P a t t e r s o n et al. 2003) based on foraging habitat: uncluttered space foragers, background-cluttered space foragers, and highly cluttered space foragers (M c K e n z i e & R o l f e 1986, A l d r i d g e & R a u t e n b a c h 1987, N e u w e i l e r 1989, S c h n i t z l e r & K a l k o 1998, S c h n i t z l e r & K a l k o 2001, S c h n i t z l e r et al. 2003). One of the habitat types ("uncluttered or open space") includes the airspace over open areas and above forest canopy. Space close above pasture or waters or between trees represents the second type ("background cluttered or edge space"). The third habitat type ("highly cluttered or narrow space") is the surface of vegetation, within vegetation, or ground, summarized as "closed habitats" (S c h n i t z l e r et al. 2003).

In the present paper, we tried to answer questions concerning the relations of habitat type and spatial scale to bat species diversity in a temperate mountain range forest: How does niche separation of bats, e.g. foraging mode, orientation by echolocation and roost selection, transfer into spatial distribution at local foraging sites? How many species forage sympatric at what scale (do single species or small groups only, from a larger group that occurs at the investigated landscape, forage at small habitat patches)? Does sympatric foraging depend on habitat structure or on the location of habitats within a landscape? If habitat structures inside the investigated region influence foraging of different bat species, what habitat structures or types differentiate between sympatric species groups?

Methods

Bat activity and related characteristics of forest patches were investigated in the area 49°22'–49°34' N, 7°31'–7°47' E of the foothills of the Palatinate Forest ("Pfälzerwald"), Germany, close to Kaiserslautern, Rhineland-Palatinate. The region belongs to the UNESCO Biosphere Reserve Vosges du Nord / Palatinate Forest. From May to September of 2005 we measured bat activity at transects of five different sites (predominantly different mountain valleys; 1 HS, "Hirschsprungtal"; 2 WT, "Wienertal"; 3 LB, "Letzbachtal"; 4 VW, Vogelwoog; 5 SH, "Schneeweiderhof") within the Palatinate Forest and at its border (5 SH), north of the Palatinate Forest (Fig. 1). The sites were chosen because they represented similar as well as different vegetation and landscape structures (patches) at different distances. We measured the relative part of closed canopy (continuous treetops) from the total transect length, and determined the occurrence of open canopy (e.g. broad forest paths with spaces between treetops), open areas (clearances or grassland areas) and of still water borders at the different transects (Table 1). We analysed the vegetation structural parameters by measurements and observations at the forest sites, and from topographical maps of scale 1:5000.

We applied a line-transect method similar as described by O ' D o n n e l l & S e d g e l e y (2001) and V a u g h a n et al. (1997). At each forest site, a distance of 4–5 km was walked, divided into four to five line-transects. Every site and transect was investigated five times during the investigation period. Transects were not always straight lines, because the forest area was not walkable everywhere. Measurements always began at half an hour
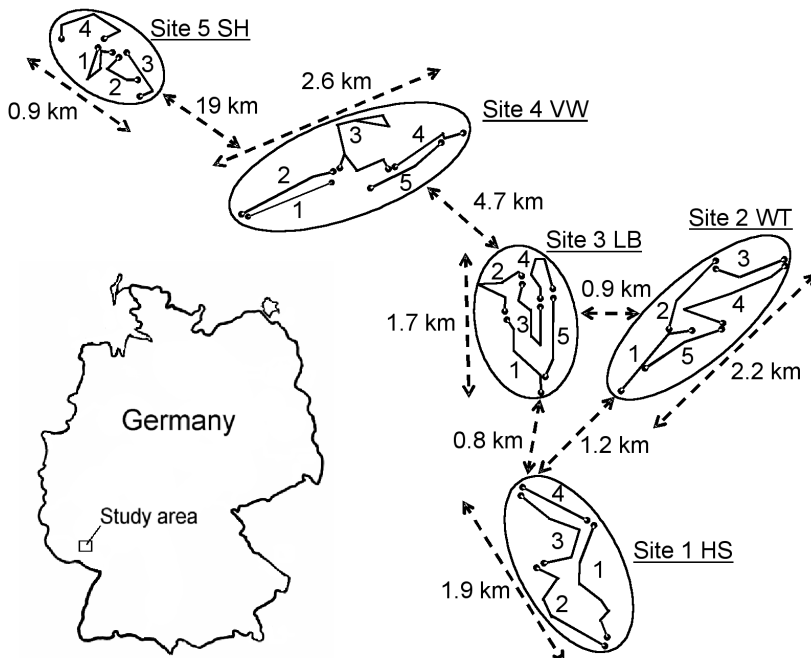

