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Assemblages of bats are phylogenetically clustered on a regional scale

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Abstract

Phylogenetically related species are assumed to be ecologically similar. Ecological similarity might lead to competition and to low distributional overlap. Therefore, if competitive interactions drive assemblages, we expect a decrease in distributional overlap with increasing phylogenetic relatedness and phylogenetic over-dispersion in assemblages. We tested this hypothesis by evaluating the mean phylogenetic distance of bat assemblages within grid cells of $\approx 36 \text{ km}^2$ across Bavaria, Germany (887 grids; 20,023 records). To calculate phylogenetic distance between species, we used a phylogenetic tree derived from sequences of three mitochondrial genes (cytb, COI, ND1), two nuclear-protein-encoding genes (vWF, RAG2) and the genes encoding 16S rRNA, 12S rRNA and tRNA-Val. Overall, bat species co-occurring within grid cells were more similar than expected from null models (phylogenetic clustering). This suggests that on the considered scale, bat assemblages are triggered more by environmental filters than by competition. Furthermore, mean phylogenetic distance decreased with the amount of anthropogenic habitats within grids. This contrasts with species richness of bats, which increased with anthropogenic habitats.

Zusammenfassung

Phylogenetisch verwandte Arten sind auch ökologisch ähnlich, was zu Konkurrenz führen kann. Wenn Konkurrenz eine Rolle spielt, dann erwartet man auch für phylogenetisch ähnliche Arten eine geringere Überlappung in ihrer Verbreitung sowie für Artengemeinschaften eine größere genetische Distanz als erwartet. Wir prüften diese Hypothese anhand der mittleren phylogenetischen Distanz von Fledermausgemeinschaften in Rasterquadraten Bayerns ($\approx 36 \text{ km}^2$; 887 Quadrate, 20.023 Datensätze). Zur Berechnung der phylogenetischen Distanz zwischen den Arten erstellten wir einen phylogenetischen Baum aus den Sequenzen von drei mitochondrialen Genen (cytb, COI, ND1), zwei Kern-Protein-kodierenden Genen (vWF, RAG 2) und den Genen für 16sRNA, 12sRNA und tRNA-Val. Im Gegensatz zur Erwartung stieg die Überlappung in der Verbreitung mit der phylogenetischen Distanz an, und Fledermausarten, die gemeinsam innerhalb eines Kartengitters vorkamen, waren phylogenetisch näher verwandt als auf Basis von Nullmodellen erwartet. Die Zusammensetzung von Fledermausgemeinschaften scheint auf der

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betrachteten Skala, mehr durch ökologische Bedingungen als durch Konkurrenz beeinflusst zu sein. Darüber hinaus verringerte sich die mittlere phylogenetische Distanz mit steigendem Anteil urban geprägter Habitate, während die Artenzahl sogar stieg. © 2012 Gesellschaft für Ökologie. Published by Elsevier GmbH. All rights reserved.

Keywords: Competition; Ecological filters; Landuse; Over-dispersion; Phylogenetic clustering; Urban environments

Introduction

Under the assumption that species within a genus are ecologically similar (niche conservatism; Losos 2008; Wiens et al. 2010), species-to-genus ratios have been used to infer interactions within assemblages of organisms (Elton 1946). A development of this approach is the analysis of phylogenetic distance between species co-occurring in assemblages (Cavender-Bares, Kozak, Fine, & Kembel 2009; Pavoine & Bonsall 2011; Vamوسي, Heard, Vamوسي, & Webb 2009). If co-occurring species are phylogenetically more related than expected by chance, environmental filters are an important force structuring communities. In contrast, over-dispersion might indicate competitive interactions. Phylogenetic over-dispersion should occur at small spatial scales, whereas phylogenetic clustering should be common in harsh environments and at large spatial scales (Vamوسي et al. 2009; Wiens 1977; but see Chesson & Huntly 1997). Furthermore, if competition is important, one expects also an increase of phylogenetic similarity with decreasing distributional overlap across species pairs.

