



Original investigation

## Different responses of attic-dwelling bat species to landscape naturalness

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## ARTICLE INFO

## Article history:

Received 10 July 2016

Accepted 15 October 2016

Handled by Danilo Russo

Available online 18 October 2016

## Keywords:

Chiroptera

Maternity roosts

House-dwelling bats

Landscape structure

Central Europe

## ABSTRACT

Although the general role of bats and the tolerance of many species to urbanized areas is well known, the relationship between urban roosts and their surrounding landscapes having different degrees of naturalness still requires our attention, mainly in species that are the most adapted to human-made structures. We used extensive data from attic-dwelling bat surveillance conducted throughout Slovakia to assess species responses to the degree of naturalness of the landscape surrounding their anthropogenic roosts. Using generalized linear mixed-effects modelling, we found that some bats established their nursery colonies in either a habitat with a higher proportion of forests mostly at sub-mountain/mountain altitudes (*R. hipposideros*, *P. auritus*, *M. emarginatus*), or they preferred lowlands with a predominance of arable land (*E. serotinus*, *P. austriacus*). Furthermore, higher habitat heterogeneity and the proportion of grassland were positively associated with the occurrence of *P. auritus*; however, negative associations with these habitat variables were found in *E. serotinus*. The predicted suitability of an area for bats to establish nursery colonies suggests the existence of two regions with different bat species composition in the study area: a region of the Pannonian Lowlands and a less urbanized mountain region of the Carpathian Mountains. Our study thus showed that landscape naturalness is a determining factor for roost-site selection by bats preferring anthropogenic roosts; however, some bat species did not express specific preferences according to the tested environmental variables, and other ecological traits in the evaluated species should be considered.

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## Introduction

Landscape urbanization is, among other human impacts, considered to be one of the most important factors influencing, either positively or detrimentally, ecological traits in many animal species (e.g. Baker and Harris, 2007; McKinney, 2006, 2008). Species' responses to specific conditions of urbanized areas as complex ecosystems are various and seem to be species-specific. We may classify taxa according to urban tolerance as urban avoiders, urban adapters or urban exploiters (Blair, 1996; Fischer et al., 2015; Germaine and Wakeling, 2001; Kark et al., 2007). Thus, different species, although closely related, may avoid such areas

or may utilize and colonize them as dwellers through the process of synurbanization (e.g. Francis and Chadwick, 2012). Among mammal species, bats represent the largest group inhabiting a variety of human-made structures within a wide urbanization gradient (Kunz, 1982). In detail, they could be characterized as urban-tolerant, urban-sensitive, suburban-habitat specialists or as adapted synurbic species (Russo and Ancillotto, 2014). However, depending on the different landscapes, habitat or climate of a region, variability in this trait has been observed between even closely related species as well as among distinct populations of the same species (e.g. Dietz et al., 2009; Lintott et al., 2015a,b; Rodrigues et al., 2003; Uhrin et al., 2010).

The influence of urbanized areas on bat communities in temperate zones was emphasized in a series of studies showing several functions of settlements for bats. Bats can find hibernacula, swarming sites, maternity roosts, foraging grounds or transient roosts in such areas (e.g. Gehrt and Chelvig, 2004; Jung and Threlfall, 2016;

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Loeb et al., 2009; Neubaum et al., 2007; Oprea et al., 2009; Rydell, 1992). Furthermore, particular species can benefit from utilization of urbanized structures in various respects, including reduced predation risk, energetic benefits and/or the presence of social or mating partners. On the other hand, several negative consequences, such as human-biased threats, buildings as ecological traps and the presence of predators and pathogens, should also be considered (Voigt et al., 2016). Thus, from a conservation point of view, the contribution of urbanized areas in hosting viable populations of endangered bat species requires our attention (Shwartz et al., 2014).

Naturalness as a visual concept of the landscape character used in modern nature conservation practices can be measured by different indicators (level of succession, number or shape of habitat patches, shape or length of edges, etc.) and it describes how close a landscape is to a perceived natural state (e.g. Ode et al., 2009). Although the occurrence of bats in urbanized sites is well known, the relationship between urban roosts and surrounding landscapes with different degrees of naturalness is not yet fully understood in such species. Radio-tracking studies have suggested that almost all European bat species roosting in urbanized sites use adjacent woodlands and to some extent also arable land as foraging habitats (e.g. Arlettaz, 1999; Ashrafi et al., 2013; Bontadina et al., 2002; Catto et al., 1996; Dekker et al., 2013; Dietz et al., 2013; Entwistle et al., 1997; Flanders and Jones, 2009; Fonderflick et al., 2015; Krull et al., 1991; Robinson and Stebbings, 1997). Landscape analyses have shown a significant impact of the foraging habitat on roost selection by a species. In a heavily deforested landscape of the British Isles, the roost location of six urban-roosting bat species was positively associated with either the extent or proximity of broadleaved woodlands (Boughy et al., 2011). Certain house-dwelling bats depend on the availability of wooded elements near their roosts (Bellamy and Altringham, 2015; Moussy, 2011; Tournant et al., 2013), while others were found to forage in areas with a significantly higher cover of arable land and grassland (Tink et al., 2014). On the other hand, some well adapted city specialists benefit even from foraging in hostile urban areas (Ancillotto et al., 2016; Maxinová et al., 2016). Furthermore, the spatial integration of maternity roosts into a connected network allowing the exchange of individuals among roosts in a heterogeneous landscape was another factor explaining bat presence (Tournant et al., 2013). The degree of landscape urbanization or naturalness influences populations of bats in many aspects (Coleman and Barclay, 2011; Hale et al., 2012); however, the influence of landscape composition surrounding roost sites is scale-dependent (Gorresen et al., 2005; Mehr et al., 2011), and highly urbanized areas may thus represent a natural refuge (represented by gardens, orchards, parks) for some bat species within landscapes dominated by unsuitable types of land cover (Fabianek et al., 2011; Gehrt and Chelsvig, 2004; Jung and Threlfal, 2016; Li and Wilkins, 2014; Smith and Gehrt, 2010; Tink et al., 2014).