Fig. 1. Relative location of investigation sites. Numbers denote transects at different forest sites (encircled). Distances between sites are not drawn by scale, but are given by numbers of km at arrows.

Table 1. Habitat structures and bat species diversity (Shannon-Wiener index, *H*; and Evenness-index, *E*) at the five investigation sites. Four different types of spatial vegetation structures were distinguished: Closed canopy (cc), open canopy (oc), clearance or grassland (cl), still water (sw); with the relative part of closed canopy given in parentheses.

Site	Closed canopy (%)	Habitat structures present at individual transects (1-5)					*H*	*E*
		1	2	3	4	5		
1 HS	60	cc (80%), oc, sw	cc (60%), oc	cc (80%), oc	cc (20%), oc	--	0.29	0.60
2 WT	37	cc (5%), oc	cc (10%), oc, cl	cc (60%), oc, cl	cc (30%), oc	cc (80%), oc	0.56	0.72
3 LB	52	cc (40%), oc, cl	cc (50%), oc	cc (80%), oc	cc (80%), oc	cc (10%), oc, cl	0.38	0.55
4 VW	25	cc (5%), oc, cl, sw	cc (10%), oc, cl, sw	cc (50%), oc, cl	cc (40%), oc, sw	cc (20%), oc	0.64	0.71
5 SH	19	oc, cl	oc, cl, sw	cc (5%), oc, cl	cc (70%), oc, cl	--	0.53	0.62

after sunset and lasted approximately 4–5 hours. The start transect changed randomly from night to night. All investigation nights were chosen to be of relative high temperature (above 14°C at sunset), low wind speed and without rain, because that conditions favour bat activity. When monitoring bats, we noticed the position of sound recordings at the respective transect and landscape structure.

Sound recording and analyses for species discrimination

Bat echolocation and social calls were recorded via a portable time expansion ultrasonic receiver ("Laar bridge box", BVL von Laar, Klein Goernow, Germany). The microphone of the detector has a flat frequency response for frequencies between 20–80 kHz. Via an amplifier a flat sensitivity of the detector up to 170 kHz is achieved. The signals were digitized in real time by the ultrasound processor that sampled at a rate of 400 kHz and time-expanded 10fold a 5.12 s digitally recorded sequence. This was stored in a memory array of the processor. The resulting sequence, lasting 51.2 seconds, was then replayed and recorded to audiotape on a Sony TCD-D8 DAT-recorder.

The time-expanded recordings were digitized and analyzed in a PC at a sampling rate of 44.1 samples/second, with 16 bits/sample, using the software Avisoft Professional (Avisoft, Berlin). In combination with the 10-fold time expansion, a real-time sampling rate of 441 kHz resulted. Digitized signals were processed through a fast Fourier transformation (FFT) using a 512 points Hamming window. FFTs were calculated with 93.75% time overlap. Oscillograms, frequency power spectra and spectrograms were evaluated. For species discrimination, four frequency parameters of the calls were measured and compared to reference recordings via discriminant function analysis. We measured the parameters total duration of the call (measured from oscillograms), the start frequency (the frequency value at the beginning of the call; measured from spectrograms), end frequency (the frequency value at the end of the call; measured from spectrograms), and the frequency of maximum energy (measured from power spectra). Measurements were taken from the fundamental harmonic.