Humans transform landscapes at an unprecedented rate (Hooke 2000). One important aspect of these changes is urbanization: more than 50% of the world's population live at present in cities (Grimm et al. 2008). Cities that developed in heterogeneous landscapes (Kühn, Brandl, & Klotz 2004) have a unique climate with elevated temperatures (Knapp, Kühn, Schweiger, & Klotz 2008) and provide numerous habitats (Niemelä 1999). Therefore, on larger spatial scales, urban environments as a whole can be astonishingly species rich, even richer than surrounding rural habitats (Knapp et al. 2008; Stadler, Trefflich, Klotz, & Brandl 2000; Wania, Kühn, & Klotz 2006). Urban environments harbour also alien species that contribute to the species richness of cities (Brunzel, Fischer, Schneider, Jetzkowitz, & Brandl 2009). However, although cities are hotspots of plant species richness, this is not reflected by phylogenetic diversity (Knapp et al. 2008): the richness is due to the occurrence of phylogenetically related species, which are assumed to be able to cope with the conditions in urbanized areas. In line with these findings, alien species in cities show a lower phylogenetic diversity than native species (Ricotta et al. 2009). Obviously, urban areas impose strong environmental filters that can be passed only by species with appropriate adaptations (Kühn et al. 2004; Ricotta et al. 2009).

Using grid cells of approximately 6 km × 6 km, Mehr et al. (2010) showed that across Bavaria (Germany), the species

richness of bats increases with the amount of urban environments. However, this correlative study was not able to infer the ecological processes driving these bat assemblages. Across Denmark, the regional occurrence of bird species shows signs of competitive interactions (Gotelli, Graves, & Rahbek 2010). These studies encouraged us to ask to what extent assemblages of bats are also influenced by competitive interactions on this scale. We re-analysed the data of Mehr et al. (2010) to answer two questions. First, are competitive interactions between species important for the regional distribution of bats? Competitive interactions should lead to a negative correlation between phylogenetic relatedness and distributional overlap as well as to phylogenetic over-dispersion. Second, do assemblages of bat species show contrasting patterns of species richness and phylogenetic diversity similar to plants when grids dominated by urban environments are compared to grids dominated by rural landscapes?

Materials and methods

Bavaria covers an area of 70,552 km². The mean annual temperature varies from 10 °C in the north to –5 °C in the south (Alps), and the annual precipitation varies from around 500 mm in the north to 2000 mm in the south. As a consequence of the climatic conditions, the northern regions are used mainly as cropland, while meadows prevail in the south.

The bat data originate from the database of the Bavarian Environment Authority (Landesamt für Umwelt, LfU). These data comprise presence/absence data of 22 bat species occurring across the sub-grids of the topographic map of Bavaria (1:25,000; TK25). The average area of a sub-grid is 33.9 km². For each grid cell, we compiled the presence/absence data of bat species using information collected from April to October between 1985 and 2008. We use the term “sampling campaign” for any set of bat records (netting, at summer roosts, bat calls) in the database. Preliminary analysis revealed a positive relationship between the number of species recorded within grid cells and the number of sampling campaigns ($r=0.31$; $n=1927$; $P<0.001$). Therefore, we decided to select only grid cells with at least seven sampling campaigns for further analyses (for details, see Mehr et al. 2010; 887 grids with 20,023 records of 22 species).

Geneious v. 5.0.3 was used to search GenBank for sequence data of the 22 bat species occurring in Bavaria. Data of three genes encoding mitochondrial proteins (ND1, COI, cyt**b**), two genes encoding nuclear proteins (vWF, RAG2)

and the genes encoding 16S rRNA, 12S rRNA and tRNA-Val were used. We selected these genes because for each bat species the sequences of at least three of these genes were available. We included also sequences for *Bostaurus*, *Rattus norvegicus*, *Taxidea taxus*, *Lynx canadensis*, *Canis lupus*, *Sorex araneus* and *Rousettus aegyptiacus*. The sequences of each gene were aligned in GENEIOUS, and the single alignments were concatenated (7952 base pairs; Appendix A: Table S1).

To construct the phylogenetic tree, we used TREEFINDER (Jobb 2008). In their phylogenetic analyses of bats, Jones, Bininda-Emonds, and Gittleman (2005) and Teeling et al. (2005) used the general time reversible (GTR) substitution model; therefore, we made no attempt to search for the overall best model or for separate models for each locus. We used the GTR substitution model, including unequal rates across sites (GTR [Optimum, Empirical]:GI[Optimum]:4), with *R. norvegicus* as the outgroup (for further details, see Appendix A: Fig. S1). We then removed the outgroup and all other non-bat species (including *R. aegyptiacus*), and scaled the data to an ultrametric tree using *chronopl* in the add-on package *ape* within R (version 2.10.1; R Development Core Team 2004) (Fig. 1). This method uses the parameter λ to implement a trade-off between a parametric rate smoothing, where each branch has its own rate, and a non-parametric term, where changes in rates are minimized. If $\lambda = 0$, then rates vary as much as possible among branches, whereas for increasing values of λ , the variations are smoother and tend toward a clock-like model. We arbitrarily used a value of $\lambda = 1$. From this ultrametric tree (Fig. 1), patristic distances between species were calculated using the function *distTips* in the add-on package *adephylo* of R. The branch length from root to tip equals 1 by definition.