In Central Europe, there is wide spectrum of bat species that use man-made structures for roosting, however, as house-dwelling species are considered to be mainly those bats that occupy similar anthropogenic roosts in the urbanized areas of towns and villages, mostly spacious attics in large and old sacral buildings, where they establish nursery colonies (Dietz et al., 2009). Nowadays, these several species roost only in such anthropogenic roosts (exceptions in underground shelters are very rare; reviewed by Krištofik and Danko, 2012) and thus, from the point of view of roosting site, they can be considered as attic-dwelling bats. To answer how habitat composition and spatial heterogeneity influence roost-site selection by these species, a large scale study within a landscape with different degrees of naturalness may be helpful. Since all of the target species express strong roost-site fidelity (evidence gathered over decades is common), information about their occurrence could

be suitable for effective spatial analysis and predictive modelling. For this purpose, we used extensive data from attic-dwelling bat surveillance conducted in urban-located roosting sites over the whole area of Slovakia. We aimed to assess the occurrence of nursery colonies in such a type of roosts and the specific responses of bat species to different naturalness of the landscape that is considered to be their expected foraging area. Furthermore, on the basis of their habitat selection, we attempted to predict potential of the landscape for bats to establish their nursery colonies in areas where they were not yet recorded. In a landscape that offers suitable foraging habitats for some species but does not have suitable roosts available, such information could provide an effective and relevant conservation tool for attic-dwelling bats.

## Material and methods

### Study area

This study covers the whole territory of Slovakia (49,035 km<sup>2</sup>, 94–2655 m a.s.l.). The main part of the area belongs to the Carpathians; the lowlands in the south-west and south-east belong to the Pannonian Lowlands. The area is in the Atlantic climatic region and has a long-term average temperature of  $-3.9^{\circ}\text{C}$  in January and  $17.4^{\circ}\text{C}$  in July, with yearly precipitation of about 740 mm. The region is characterized by various vegetation zones divided into eight forest vegetation levels (oak, beech-oak, oak-beech, beech, fir-beech, spruce-beech-fir, spruce and dwarf pine) with a natural timber line at 1450–1700 m a.s.l. More than 42% of the country's area is forested. Although the area is relatively densely populated by humans (110 inhabitants per km<sup>2</sup>) living in 138 towns and 2885 villages, settlements are concentrated in rural landscapes. There are only three larger towns – that is heavily build-up sites – that have 100–500 thousands inhabitants.

### Data collection

We collected all available data (ca. 2700 records collected during 1960–2009), both published (compiled by Uhrin and Polakovičová, 2000; Uhrin, 2006; Uhrin and Ševčík, 2011) and unpublished, on attic-dwelling bats occurring in the attics of buildings in Slovakia. From this large source of data, we selected records on bat species that dominate in this type of building roost in Slovakia and that establish nursery colonies for reproduction almost exclusively in them (Krištofik and Danko, 2012). Bats roosting in other parts of buildings (e.g. behind gutter pipes and claddings, in wall crevices, etc.) were thus omitted from our survey. Using this criterion we analysed the occurrence of the greater horseshoe bat *Rhinolophus ferrumequinum* (Schreber, 1774), the lesser horseshoe bat *Rhinolophus hipposideros* (Borkhausen, 1797), the greater mouse-eared bat *Myotis myotis* (Borkhausen, 1797), the lesser mouse-eared bat *Myotis blythii* (Tomes, 1857), Geoffroy's bat *Myotis emarginatus* (Geoffroy, 1806), the serotine bat *Eptesicus serotinus* (Schreber, 1774), the brown long-eared bat *Plecotus auritus* (Linnaeus, 1758) and the grey long-eared bat *Plecotus austriacus* (Fischer, 1829).

### Statistical analysis

In order to identify the factors influencing the presence of nursery colonies of attic-dwelling bats in landscapes of different degree of naturalness, we used seven environmental variables which characterise the habitat surrounding bat roosts. We recorded altitude and calculated the relative proportion of main habitat types (forest, arable land, gardens [including hop-gardens, vineyards and orchards], grassland, and urban land) within a circle of 5-km radius around each roost (78.5 km<sup>2</sup>). We then estimated the landscape heterogeneity as the length of the boundaries between the five

**Table 1**

The number of roosts in which single individuals of attic-dwelling bats were found and the number of roosts with nursery colonies in the estimated size categories according to the number of individuals.