We performed discriminant function analysis according to Russo and Jones (2002) with the help of the statistics software package STATISTICA 6.0 (StatSoft, Tulsa, USA). We

compared the echolocation calls in question to calls of twenty bat species that potentially occurred in the investigation area (*Barbastella barbastellus* Schreber, *Eptesicus serotinus* (Schreber), *E. nilssonii* Keyserling & Blasius, *Myotis bechsteinii* Kuhl, *M. myotis* Borkhausen, *M. brandtii* Eversmann, *M. dasycneme* Boie, *M. daubentonii* (Kuhl), *M. mystacinus* Kuhl, *M. nattereri* Kuhl, *Nyctalus leisleri* Kuhl, *N. noctula* Schreber, *Plecotus auritus* L., *P. austriacus* J. Fischer, *Pipistrellus kuhlii* Kuhl, *P. nathusii* Keyserling & Blasius, *P. Pipistrellus* (Schreber), *P. pygmaeus* (Leach), *Rhinolophus ferrumequinum* (Schreber), *R. hipposideros* Bechstein, *Vespertilio murinus* L.). Twenty echolocation calls of the unknown bat and twenty echolocation calls of each of the known bat species were compared simultaneously by this method. Reference data of known species were obtained from flying bats identified at their roosts (P f a l z e r & K u s c h 2003) and from B a r a t a u d (1996). Squared Mahalanobis distances were evaluated to indicate the nearest distance of the calls of unknown and known bats. *Myotis* species, except *M. myotis* and *M. daubentonii*, could not certainly be distinguished. A further bias of the use of ultrasonic detectors to record bat activity was that soft-calling species, or species flying at greater height, may be detected less frequently than loud-calling species, or those at lower height.

S t a t i s t i c a l   a n a l y s e s   o f   c o m m u n i t i e s

We calculated the Shannon-Wiener index H as a measure of species diversity.

$$H = -\Sigma p_i \cdot \log(p_i)$$

$$p_i = \frac{n_i}{N}$$

where p_i = the proportion of the ith species in the sample. The proportion of species was their number of recorded calls (n_i) from all recorded calls (N) of that site (sample). So, the flight activity of species at sites rather than their abundance was compared. The evenness E was calculated as

$$E = \frac{H}{log\ S}$$

where S is the species richness.

To correlate the geographical distance and community similarity we estimated the latter by Wainstein's index $K_w = JN$ x Re; with JN = Jaccard's similarity coefficient, and Re = Renkonen's coefficient. Jaccard's coefficient is calculated by dividing the number of species found in both of two samples by the number found in only one sample or the other and then multiplying by 100. Renkonen's coefficient, which can be termed "percentage similarity", was calculated as

$$Re = \sum_{i=1} \min p_{Ai}, p_{Bi}$$

$$\text{with } p_{Ai} = \frac{n_{Ai}}{N_A}, p_{Bi} = \frac{n_{Bi}}{N_B}$$

where p_{Ai} = the proportion of the ith species in sample A; p_{Bi} = the proportion of the ith species in sample B.

Cluster analyses were performed with the help of the statistics software package SPSS 13.0.1 (SPSS Inc., Chicago, USA). As distance measures the Euclidean distance and the squared Euclidean distance were applied. As linkage methods the average linkage (between groups), single linkage and the unweighted pair-group average methods were used. All resulting trees were basically similar.

Results

From a total of 1243 sequences of echolocation calls recorded at five different landscape sites (Table 1) we determined 60.7% to be from *Pipistrellus pipistrellus*, 9.5% from *Nyctalus leisleri*, 8.9% from *Myotis daubentonii*, 5.9% from *Myotis myotis*, 3.5% from *Nyctalus noctula*, 2.5% from *Eptesicus serotinus*, 0.9% from *Plecotus austriacus* and 8.0% from other *Myotis* species (Table 2). Analysis of these calls revealed an uneven distribution of the species among different sites of the investigated area. Species diversity and evenness differed between sites (Table 1), with the largest as well as the lowest diversity at still water sites inside the forest. Because the Shannon-Wiener index H differed more than the evenness-index E, we conclude that the number of species present at a site did more than flight activity of those species influence the differences between bat communities. Cluster analyses confirmed that species differed in their presence and flight activity at the sites (Fig. 2). Bat communities at sites 1 HS and 3 LB were most similar, and both differed with increasing degree to communities at sites 4 VW, 2 WT and 5 SH. Pair-wise calculation of community similarity between forest sites by Wainstein's index resulted values from 21% to 68% with a mean of 41.7 ± 14.9% (SD)

Table 2. Numbers of call sequences from different bat species recorded at five forest sites (1 HS, 2 WT, 3 LB, 4 VW, 5 SH), and 4–5 transects, respectively.