To test for correlations between co-occurrence patterns of species and phylogenetic distance between species, we calculated an interspecific similarity matrix based on the occurrence of species across grids using Schoener's index. Originally this index was used to measure overlap in habitat use or diet (Renkonen 1938; Schoener 1970). An index of 0 indicates that two species never occur in the same grid; an index of 1 indicates that the two species always occur together. For these analyses, we used the function *comm.phylo.cor* within the add-on package *picante* in R and two null models to test for significance with 999 null communities. First, we reshuffled the tip labels in the phylogenetic tree. This null model retains the community matrix and tests whether the phylogenetic composition of species within grids is random with respect to the phylogeny. Second, we used the independent swap algorithm to generate reshuffled assemblages (Gotelli & Entsminger 2001). This fixed-fixed (*FF*) null model maintains species occurrences across grids and species richness within grids.

To evaluate the phylogenetic structure of assemblages from the distance matrix, we calculated the mean phylogenetic distance between co-occurring bat species within each grid using the add-on package *picante*. We calculated the

standardized effect size of the mean phylogenetic distance (Webb, Ackerly, McPeck, & Donoghue 2002):

$$\frac{(mpd.obs - mpd.rand.mean)}{mpd.rand.sd},$$

with *mpd.obs* being the observed mean phylogenetic distance in communities, *mpd.rand.mean* being the mean distance in null communities (see above) and *mpd.rand.sd* being the standard deviation of mean distance across null communities. Values < 0 indicate ecological clustering, whereas values > 0 indicate phylogenetic over-dispersion. Note that sometimes the sign is inversed, and the resulting index labelled as the net relatedness index (Webb et al. 2002). As the regional species pool is composed of only 22 bat species, species richness in the different cells should be much lower. Otherwise, for cells with high species richness, *mpd.rand.mean* converges to *mpd.obs*, and *mpd.rand.sd* converges to zero. However, maximum species richness was 14, and most grids showed values < 10 .

Recently, Ulrich, Piwczynski, Maestre, and Gotelli (2012) linked phylogenetic community structure and environmental variables to pair-wise patterns of species co-occurrences to account for matrix-wide differences in species associations (cf. Gotelli & Ulrich 2012). They used average phylogenetic and environmental distances of all species pairs that co-occur in three distinct patterns: aggregated (defined by clumped $\{\{1,1\},\{1,1\}\}$ 2×2 species \times sites submatrices), segregated (checkerboard $\{\{1,0\},\{0,1\}\}$ submatrices), and togetherness ($\{\{1,1\},\{0,0\}\}$ submatrices) (cf. Ulrich & Gotelli 2012). The aggregated and checkerboard patterns are commonly linked to filtering and reciprocal species exclusion, respectively, while the togetherness pattern indicates similar niche requirements (cf. Stone & Roberts 1992; Ulrich et al. 2012). Average phylogenetic distances of the species involved in these co-occurrence patterns are then compared to the random expectation inferred from a null model that reshuffles the occurrences in the underlying presence/absence matrix (Ulrich et al. 2012). Here we again used the *FF* null model. Positive correlations between phylogenetic distance and the distance of the pre-defined site-specific variables with respect to a clumped or togetherness pattern (and respective negative correlations in the case of segregated co-occurrences) indicate niche conservatism.