Species	Solitary individuals	Nursery colonies		
		tens	hundreds	thousands
<i>Eptesicus serotinus</i>	169	148	1	0
<i>Myotis blythii</i>	29	14	6	0
<i>Myotis emarginatus</i>	39	21	17	0
<i>Myotis myotis</i>	328	88	111	10
<i>Plecotus auritus</i>	66	41	0	0
<i>Plecotus austriacus</i>	232	113	0	0
<i>Rhinolophus ferrumequinum</i>	92	3	7	0
<i>Rhinolophus hipposideros</i>	170	163	18	0

main habitats evaluated within the circular area. Reviewing the average distance between the roost and the foraging area (if available, we considered also the size of foraging areas or home ranges) in the examined attic-dwelling bats, we found that the 5-km distance had the best overlap across different species (Table S1 of Supplementary information; Arlettaz, 1999; Ashrafi et al., 2013; Audet, 1990; Bontadina et al., 2002; Catto et al., 1996; Dekker et al., 2013; Dietz et al., 2013; Flanders and Jones, 2009; Fonderflick et al., 2015; Holzhaider et al., 2002; Krull et al., 1991; Razgour et al., 2011; Robinson and Stebbings, 1997; Rudolph et al., 2009; Zahn et al., 2005). Although individual foraging range in few species can usually exceed five kilometres (it is notably the case of *M. myotis*; Audet, 1990; Rudolph et al., 2009; Zahn et al., 2005), larger radius will more likely increase proportion of area that is largely unproductive regarding to main foraging grounds of the whole colony. This could underestimate possible effects of measured landscape variables, thus, we employed this value as a fixed-length radius to characterise only the core area of the surrounding landscape that could determine roost site selection of these bats. The spatial data were obtained from different map sources (Slovak Forest National Database, Land Parcel Identification System and basic topographic map of the Slovak Republic using grid layers with 25 m pixels) and processed in the QGIS 2.8 software (QGIS Development Team, 2015).

The size of nursery colonies is species-specific (Table 1), and it is often difficult to properly estimate the number of bats, especially in large colonies and in species that roost in narrow shelters or behind timbers. Further, colony size changes during the reproduction period (juveniles were not always distinguished from adult females in our dataset), and it may also change significantly over years; thus, we used species presence information only. Such conservative approach had support also in preliminary modelling of count data (model formula was similar as described below) which did not yield more statistically significant results or different patterns comparing to binary data. For example, none relationship between colony size and environmental variables was observed also in the species *M. myotis* that had the largest variation in colony size (Table 1). From the set of all roosts inhabited by colonies of females and their offspring ( $n = 632$  buildings, Fig. 1) we obtained positive occurrences for each bat species (Fig. S1 of Supplementary information). Although our source of bat occurrence data covered a period of 50 years, majority of nursery roosts (85%) was recorded or rediscovered in the recent period of 1990–2010, while most field work was done in the period 1995–2000 (Fig. S2 of Supplementary information). During this time main landscape characteristics could change only insubstantially overall in the study area, whereas on the other hand, some old bat data came from the regions where no recent field work was performed. Thus, we were confident that the small proportion of historical records should not produce statistical bias when using only recent spatial data in the analysis. The remaining nursery roosts which were not occupied by a particu-

**Table 2**

Factor loadings of the two first principal components extracted by principal component analysis. Important loadings are in bold print.

Variable	PC1	PC2
altitude	<b>0.48</b>	0.00
forest	<b>0.47</b>	-0.36
arable land	<b>-0.52</b>	0.00
gardens	-0.25	-0.11
grassland	0.33	<b>0.58</b>
urban land	-0.33	0.20
heterogeneity	0.00	<b>0.69</b>
Proportion of variance	0.42	0.24

lar species were considered as negative roosts (the ratio of positive to negative occurrences ranged from 1:3 to 1:63). For modelling the binary response, we employed generalized linear mixed-effects models (GLMM) with a logistic link function. As we found significant correlations between most of the environmental variables ( $r_s = |0.17-0.80|$ ,  $p < 0.001$ ), we used principal component analysis (PCA) to convert them into linearly uncorrelated principal components (PC). Prior to PCA, data were standardised by subtracting the mean and dividing by the standard deviation. The scores of the first two PCs (Fig. S3 of Supplementary information), which accounted for the most variability in the data (66%), were included in the GLMM as fixed factors together with their interactions. Variables with loadings  $>|0.4|$  were considered to be important for factor interpretation (Table 2). As some roosts were occupied by more than one species (range 1–5), which could be linked to building characteristics (e.g. construction, size, age) or regional differences (e.g. karst phenomena presence, density of roosts, availability of hibernacula), the number of other species nursing in the same roost was incorporated as a random factor in all models. The pattern of species co-occurrence was assessed using  $\phi$  correlations and the significance of this relationship was tested using the  $2 \times 2 \chi^2$  test. Finally, we used the scores of the first two PCs for the surrounding habitat of all roosts ( $n = 1299$  buildings) which were occupied by bat species, irrespective of whether they were occupied by nursery colonies or solitary individuals only, to predict suitability of the landscape surrounding these roosts to establish nursery colonies. This prediction has arisen from the fact that if solitary individuals occurred in the roost, one can expect species reproduction and roost accessibility at least in the area. It was calculated in species where tested factors (PC1 or PC2) had a significant effect on occurrence of their nurseries. We utilized parameter estimates of the respective GLMM models, which predicted probabilities of species occurrence in relation to habitat characteristics and ranged from 0 – negative to 1 – positive occurrence. We then created a raster in the QGIS software as an interpolation of the predicted probabilities across whole study area. To visualise the effect of the two significant factors together, the two rasters were merged.