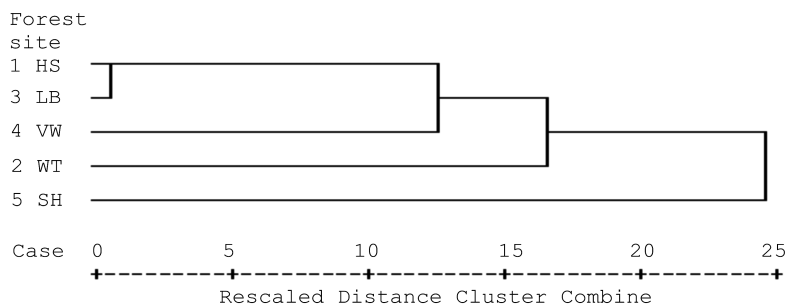| Forest site	Transect	*E. serotinus*	*M. daubentonii*	*M. myotis*	*Myotis* sp.	*N. leisleri*	*N. noctula*	*P. austriacus*	*P. pipistrellus*
1 HS	1	0	0	2	18	0	0	0	100
	2	0	0	1	6	0	0	0	9
	3	0	0	2	1	0	0	0	8
	4	0	0	1	16	0	0	0	23
2 WT	1	2	0	2	0	19	4	0	15
	2	4	0	1	0	16	6	0	41
	3	13	0	1	3	17	0	0	22
	4	0	0	0	1	3	1	0	11
	5	0	0	0	0	0	0	0	0
3 LB	1	0	0	8	19	1	3	0	72
	2	0	0	6	2	0	0	0	7
	3	0	0	2	3	0	0	0	7
	4	0	0	3	0	0	0	0	15
	5	0	0	6	8	1	2	0	59
4 VW	1	0	8	2	0	8	16	0	13
	2	3	12	0	1	6	2	0	17
	3	9	2	0	15	7	8	2	21
	4	0	33	0	0	4	0	0	80
	5	0	0	0	0	0	0	0	6
5 SH	1	0	7	4	0	2	0	1	47
	2	0	48	20	1	18	2	6	120
	3	0	1	10	0	16	0	2	55
	4	0	0	2	6	0	0	0	7
Sum		31	111	73	100	118	44	11	755

Fig. 2. Cluster analysis of bat communities at five different forest sites (1 HS, 2 WT, 3 LB, 4 VW, 5 SH) using Euclidean distances and Average Linkage (between Groups).
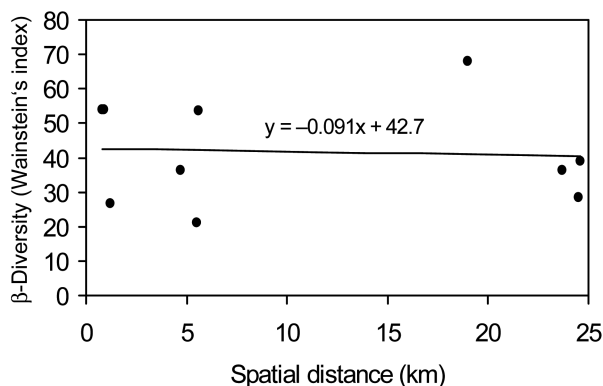

Fig. 3. Correlation of the beta-Diversity (Wainsteins`s-Index) of bat communities to spatial distances of the compared sites.

(Fig. 3). There was no significant increase of the beta-diversity with geographical distance (regression analysis; MSq: 8.224; F: 0.03; $p = 0.861$ for significant changes; see Fig. 3).