We used the 19 bioclimatic variables (WorldClim; see Hijmans, Cameron, Parra, Jones, & Jarvis 2005; Peres-Neto & Jackson 2001; Appendix A: Table S2) as well as land-cover data from the mapping project CORINE (from LANDSAT-7 images collected during 2000; <http://www.corine.dfd.dlr.de>) to analyse the phylogenetic structure according to variation of environmental variables. In contrast to Mehr et al. (2010), we reduced the set of bioclimatic variables using principal component analysis based on the correlation matrix. We used the scores of the first two principal components for further analyses. PC1 is a measure of annual temperature and precipitation; PC2 measures the seasonal variability of the

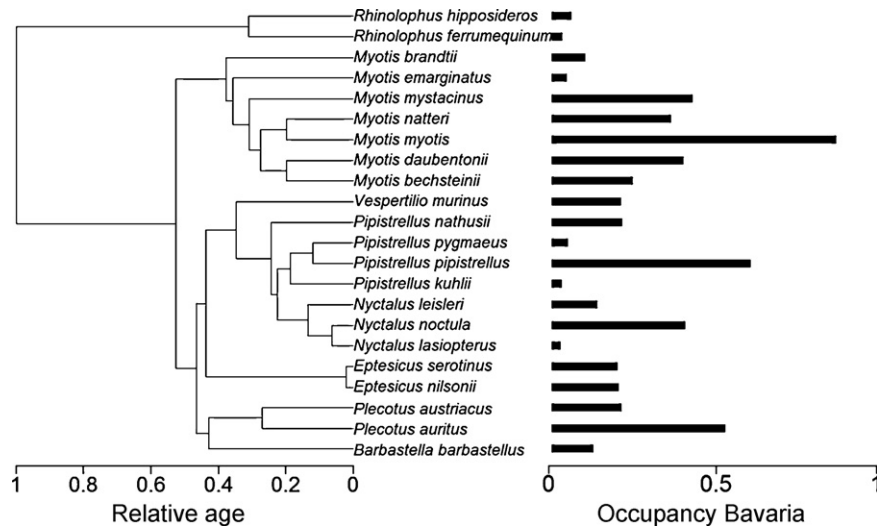


Fig. 1. Ultrametric tree of the molecular phylogeny estimated for 22 bat species occurring in Bavaria and their relative occupancies across the 887 analysed grids in Bavaria. Presence/absence data from April–October 1985–2008 were used. For details, see “Materials and methods” section.

climate (Appendix A: Fig. S2). We grouped several classes of the available land-use data to form seven land-use types and calculated for each type the percentage cover within each grid cell (Pfeifer, Müller, Stadler, & Brandl 2009; Appendix A: Table S3). In contrast to Mehr et al. (2010), we combined all structures related to cities and human activities (without agricultural areas) in one variable (“anthropogenic habitats”; Appendix A: Table S3).

To analyse species richness and phylogenetic diversity in response to the environmental variables, we used Bayesian model averaging (Clyde, Ghosh, & Littman 2010) using the add-on package *BAS* with the default settings. By averaging across a large set or all models, this method determines the variables that are relevant for the data-generating process. Here we focused on the importance of anthropogenic habitats across all possible models.

Results

The phylogenetic distance of the bat species showed a significant negative correlation with co-occurrence measured by the Schoener index (matrix correlation = -0.31 ; $P < 0.001$ for both null models). This indicates that phylogenetically related species tend to co-occur across Bavaria. The two standardized effect sizes of phylogenetic relatedness of bat species co-occurring within the grid cells were correlated ($r = 0.76$). However, very few effect sizes of individual grids were significant (>1.96 or <-1.96). Overall grids, effect sizes were significantly <0 , indicating environmental filtering. For the null model that reshuffles the labels of the phylogenetic tree, the mean effect size was -0.70 ($t = -36$; $P < 0.001$; two-tailed). For the independent swap null model, the effect sizes were much smaller (mean = -0.0085).

Nevertheless, the mean still differed from zero ($t = -2.3$; $P = 0.02$; two-tailed). The co-occurrence with respect to environmental variables revealed significant negative effect sizes of *clumping* and *togetherness* and a positive effect size for checkerboard species associations in broadleaf and coniferous forests, farmlands, and anthropogenic habitats (Table 1). The highest effect sizes were found for anthropogenic habitats.

Species richness and phylogenetic diversity showed contrasting patterns with respect to the percentage of anthropogenic habitats within grid cells: species richness increased, whereas phylogenetic diversity decreased (Fig. 2 and Appendix A: Fig. S3). This result was robust and did not depend on the branch length of the tree (Appendix A: Fig. S4). Also the averaged model coefficients showed that species

Table 1. Standardized effect sizes calculated by using the *FF* null model of the average phylogenetic distances between species or distances of environmental variables with respect to *clumping*, *togetherness*, and checkerboard species pairs.