Data was analysed in the R 3.3.0 environment for statistical computing (R Core Team, 2016). For graphical display of the correlation matrix we used the package ‘corrplot’ (Wei, 2015). The function *glmer* with Laplace approximation was used for parameter estimation in the package ‘lme4’ (Bates et al., 2016). Variance explained by the fixed factors only (marginal  $R^2$ ) and by the whole model, including the random factor (conditional  $R^2$ ), was computed using the package ‘MuMIn’ (Bartoń, 2016).

## Results

We obtained 1886 records in 1299 roosts for the set of eight attic-dwelling bat species selected. Four species – *M. myotis*, *R. hipposideros*, *P. austriacus* and *E. serotinus* – were recorded most frequently. The proportions of nursery colonies in these records (761 nursery colonies roosted in the attics of 632 buildings) were

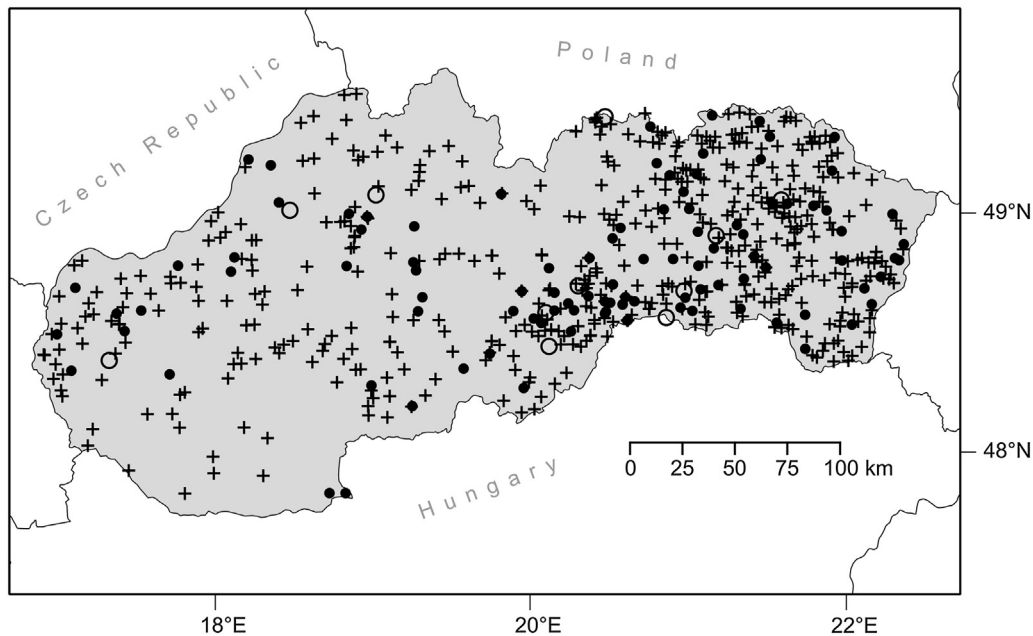


Fig. 1. Spatial distribution of single (crosses), double (full circles) and multi-species 3–5 (open large circles) roosts of bats in the study area of Slovakia.