By cluster analyses, we also compared bat communities at different transects of the five forest sites. Within the resulting trees communities at transects did not form cluster according to their geographical location at the five forest sites (Fig. 4). The cluster showed that communities differed among transects of individual forest sites, and most often were more similar at transects of different sites. Therefore, communities of individual forest sites disaggregated into different smaller communities at transects of that site. Those small "transect communities" partly were similar at transects of different forest sites. Cluster one (Fig. 4) represented transects where few species (*M. myotis*, *Myotis* sp., *P. pipistrellus*; Table 2) were present with high evenness. The second cluster (group 2) consisted of communities with high species diversity. At these transects most species (*E. serotinus*, *M. myotis, M. daubentonii, Myotis* sp., *N. leisleri*, *N. noctula*, *P. pipistrellus*) of the total number detected in the area were present. A third species group (transect cluster 3) consisted of many species, but was dominated by *P. pipistrellus*. The fourth group was represented by less diverse communities that were dominated by *P. pipistrellus*. Species accordingly differed in the breadth of use of different habitat transects. As a generalist species *P. pipistrellus* flew at 100% of all bat foraging patches (22 forest transects with bat activity of 23 investigated transects). *M. myotis* was present at 77%, *N. leisleri* at 59%, *N. noctula* at 41%, *M. daubentonii* at 32%, *E. serotinus* at 23%, *P. austriacus* at 18% of transects with bat activity (Table 2).
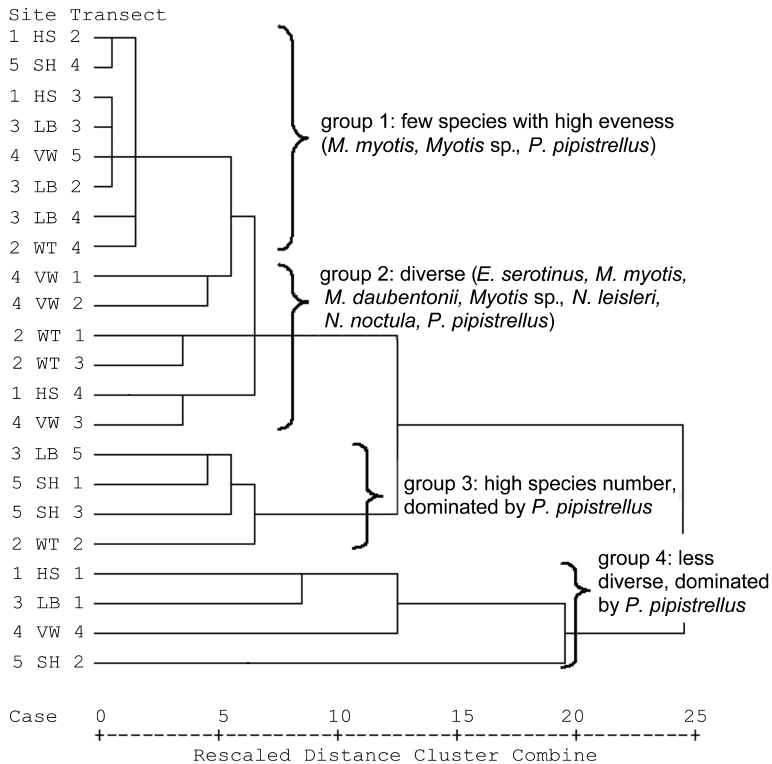
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Fig. 4. Cluster analysis of bat communities at different transects (1-5) of five forest sites (1 HS, 2 WT, 3 LB, 4 VW, 5 SH) using Euclidean distances and Average Linkage (between Groups).