	Clumping	Togetherness	Checkerboard
Phylogenetic distance	-4.24	-5.18	4.77
Environmental variables			
Farmland	-6.63	4.09	4.02
Meadows	-3.36	1.89	1.84
Wetland	-2.09	1.61	1.66
Broadleaf forest	-2.53	2.59	2.66
Coniferous forest	-1.89	3.44	3.45
Mixed forest	-1.61	1.20	1.30
Anthropogenic habitats	-5.77	7.56	7.64

Significant standardized effect sizes are in boldface (inferred from respective confidence limits; 1% two-sided error level).

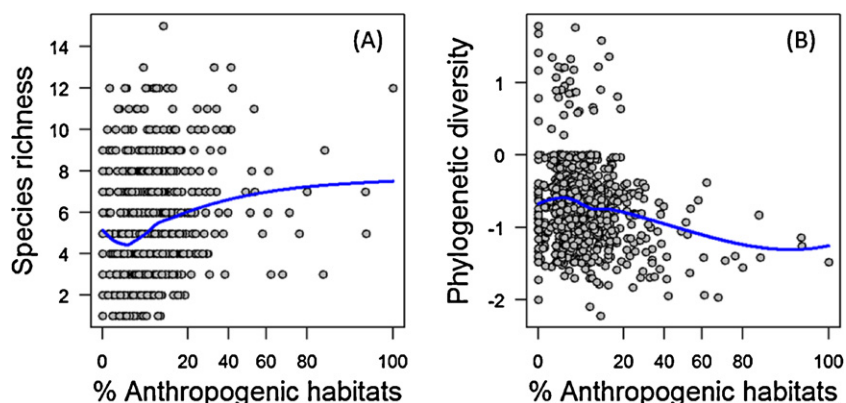


Fig. 2. Plots of the relative amount (in %) of anthropogenic habitats within grids of $\approx 6 \text{ km} \times 6 \text{ km}$ versus (A) species richness and (B) the effect size of phylogenetic diversity. Effect size was calculated using a null model that randomizes the species labels across the tree shown in Fig. 1. The blue lines show the trend of local polynomial regressions (species richness $r^2 = 0.066$; phylogenetic diversity $r^2 = 0.053$). Note that the x -values were arcsine-transformed.

richness increased and phylogenetic diversity decreased with anthropogenic habitats (Table 2). Compared to land-use variables, the inclusion probability of the principal components characterizing the climate was low (Table 2).

Discussion

Our analyses of bat assemblages across Bavaria revealed two important results. First, distributional analysis showed that environmental filtering is more important than competition for the regional distribution of bats. Second, although species richness increased with increasing anthropogenic habitats, phylogenetic diversity decreased.

Bats are volant and therefore highly mobile mammals despite their small body size. Single individuals regularly

bridge distances up to 5 km (Dietz, Helversen, & Nill 2007). Thus, bat species might interact on a scale of $6 \text{ km} \times 6 \text{ km}$, and it was promising to test whether bat assemblages are triggered by competitive interactions (Gotelli et al. 2010). All our analyses, however, ranging from plotting phylogenetic distance versus distributional overlap, to testing the sign of the mean phylogenetic relatedness, to co-occurrence analysis with respect to phylogeny and environment, indicated clustering. Thus, competition played no important role in European bat assemblages on the considered scale. However, this result may not be transferable to bat assemblages in the tropics, which are species rich and seem to be saturated compared to the temperate European bat assemblages (Stevens & Willig 2002).

Our analyses indicated that particularly strong signals of environmental filtering appeared not only for anthropogenic

Table 2. Posterior means and standard deviations of climatic and land-use variables as regressors.