Table 3

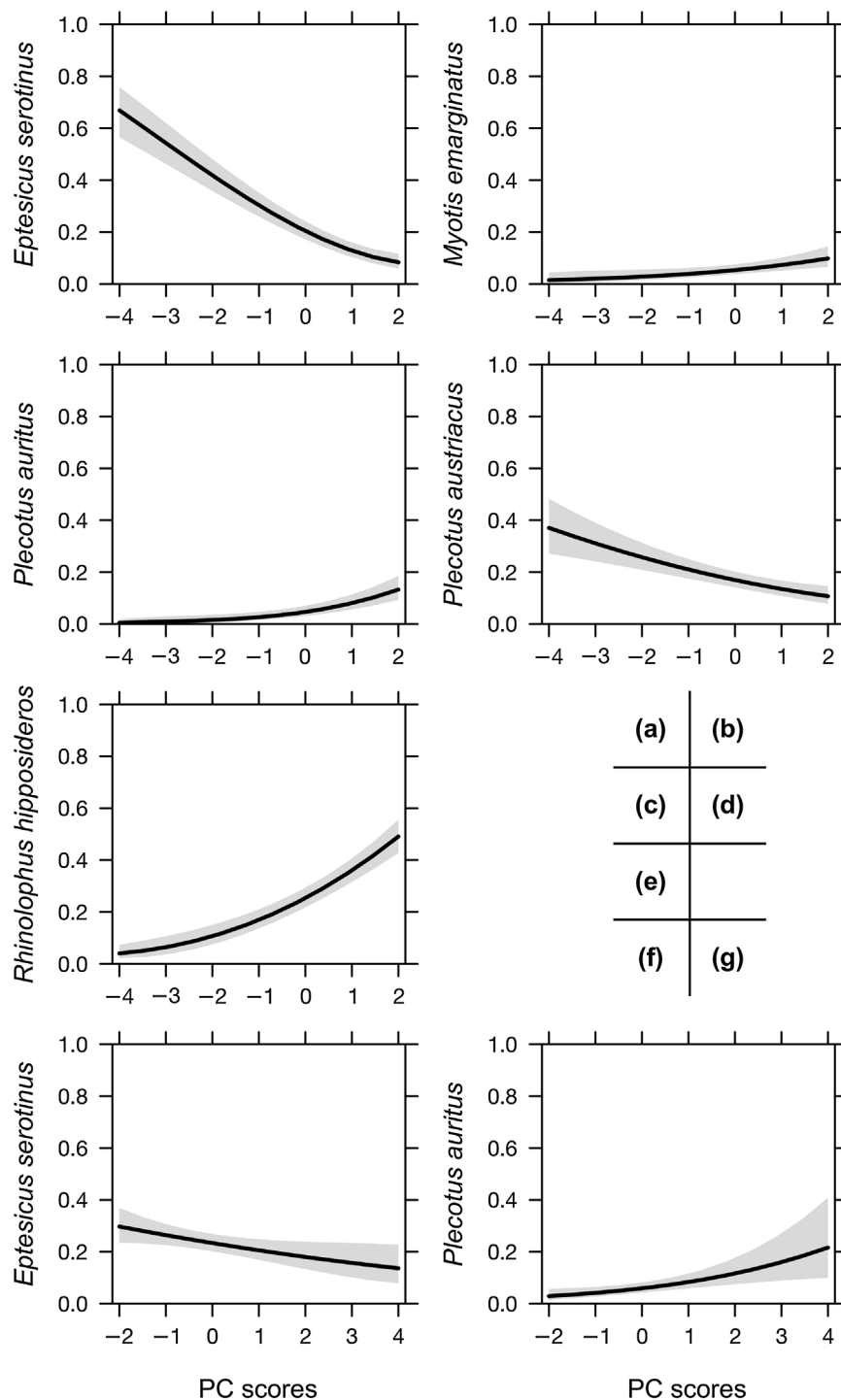
Matrix of roosting co-occurrence of species showing  $\phi$  coefficient (above diagonal) with  $p$ -values of  $2 \times 2 \chi^2$  test (under diagonal).

	<i>Eptesicus serotinus</i>	<i>Myotis blythii</i>	<i>Myotis emarginatus</i>	<i>Myotis myotis</i>	<i>Plecotus auritus</i>	<i>Plecotus austriacus</i>	<i>Rhinolophus ferrumequinum</i>	<i>Rhinolophus hipposideros</i>
<i>Eptesicus serotinus</i>								
<i>Myotis blythii</i>	0.05							
<i>Myotis emarginatus</i>	0.02	0.85						
<i>Myotis myotis</i>	0.00	0.00	0.05					
<i>Plecotus auritus</i>	0.00	0.23	0.09	0.00				
<i>Plecotus austriacus</i>	0.00	0.03	0.00	0.00	0.02			
<i>Rhinolophus ferrumequinum</i>	0.31	0.57	0.00	0.12	0.40	0.14		
<i>Rhinolophus hipposideros</i>	0.00	0.72	0.02	0.00	0.00	0.00	0.19	

all at a similar level (range 33–52%). The only exception was *R. ferrumequinum*, for which records of solitary individuals predominated (90%; Table 1). The size of the nursery colonies differed among species, with the highest number of individuals in *M. myotis* and the smallest in both *Plecotus* species and *E. serotinus* (Table 1). The majority of roosts (82%) were occupied by a single species; however, some roosts were used by two (16%), three (1.2%), four (0.3%) or even five (0.2%) species. Bats that mainly formed single-species nursery colonies were *E. serotinus* and both *Plecotus* species. On the other hand, some species often occurred together with other bats. The multi-species roosting of *M. emarginatus* with both *Rhinolophus* species and the very frequent co-occurrence of the two sibling mouse-eared bat species (*M. myotis*, *M. blythii*) in a common roost were found to be statistically significant (Table 3). Despite uneven spatial sampling in the study area, upon exploring the occurrence of roosts that were occupied by two or more species it was apparent that their occurrence is well-proportioned when compared with single-species roosts (Fig. 1).

The PC1 (strong positive contribution received from altitude and forest while negative contribution from arable land on the other hand) and PC2 (strong positive contribution from grassland and overall landscape heterogeneity) factors could be associated with the probability of occurrence of nurseries in most of the analysed attic-dwelling species. The PC1 had a significant effect in five of the eight selected species, while the PC2 had an additional effect in *E. serotinus* and *P. auritus*. A significant interaction between the

two tested factors was found in *P. austriacus* only (Fig. 2, Table 4). According to the loadings of the principal components in the study area (Table 2), some bats established their nurseries in either a habitat with a higher proportion of forests in sub-mountain/mountain altitudes (*R. hipposideros*, *P. auritus*, *M. emarginatus*), or they preferred arable land in lowlands (*E. serotinus*, *P. austriacus*). Higher habitat heterogeneity and proportion of grassland was positively connected with the occurrence of *P. auritus* while nurseries of *E. serotinus* occurred mostly in lowland regions where these variables had smaller values. Fixed effects in significant GLMM models explained 5–27% of the variability only when another proportion could be explained by random factors (up to 63%). Zero difference was found between conditional and marginal  $R^2$  in *E. serotinus* and both *Plecotus* species (Fig. 2, Table 4), that is, in species that have smaller colonies (Table 1) and do not often roost with other bats (Table 3). Although some species models resulted in non-significant estimates, the predicted occurrence of nursery colonies based on habitat suitability suggests that the area of Slovakia could be divided into two regions with different bat species composition. These regions are environmentally well defined, thus specific requirements for management practices are then expected; they are (1) a region with a warm continental climate in the Pannonian Lowlands (SW and SE Slovakia) and (2) a less urbanized mountain region with a temperate continental climate in the Western Carpathians (central and N Slovakia; Fig. 3).