Bat diversity (Shannon-Wiener index H) decreased with the relative part of closed canopy at the investigated forest sites (regression analysis: y = -0.0072x + 0.7574; MSq: 0.062; F: 10.32; p: 0.0488; Table 1). To elucidate whether different landscape or vegetation structures (patch types) were responsible for a discrimination of species or communities, we performed cluster analyses of bat communities at four landscape structures present at the total length of all transects of a forest site, respectively (Table 3). We omitted site 5 SH from the analysis, because different landscape structures lay too close together, to make a clear distinction. The number of species at the different patch types was 3–8 species at open canopy forest with Shannon-Wiener index H = 0.58 (0.33–0.64), 1–4 species at closed canopy forest with H = 0.26 (0.00–0.38), 3–4 species at still water borders with H = 0.34 (0.18; 0.49), and 1–5 species at clearances or other open areas with H = 0.32 (0.00–0.57) (Table 3). Bat communities clustered into three groups according to the patch types a) closed or open canopy forest, b) clearance or open area, and c) still water; with several exceptions (Fig. 5). The clusters were independent of the geographical location of the patches within the landscape. Bat species and activity were similar at clearances from different forest sites (sites 1 HS, 4 VW, 2WT). Likewise, open and closed canopy at sites 1 HS, 3 LB, 2 WT and 4 VW clustered to one group of similar bat communities. Both still waters were different from most other sites, but also from each other. So, similar species groups foraged, where similar patches occurred. These results showed the importance of local patch types for the discrimination of species groups, instead of the geographical location of patches.

Table 3. Numbers of call sequences recorded from different bat species and diversity measured at four investigation sites* (1 HS, 2 WT, 3 LB, 4 VW) and at four different landscape structures (closed canopy, cc; open canopy, oc; clearance or grassland, cl; still water, sw).

Species and diversity measure	1 HS oc	cc	sw	cl	2 WT oc	cc	cl	3 LB oc	cc	cl	4 VW oc	cc	sw	cl
E. serotinus	0	0	0	0	9	3	7	0	0	0	8	0	0	4
M. daubentonii	0	0	0	0	0	0	0	0	0	0	2	0	53	0
M. myotis	1	4	1	0	4	0	0	13	10	0	2	0	0	0
Myotis sp.	16	14	11	0	6	0	0	14	6	12	15	0	0	1
N. leisleri	0	0	0	0	37	5	13	2	0	0	9	0	8	8
N. noctula	0	0	0	0	10	1	0	3	0	2	7	0	16	3
P. austriacus	0	0	0	0	0	0	0	0	0	0	2	0	0	0
P. pipistrellus	26	28	86	1	53	31	2	83	39	38	54	5	64	14
Sum of species	3	3	3	1	6	4	3	5	3	3	8	1	4	5
Shannon Index *H*	0.33	0.38	0.18	0.00	0.60	0.32	0.39	0.39	0.35	0.30	0.64	0.00	0.49	0.57
Evenness *E*	0.69	0.80	0.37	--	0.78	0.54	0.81	0.56	0.72	0.63	0.70	--	0.82	0.82

*(site 5 SH is not included because of the narrowness of different landscape structures, and the occurrence of properties)
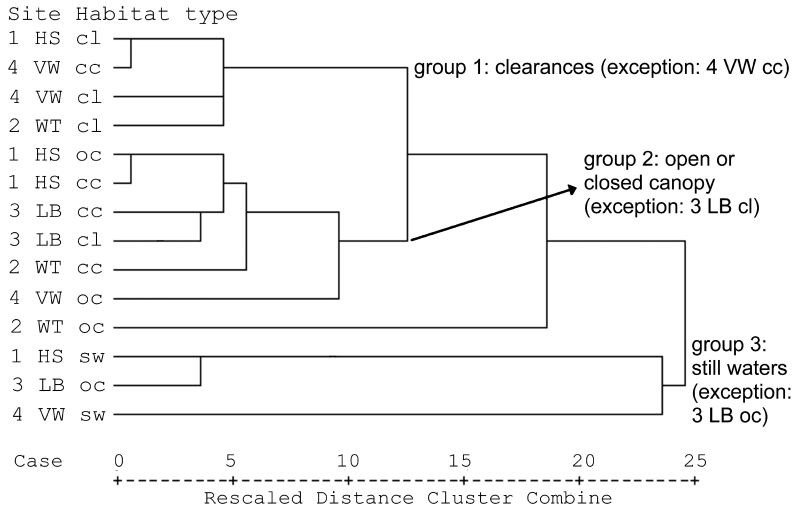

Fig. 5. Cluster analysis of bat communities at different habitat types (cl, clearance; cc, closed canopy; oc, open canopy; sw, still water) of five forest sites (1 HS, 2 WT, 3 LB, 4 VW) using Euclidean distances and Average Linkage (between Groups).

