Environmental correlates of species richness of European bats (Mammalia: Chiroptera)

WERNER ULRICH[1, 2], KONRAD SACHANOWICZ[1], and MARIUSZ MICHALAK[1]

[1]*Nicolaus Copernicus University in Toruń, Department of Animal Ecology, Gagarina 9, 87-100, Toruń, Poland*
[2]*Corresponding author: E-mail: ulrichw@uni.torun.pl*

We use data of bat species richness of 58 European countries and larger islands from Fauna Europaea augmented by recent faunal surveys of particular countries to evaluate the effects of area, latitude, annual temperature range, and mean winter length (days < 0°C), geographical heterogeneity, number of plant species, and distance from Turkey on bat species richness. Area, latitude, and temperature range explained more than 73% of the total variability in European bat species richness. Latitude and temperature corrected species-area relationships of vespertilionid bats were fitted by the power function model with mainland countries having a lower slope ($z = 0.09$) than islands ($z = 0.15$) consistent with current theory. The area corrected centre of vespertilionid species richness was at about 46°N with Croatia being most species rich (34 species). Non-vespertilionid bats peaked at 41°N and did not show a simple latitudinal gradient. The inclusion of plant species richness in the model for Vespertilionidae did not lower the significant influence of area and latitude on species richness. Plant species richness itself was not a major predictor of bat species richness. Three environmental characteristics (latitude, area and temperature) are the main predictors of bat species richness in Europe. These attributes act in an additive manner. This phenomenon allows potential covariates to be eliminated from species-area relationships using simple regression techniques. Further, additive models constructed in this way allow for a ranking of countries with respect to species richness.

Key words: Chiroptera, species-area relationship, macroecology, latitudinal gradients, non-linear regression

INTRODUCTION

Area and latitude are major predictors of large-scale variation in species richness of animals and plants (cf. Rosenzweig, 1995; Maurer, 1999; Brown and Lomolino, 2005). With few exceptions (sawflies, ichneumonids, aphids) species richness of a given taxon peaks at lower latitudes (Rhode, 1992; Blackburn and Gaston, 2003). Bats are no exception to this rule. Species richness peaks around the equator (Procheş, 2005) and sharply declines from lower to higher latitudes (Kaufman and Willig, 1998;

Horáček *et al.*, 2000). Centres of bat species richness are tropical America, eastern tropical Africa and south-eastern Asia (Procheş, 2005), each having more than 120 species. On the other hand, Europe and the major part of North America each have fewer than 50 species. An exception to this latitudinal trend in bats is the family Vespertilionidae that reaches its highest species richness in temperate climates (Simpson, 1964; Patten, 2004). Vespertilionidae are the most dominant family of European bats accounting for 38 of the 46 bat species (Mitchell-Jones *et al.*, 1999; see Table 1).

Species richness increases usually with area (Rosenzweig, 1995; Lomolino, 2000; Scheiner 2003; Ulrich and Buszko, 2003, 2004; Turner and Tjørve, 2005). This species-area relationship (SAR) often follows an allometric function of the form:

$$S = S_0 A^z \text{ [equation 1]}$$

where S denotes the number of species in a given area A. S_0 and z are the parameters of the model with S_0 being an estimate of the mean number of species per unit area (the species density).

The influence of area on bat species richness is not as unequivocal as for latitude. Several studies failed to find a significant SAR for bats (Willig and Selcer, 1989; Kaufman and Willig, 1998; Lyons and Willig, 1999; Willig *et al.*, 2003*a*; Patten, 2004). This would make bats one of the very few exceptions to the general SAR pattern (Lyons and Willig, 2002). In turn, Ricklefs and Lovette (1999) reported a significant SAR for bats of the Lesser Antillean Islands. These contrasting results might be explained by the work of Lyons and Willig (2002) who reported overall low (and often insignificant) slope values below 0.1 of New World bats. Slopes appeared to be higher (> 0.1) only in temperate regions.

In contrast to North America, where Lyons and Willig (1999) and Patten (2004) analyzed large scale patterns of species richness, the macroecology of European bats is known insufficiently, despite many detailed studies and species lists for nearly all European countries and regions (cf. Mitchell-Jones *et al.*, 1999; Horáček *et al.*, 2000; Fauna Europaea, 2004). Only Horáček *et al.* (2000) studied the biogeography of Palaearctic bats in detail. They considered 65 Palaearctic core species and used principal component analysis to categorize them into several faunal groups defined by the main foraging type and geographic distribution. They also pointed to the high correlation between geographical distance and faunal similarity. The present study extends this line of analysis and investigates whether European bat species richness can be explained by important environmental characteristics. We use the species list of Fauna Europaea (2004) and a series of additional publications (Table 1) to infer the geographical distribution of 46 bat species.