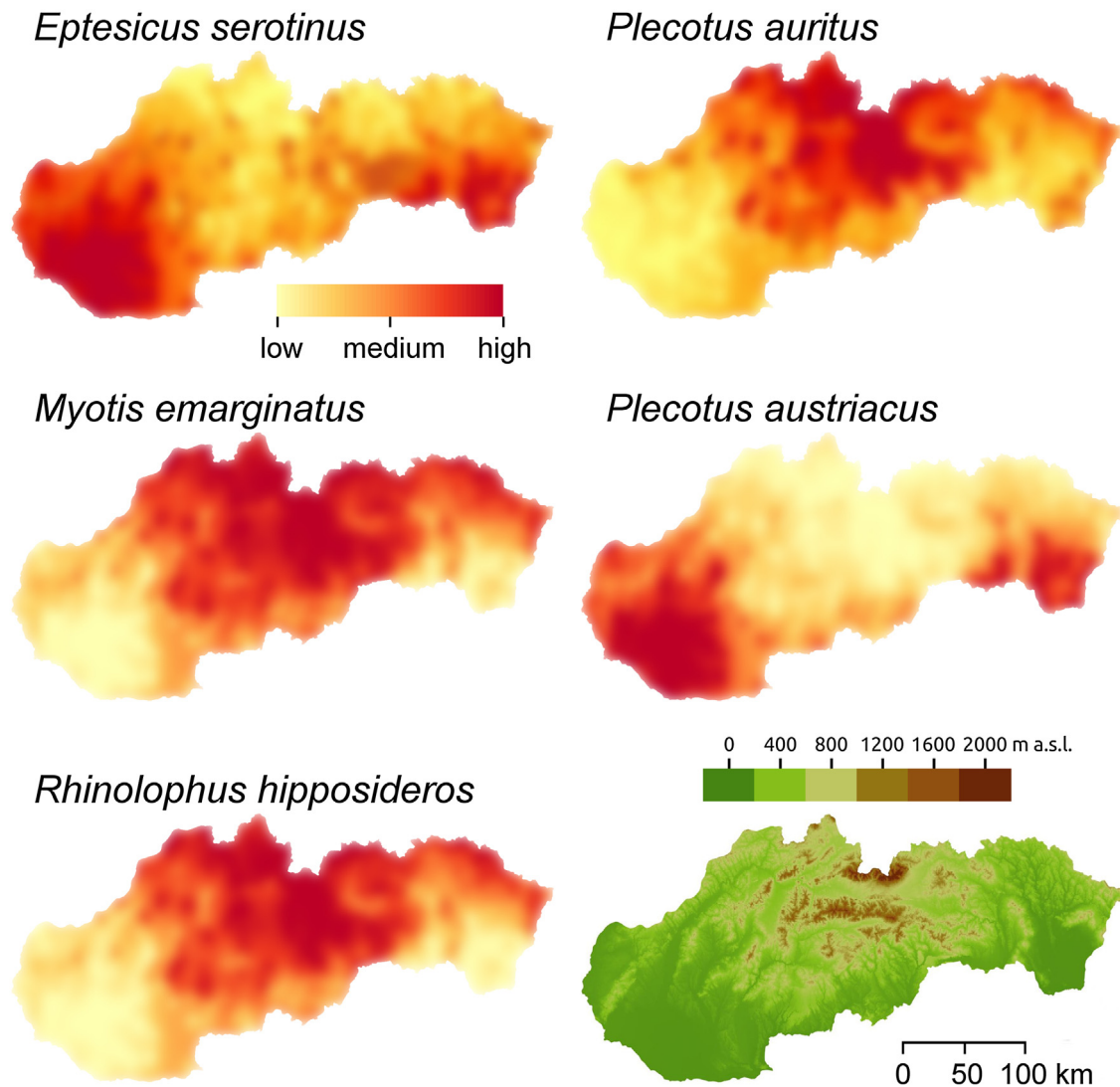


**Fig. 2.** Predicted probabilities of species occurrence in relation to habitat characteristics. Logistic probabilities with 95% confidence intervals are derived from generalized linear models with a binary response (0–negative, 1–positive occurrence). Only significant ( $p < 0.05$ ) main effects of PC1 (a–e) and PC2 (f–g) are shown. For habitat characteristics associated with principal components, see [Table 2](#).