Discussion

The results confirm that within a landscape community, species or species groups favour small foraging patches according to their morphological and physiological adaptations. Four types of bat communities were detected at different forest transects: 1. A diverse group consisting of at least seven species, including aerial, trawling and gleaning foragers; 2. a species rich group dominated by *P. pipistrellus*; 3. a less species rich group of high evenness consisted of *Myotis* species (gleaning and aerial / trawling foragers), and of *P. pipistrellus*; and 4. a less diverse group with dominance of *P. pipistrellus*. We observed that specific bat

communities foraged at "within forest" sites, at "open area" sites and at still waters. The highest bat diversity foraged predominantly at open canopy forest. This habitat type may more than others fulfill the requirements of different functional bat groups simultaneously. Based on foraging patch types, bat species communities of insectivorous bats were divided into three guilds (S c h n i t z l e r et al. 2003). Our results concerning bat species that are active in a forest area met these considerations largely. Open canopy forest should represent a larger number of different foraging patches than do other forest sites (open spaces between canopy, surface of vegetation, within and close to vegetation, above canopy, ground), and thereby supports foraging of diverse bat species.

The observed local communities were similar at similar landscape structures, whereas the overall communities at different forest areas differed. Different bat species should forage together, where the local habitat meets the special requirements. Similar bat species groups develop at geographically distant sites, when similar habitat types are present. Several reports direct to how niche separation of bats does transfer into spatial distribution at local foraging sites (e.g., D e J o n g 1995, W a l s h & H a r r i s 1996, C e ľ u c h & K a n u c h 2004, Z u k a l & Ř e h á k 2006, K a n u c h et al. 2007, for European bats). J a b e r g & G u i s a n (2001) noticed an aggregated distribution of bat species at the landscape level within the Swiss Alps. They predicted overall community patterns and distribution of potential species' habitats from quantitative models that used landscape structure in combination with a geographical information system (GIS). Descriptors of landscape structure accounted for 30% of the variation in bat community composition. For some species, more than 60% of the variance in distribution could be explained by landscape structure. Elevation and vegetation structure (forest or woodland cover, lakes and suburbs) were the most frequent predictors. Geographic location, presence of a lake and residential buildings seemed to affect the overall community composition, but they appeared to be good predictors of distribution only for particular species. Our results concerning different community structures at different landscape sites confirm this prediction. We also observed that some species are widely distributed at different places, whereas others were more specialized to few sites. In a quite different desert habitat K o r i n e & P i n s h o w (2004) observed that bats of the background-cluttered space guild foraged over a variety of habitats while bats from the other guilds were more restricted with regard to their foraging spaces. Bat activity and species richness of a fragmented forest landscape were compared with the help of ultrasonic detectors in New South Wales, Australia. A gradient in forest area, habitat diversity and structural complexity was the most consistent predictor of activity for four taxa. Most fragmentation tolerant species were active over open areas and probably used resources in the agricultural mosaic. Typically they were fast flying, low manoeuvrable species which are predicted to forage in uncluttered habitats (L a w et al. 1999). In a lowland tropical rain forest with frugivores being the dominant bat species the most common species of bat were fully partitioned in a resource niche matrix of size and trophic guild when vertical stratification was included as a variable (L i m & E n g s t r o m 2001). The different observations from a variety of regions all direct to the formation of bat species groups in correlation to physiological and morphological adaptations. The species richness and structure of those communities depend on the patch type and structural diversity. The local bat fauna thereby differentiates into smaller patch communities, whereby some habitat generalists are more wide spread than other, more specialized species.