We test six major predictions about geographical factors that should influence large-scale patterns of species richness: (i) according to the SAR, area should explain a major part of the variability in species richness. Hence, we test whether bats are in fact an exception to the common pattern. In other mammals and birds, area frequently explains more than 50% of variability in species richness (Rosenzweig, 1995); (ii) species richness and latitude should correlate negatively (Willig *et al.*, 2003*b*). Accordingly, species richness should peak in Mediterranean countries and decrease monotonically towards Great Britain, Scandinavia and other northern countries (Kaufman and Willig, 1998; Lyons and Willig, 1999; Horáček *et al.*, 2000; Patten, 2004); (iii) regions that are topographically more diverse should have enhanced numbers of species because of greater habitat heterogeneity (Wilson, 1974; Rosenzweig, 1995); (iv) temperature should influence species richness. Bats are sensitive to two aspects of temperature: yearly temperature range and absolute length of the winter (Horáček *et al.*, 2000; Neuweiler, 2000; Patten, 2004); (v) islands and mainlands should differ in species numbers after correcting for area, heterogeneity, temperature and latitude. Classical island biogeography (MacArthur and Wilson, 1967) and recent models about island colonization (Lomolino and Weiser, 2001; Rosenzweig, 2001) predict islands to have lower intercepts (expected

TABLE 1. Numbers of bat species (*S*) for European countries and islands, and the respective sources: 1 — Benda and Horáček (1998); 2 — Benda *et al.* (2003*a*); 3 — Benda *et al.* (2003*b*); 4 — Benda and Tsytsulina (2000); 5 — Bogdanowicz (2004); 6 — Celuch and Sevcik (2006); 7 — Ciechanowski *et al.* (2005); 8 — Grimmberger (1993); 9 — Hanák *et al.* (2001); 10 — Hulva *et al.* (2004); 11 — Ibáñez *et al.* (2006); 12 — Kryštufek and Petkovski (2003); 13 — Kryštufek and Vohralík (2001); 14 — Lehotska and Lehotsky (2006); 15 — Mayer *et al.* (2007); 16 — Mayer and von Helversen (2001); 17 — Niethammer and Krapp (2001); 18 — Niethammer and Krapp (2004); 19 — Paunović *et al.* (1998); 20 — Pavlinić and Tvrtković (2003); 21 — Petersons (2003); 22 — Sachanowicz and Ciechanowski (2006); 23 — Sachanowicz *et al.* (2006*a*); 24 — Sachanowicz *et al.* (2006*b*); 25 — Sachanowicz *et al.* (2006*c*); 26 — Schunger *et al.* (2004); 27 — Siivonen and Wermundsen (2003)

Country / region	*S*	Source	Country / region	*S*	Source
Albania	26	5, 22, 25	Italian mainland	31	5, 15, 17
Austria	25	5, 17	Kaliningrad Region	13	5, 17, 18
Azores	2	5	Latvia	16	5, 17, 21
Balearic Is.	15	5	Liechtenstein	6	5
Belarus	18	5, 20	Lithuania	14	5
Belgium	20	5, 16, 17	Luxemburg	18	5
Bosnia and Herzegovina	24	5, 7, 25	Macedonia	24	5, 11, 12
Britain Is.	18	5	Madeira	5	5
Bulgaria	33	3, 5, 25, 26	Malta	8	5
Canary Is.	9	5,11, 15	Moldova	21	5, 17, 18
Channel Is.	5	5	North Aegean Is.	9	5
Corsica	21	5, 18	Northern Ireland	8	5
Crete	17	5, 18	Norwegian mainland	11	5
Croatia	34	4, 5, 8, 18, 20	Poland	24	5, 23, 24
Cycladic Is.	3	5	Portugal mainland	24	5
Cyprus	18	5	Romania	30	5, 8, 17, 18, 24
Czech Republic	24	5, 18	Russia (European part)	30	5, 10, 18
Danish mainland	14	5	Sardinia	20	4, 5, 17, 18
Dodecanese Is.	14	5	Serbia and Montenegro	29	4, 5, 7, 19, 25
Estonia	11	5	Sicily	22	4, 5, 17
European Turkey	26	1, 2, 4, 5	Slovakia	28	5, 6, 14, 22
Faroe Is.	0	5	Slovenia	27	4, 5, 17, 18
Finland	11	5, 27	Spanish mainland	32	5, 11, 15
French mainland	32	5	Svalbard & Jan Mayen	0	5
Germany	25	5, 6, 18	Sweden	18	5
Gibraltar	5	5	Switzerland	29	5, 17
Greek mainland	33	5, 9, 15	The Netherlands	17	5, 18
Hungary	28	5, 16, 17	Ukraine	26	5, 17, 18
Iceland	1	5			
Ireland	11	5	Sum	46	