## Discussion

Our results, based on extensive occurrence data collected in the heterogeneous landscape of Slovakia, has shown different responses of synurbic and highly philopatric bat species (e.g. [Catto et al., 1996](#); [Harbusch and Racey, 2006](#); [Horáček, 1985](#)) to the quality of habitats that surround their urban-located roosts. Along with species occurring more in forest/mountain landscapes that possess a higher degree of naturalness (*R. hipposideros*, *P. auritus*, *M.*

*emarginatus*) and species that dominate in more urbanized, but heterogeneous, lowland areas (*E. serotinus*, *P. austriacus*), there were also some species (*M. blythii*, *M. myotis*, *R. ferrumequinum*) that did not express any specific preferences according to the tested variables. Overall species distribution is always larger comparing to distribution of nursery colonies only as males should have lower requirements on roost quality than females ([Kunz, 1982](#)). Our predictive modelling demonstrated that potential of establishing nursery colonies is besides suitable/available roosting site also



**Fig. 3.** Suitability of the area for bats to establish nursery colonies (the darkest areas are highly suitable) according to habitat characteristics. The raster was created as an interpolation of predicted probabilities of species occurrence from generalized linear mixed-effects models (Table 4, Fig. 2) for all roosts. If both factors had significant effects in the model, the two rasters for PC1 and PC2 were merged.

limited by surrounding landscape characteristics that are related to foraging grounds of these colonies. In heterogeneous landscape, where several species depend on one type of man-made shelter thus possible competition for roosting site or other mutually determined interactions are expected (Arlettaz, 1999; Arlettaz et al., 2001; Ashrafi et al., 2013; Ekman and de Jong, 1996), understanding of species occurrence needs more complex view. Comparing to previous studies which analysed the species-specific patterns often separately and in different environmental conditions, presented large scale analysis (more than one thousand of roosts inhabited by eight bat species and distributed across 49 thousands square kilometres) figured out the influence of landscape naturalness on the presence of nursery colonies of each species with regard to common area. Therefore, obtained results make better opportunity to generalize previous knowledge about species responses in different local conditions. The degree of landscape naturalness was clearly a determining factor for roost-site selection by most attic-dwelling bats in our study; however, to understand its influence on the observed patterns, one should also consider other ecological traits in the evaluated species.

A strong association of gleaners that forage in closed tree vegetation with forest habitats is well documented and widely accepted thanks to data from telemetry studies (Ashrafi et al., 2013; Bontadina et al., 2002; Dekker et al., 2013; Fonderflick et al., 2015; Holzhaider et al., 2002; Krull et al., 1991) and analyses of distributional patterns (Boughey et al., 2011; Entwistle et al., 1997). In the study area, the attic-dwelling gleaner species, *P. auritus* and *M. emarginatus*, were found foraging mainly in natural and old forests (Kaňuch et al., 2008). Together with *R. hipposideros* their roost locations were found to be dependent on surrounding broadleaved woodland or similar habitats, like orchards and riparian vegetation (Entwistle et al., 1997; Boughey et al., 2011). This is also supported by our results. In contrast, habitat heterogeneity in the forested landscape was not important for *R. hipposideros* and *M. emarginatus* in the examined models (Table 4). Although *M. emarginatus* often occurs in semi-open highly structured forest and farmlands (Dietz et al., 2013), fine determination of stand structure was beyond the limits of spatial resolution in our study design. Still, some preferences of highly structured habitats could be observed in *P. auritus*, the occurrence of which was also positively influenced by the proportion of grassland and higher level of landscape heterogeneity

**Table 4**

Effect of habitat characteristics (explained by PC1 and PC2 components) on the probability of species occurrence (binary response) in generalized linear mixed-effects models, where the number of other bat species in the roost was incorporated as a random factor.  $R^2_m$ —variance explained by fixed factors only (marginal),  $R^2_c$ —variance explained by all factors (conditional),  $df=1$  for all terms. For habitat characteristics associated with PC components see Table 2.

Species/ $R^2_m/R^2_c$	Factor	$\chi^2$	$p$
<i>Eptesicus serotinus</i> 0.21 0.21	PC1	72.59	<0.001
	PC2	4.80	0.028
	PC1*PC2	0.75	0.386
<i>Myotis blythii</i> 0.03 0.69	PC1	3.44	0.063
	PC2	0.20	0.655
	PC1*PC2	0.60	0.439
<i>Myotis emarginatus</i> 0.05 0.48	PC1	4.63	0.031
	PC2	2.48	0.116
	PC1*PC2	0.14	0.711
<i>Myotis myotis</i> 0.01 0.29	PC1	2.23	0.135
	PC2	1.79	0.181
	PC1*PC2	3.21	0.073
<i>Plecotus auritus</i> 0.27 0.27	PC1	17.56	<0.001
	PC2	8.02	0.005
	PC1*PC2	3.18	0.074
<i>Plecotus austriacus</i> 0.10 0.10	PC1	18.24	<0.001
	PC2	0.17	0.682
	PC1*PC2	13.47	<0.001
<i>Rhinolophus ferrumequinum</i> 0.17 0.68	PC1	1.15	0.283
	PC2	0.72	0.395
	PC1*PC2	1.71	0.191
<i>Rhinolophus hipposideros</i> 0.07 0.70	PC1	56.97	<0.001
	PC2	0.02	0.890
	PC1*PC2	0.02	0.895

(Table 4). This has already been suggested for various populations of this bat (Ashrafi et al., 2013; Bellamy and Altringham, 2015; Moussy, 2011); however, extremely high forest fragmentation may turn into a negative factor influencing species occurrence (Ekman and de Jong, 1996).