The question, how many species forage sympatric at a special patch type could be answered in the present publication only partly. We detected one to at least eight different

species at single patches, with the largest number (mean = 6) at open canopy forest patches, the lowest numbers (mean = 3) at closed canopy forest patches. Yet, further species do occur in the investigated area, e.g. *Pipistrellus nathusii* and *P. pygmaeus*, as well as *Plecotus auritus* were detected (seldom) in other investigations (unpublished). We furthermore could not distinguish all *Myotis* species. The largest numbers of bat species that forage sympatric at patches in the studied temperate low mountain range forest may therefore be higher than the observed eight species. J a b e r g & G u i s a n (2001) concluded from GIS-modelling that a "low elevation species group" in a Swiss Alps region consists of five species (*Pipistrellus kuhlii*, *Plecotus austriacus*, *Vespertilio murinus*, *Pipistrellus nathusii* and *Eptesicus serotinus*). A unique "high elevation species", which also relies on urbanized areas (*Eptesicus nilssonii*) was modelled, as well as an "urban species group", comprising three species (*Nyctalus leisleri*, *N. noctula* and *Pipistrellus pipistrellus*), and a "forest-dwelling species group", including at least 5 species (*Plecotus auritus*, all *Myotis* sp., *Miniopterus schreibersi*, *Barbastella barbastellus* and *Rhinolophus ferrumequinum*). These findings agree in the observation that a relatively large number of species co-occur in special patch types, also in the non-tropical region. In the tropics, bat species numbers that may build communities are even larger (L i m & E n g s t r o m 2001, K i n g s t o n et al. 2003). It remains unclear at which spatial scale the observed large species numbers co-occur.

The overall bat diversity varied between different forest sites (mountain valleys and forest border sites). The question arises, to what extent the spatial location of patches within the surrounding landscape influences the bat diversity, besides the patch quality. Several factors, including the availability of roosts, food and water, flight morphology, colony size, and reproductive cycle influence the relationship between roosts and foraging areas (K u n z & L u m s d e n 2003). The beta-diversity measured in the present investigation did not correlate to the geographical distance of the sites, indicating that a gradient of overall species occurrence was absent. Such a gradient may arise where resources like roost availability are locally limited. As an example, the greater mouse-eared bat (*Myotis myotis*) typically uses buildings as day roosts. This species was present at all of the sites despite the local absence of buildings. The commuted distances from roost sites to foraging patches were observed to differ considerably among different bat species (K u n z & L u m s d e n 2003). Only for some (small) bat species flight distances seem to be of significance and proximity of roosts to food resources may then be an important determinant in roost site selection. Pipistrelle bats were observed to change foraging patches during the active season (K u s c h & I d e l b e r g e r 2005). This may depend on changes of food availability, or on the distance to day roosts, also. Lactating females may prefer foraging patches nearby the nursery roost. The population density monitored from colony sizes of greater mouse-eared bats in Bavaria (Germany) was positively correlated to mixed forest area around the nursery roosts (Z a h n et al. 2006). Bats that use abundant roost types are more likely to move their day roosts in response to food availability (K u n z & L u m s d e n 2003). However, many species of bats fly greater distances up to 10–30 km from roost sites and have large home ranges (B a r c l a y 1989, A r l e t t a z 1999, O ' D o n n e l l 2001). The choice of foraging patches by some less distant flying species that roost in buildings, e.g. *Plecotus austriacus*, may be more influenced by the geographical location of roosts. This may especially hold true for horseshoe bats, which went extinct in the investigated area. The lesser horseshoe bat, *Rhinolophus hipposideros*, was observed to forage predominantly in broad-leafed woodland. Females foraged most time within a distance of only 600 m from nursery roosts

(B o n t a d i n a et al. 2002), which are always in buildings in the investigated northern part of the total distribution area of this species.

We therefore assume a mode of species diversity regulation at foraging patches of the investigated forest region that includes predominantly the patch type (vegetation structure), but also the location of patches in relation to day roosts. The results direct to the importance of an adequate forest management for a conservation of bat diversity. Forest management modes should favour small scale structural diversity and should avoid area-wide high tree densities as they are given by age class monocultures.

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