	Species richness			Phylogenetic diversity		
	Mean	SD	P	Mean	SD	P
Intercept	5.10	7.77×10^{-2}	1.00	-7.0×10^{-1}	1.77×10^{-2}	1.00
PC1	-8.21×10^{-3}	2.50×10^{-2}	0.17	-9.9×10^{-4}	4.14×10^{-3}	0.11
PC2	2.65×10^{-2}	4.37×10^{-2}	0.34	-1.4×10^{-3}	5.06×10^{-3}	0.13
Farmland	-1.69×10^{-1}	4.68×10^{-1}	0.22	-1.1×10^{-2}	5.14×10^{-2}	0.12
Meadow	1.80	7.58×10^{-1}	0.92	2.2×10^{-1}	1.71×10^{-1}	0.72
Wetland	6.34	2.75	0.93	2.0×10^{-2}	1.52×10^{-1}	0.08
Broadleaf forests	3.18	1.19	0.96	-4.5×10^{-1}	3.02×10^{-1}	0.78
Coniferous forests	2.77×10^{-1}	5.64×10^{-1}	0.30	-3.9×10^{-3}	4.80×10^{-2}	0.09
Mixed forests	2.87	1.09	0.95	8.0×10^{-2}	1.70×10^{-1}	0.24
Anthropogenic habitats	6.07	8.03×10^{-1}	1.00	-1.1	1.61×10^{-1}	1.00
Easting	5.37×10^{-6}	1.33×10^{-6}	1.00	-2.8×10^{-8}	1.27×10^{-7}	0.11
Northing	6.71×10^{-6}	1.42×10^{-6}	1.00	-1.2×10^{-6}	2.86×10^{-7}	1.00

We also include easting and northing to account for spatial trends. The dependent variable is either species richness or the effect size of phylogenetic diversity calculated by randomizing the labels across the tree in Fig. 1. P reports the Bayesian posterior inclusion probability. Note that the estimator of anthropogenic habitats for predicting species richness is positive, whereas the estimator is negative for phylogenetic diversity (shaded row). In both models, the Bayesian posterior inclusion probability for anthropogenic habitats is 1. Since the number of explanatory variables is small, a full enumeration of the model space is possible.

habitats and farmlands, but also for broadleaf and coniferous forests. The signal of over-dispersion in the analysis of togetherness is also an indicator of environmental filtering (Table 1). The respective high positive standardized effect sizes mean that sites where two species are jointly absent deviate from jointly occupied sites significantly more than expected by chance. These signals of clustering do not point to competitive effects that structure local bat communities but rather highlight the role of phylogenetic history and similar habitat requirements. The largest effect sizes of the co-occurrence of bat species indicating clustering of species pairs with respect to these particular habitats were found for anthropogenic habitats.

At certain scales, cities harbour a surprisingly large number of species and bats are no exception (Mehr et al. 2010; see also Coleman & Barclay 2012). Buildings in cities provide artificial roosts (Neubaum, Wilson, & O'Shea 2007), and the abundance and biomass of insects is comparatively high within cities (Faeth, Warren, Shochat, & Marussich 2005), providing rich food bonanzas for bats. Gehrt and Chelvig (2004) regarded urban environments as islands of habitats within the intensive desert of agriculture. All these effects might explain the increase in bat species richness with the increasing amount of anthropogenic habitats (Mehr et al. 2010). In contrast to species richness, however, phylogenetic diversity declined with increasing anthropogenic habitats. Our results support the idea that only phylogenetically related species that share similar functional traits inhabit this land-use type (see Knapp et al. 2008 for plants). Anthropogenic habitats are therefore environmental filters that only pre-adapted species can pass (Shochat, Warren, Faeth, McIntyre, & Hope 2006). As a consequence, urban environments impose unique selection pressures (Partecke & Gwinner 2007). Knapp et al. (2008) noted that the diminished phylogenetic information might decrease the capacity of assemblages to respond to environmental changes.

Despite the clear and robust decrease in phylogenetic diversity with an increase in anthropogenic habitats, there was a lot of scatter and unexplained variance (see Fig. 2B). This scatter suggests that numerous other factors influence the distribution and therefore species richness and phylogenetic diversity of bat species across Bavaria. In grids with almost no anthropogenic structures, the effect size of phylogenetic diversity was high or low, whereas in grids with a large cover of urban structures, it was always low. Such a triangular pattern is typical when many other factors influence the pattern (Cade & Noon 2003). For example, broadleaf forests have a strong negative effect on phylogenetic diversity; within forests, only bats with particular adaptations are able to hunt (Müller et al. 2012). Nevertheless, the low number of bat species occurring within the borders of Bavaria may also contribute to the low amount of explained variance. Furthermore, most species occurring in Bavaria are widely distributed (see also Fig. 1), which leads to limited spatial variation of assemblages. However, a study of bird species richness across Bavaria also found low levels of explained variance (Pfeifer et al. 2009),

and therefore the small amount of explained variance is not unusual.

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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.baae.2012.11.006>.

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