In contrast to the previous group of species, the presence of *E. serotinus* and *P. austriacus* nurseries was positively affected by a higher proportion of open habitats in arable and grasslands (Fig. 2). Generally, the roosts of *E. serotinus* are often located in sparsely forested, predominantly agricultural lowlands (Catto et al., 1996; Robinson and Stebbings, 1997). However, in some regions *E. serotinus* also selected different habitats (villages, roads through coniferous forests or coastal dunes) due to its very opportunistic foraging strategy (Ciechanowski, 2015), which may explain the correlation between the higher level of landscape heterogeneity and the occurrence of nursery colonies in our study area. Foraging along hedges and tree lines in open habitats or in proximity to unimproved grasslands near roosting sites, as observed by some authors (Ashrafi et al., 2013; Razgour et al., 2011), could also explain the only significant interaction term of the two tested principal components in the model constructed for *P. austriacus* (Table 4).

Although habitat composition and structure have previously been found to be factors determining spatial activity in the remaining evaluated bat species, *M. myotis*, *M. blythii* and *R. ferrumequinum* (Arlettaz, 1999; Flanders and Jones, 2009; Fonderflick et al., 2015; Zahn et al., 2005, 2006), we did not find any such association with surrounding roost habitats in our analysis. Other factors, which were not tested for, could be therefore more responsible for their roost-site selection here. For example, food availability was found to be the major factor regulating the patterns of life history traits in the mouse-eared bats, *M. myotis* and *M. blythii*, and furthermore, both species may search for very distant foraging grounds, where they prey opportunistically on temporary swarms of large

arthropods (Arlettaz et al., 2001). Compared with the other species evaluated, the average colony size of these, the largest of the attic-dwelling bats, is much bigger, usually representing hundreds or even thousands of individuals (Table 1). This probably limits the availability of roosts for such big colonies and may impact other species, too. This factor may also explain the very long-term fidelity to some roosting sites; many attics are known to be occupied for decades (Güttinger et al., 2001; Topál and Ruedi, 2001), while avoidance of roosting with other species (*E. serotinus*, *P. austriacus*) in the same roost was found (Table 3). Thus, their roost selection in urban habitats is probably determined by a complex of factors rather than by a few analysed landscape elements only. In the specific case of *R. ferrumequinum*, non-significant habitat variables could have probably resulted from the small sample size. This species reproduces only in isolated regions that are geographically characterized by a warm limestone landscape, similarly to other congeneric species occurring there at their northern range limits (Uhrin et al., 1996, 2012). The geographical character, combined with climatic variables, may thus explain the distribution of some of the bat species in our study (cf. Michaelsen et al., 2011; Milne et al., 2006).

Because we analysed data that were collected over a long term, though the majority were collected during the last 15 years (Fig. S2 of Supplementary information), one could speculate further about possible effects of the temporal aspect in landscape change. However, upon removing this smaller proportion of historical records before 1990 from the analyses, the results did not change, and all significant effects of landscape characteristics on the presence of species remained consistent (Table S2 of Supplementary information). If recent bat roosts established in the past would reflect in some extent also landscape structures that no more exist, then spatial robustness of our study should suppress such effect. Bats are considered to be reliable bioindicators due to their sensitivity to environmental changes (Russo and Jones, 2015); thus, knowledge about landscape potential to accommodate and nourish specific bat species could be useful in adaptive decision-making process as a tool for integrated natural resource management. The efficiency of bat conservation by protected areas in Europe is not well analysed (Lisón et al., 2015; Maiorano et al., 2015). Most of the species analysed in this study were evaluated as being particularly sensitive to a high level of habitat fragmentation (Frey-Ehrenbold et al., 2013), and thus, effective conservation measures should be applied in the important habitat types identified (e.g. bat friendly forest management, pesticides regulations in farmland), considering the functional level of heterogeneity and connectivity between them (Lintott et al., 2015b; Park, 2015). The diverse landscape with various types of connected habitats positively supports species diversity, which may be, especially in agricultural landscape, important for potential ecosystem services offered by bats (e.g. insect pest control, nutrients from guano), which include synurbic species too (Puig-Montserrat et al., 2015; Williams-Guillén et al., 2016). Furthermore, in addition to appropriate habitat management in the vicinity of roosts, it is still necessary to protect the roosts themselves, as they may be permanently affected by several detrimental factors such as destroying of old buildings and reconstructions making bats entry restraints, human disturbance or even killing (e.g. Rowse et al., 2016; Stone et al., 2015; Voigt et al., 2016).

## Acknowledgements

We are grateful to all colleagues who kindly provided their data, but mainly (in alphabetical order) Martin Cel'uch, Blanka Lehotská, Edita Maxinová, Michal Noga, Mária Petrášová, Michal Rendoš and Martin Ševčík. In this study, data gathered by the 'Information

System of Taxa and Biotopes' (State Nature Conservancy of the Slovak Republic) were also used. Valuable corrections and suggestions by Karen Haysom and comments from one anonymous reviewer helped to improve the previous version of the manuscript. The study was supported by grants from the Cultural and Educational Grant Agency (KEGA 012UPJŠ-4/2014) of the Ministry of Education, Science Research and Sport of the Slovak Republic, and the Ministry of Culture of the Czech Republic (DKRVO 2016/15, 00023272).

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.mambio.2016.10.001>.

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