species densities) and steeper slopes of SARs when fitted by the power function model; (vi) after the last glaciation, Europe was invaded by bats from the Mediterranean (Horáček *et al.*, 2000). Probably, the main centre of invasion for central and eastern Europe was in the southern part of the Balkans and Turkey. Under this assumption, a signal of this invasion should appear in the pattern of species richness. Hence, the distance from the southeastern Europe (Greece and Turkey) should also affect species richness of European bats.

MATERIALS AND METHODS

Our basic source of data on bat distribution was the internet data base Fauna Europaea (Bogdanowicz, 2004). We further used recent taxonomic revisions and faunal surveys to update the faunal composition of 58 countries (mainlands and larger islands regardless of national affiliation) mentioned in Fauna Europaea (Table 1 and Appendix). We did not consider

data for San Marino, Andorra, Monaco, and Vatican City because of insufficient survey work.

According to the six hypotheses mentioned above, we evaluated the influence of five geographical variables on bat species richness. For each European country and larger island (Table 1), we determined the area in km^2 and the latitude of its capital or (in the case of islands) its main city (data from World Atlas, http://www.worldatlas.com/aatlas/world.htm). We used the distance of a given capital or main city from Ankara (from World Distance Calculator, http://www.airportaccommodation.co.uk/worlddistances.php) as the distance from the presumed eastern glacial refugium (Turkey) ΔD. We compiled mean temperatures in January ($T_{January}$) and July (T_{July}) from data in Weatherbase (http://www.weatherbase. com) and estimated the yearly temperature difference ΔT of a country or island from $\Delta T = T_{July} - T_{January}$. Next, we estimated the mean length of the winter from the mean number of days below 0°C ($N_{T<0}$).

Further, we compiled data of the number of vascular plants from data in EarthTrends: The Environmental Information Portal (http://earthtrends. wri.org) and used these as a second estimate of habitat heterogeneity. However, because reliable data were available for only six islands and 35 countries, we did not include plant species numbers in our basic model. As an estimate of topographical heterogeneity (H) we used the quotient of highest elevation through country or island area (Ricklefs *et al.*, 2004). Because this is a very crude measure we use H mainly to have an additional variable to control for possible heterogeneity effects. We did not use mean precipitation due to the large variability within most countries that often exceeded 200%. Patten (2004) found precipitation not to be a significant predictor of North American bat species richness.

To infer the influence of these five environmental characteristics we applied the non-linear estimation module of Statistica 7.1 (Statsoft, 2005) (Model I least squares, Levenberg-Marquardt estimation) to fit additive non-linear models separated for Vespertilionidae and for all other bats. Small numbers of species (near the lower boundary of zero) pose a problem to this modelling approach because the distribution of errors might be distorted that leads to increased type II error probabilities. In this case Poisson error models are widely used (Jiao *et al.*, 2004). However these models have inflated type I error probabilities if the data are overdispersed (variance >> mean). This was the case for the species richness data across countries (all species: $\sigma^2 = 107$; $\mu = 17$). Therefore, we used the more conservative normal error model. To estimate the relative influence of each of the predictors, we used squared semi-partial correlations between these predictors (ln-transformed in the case

of area — Statsoft, 2005). We applied the Akaike information criterion for model choice using R^2 as the measure of goodness of fit. Errors refer to standard errors.

RESULTS

Of the 46 European bat species 38 stem from the family Vespertilionidae (see Appendix). The Rhinolophidae are represented by five species from the genus *Rhinolophus*. Additionally, *Rousettus aegyptiacus* (Pteropodidae), *Miniopterus schreibersii* (Miniopteridae), and *Tadarida teniotis* (Molossidae) occur in Europe. Croatia (34 species) as well as Greece and Bulgaria (33 species each) are most species rich countries (Table 1).

The SAR of the European vespertilionid bats is well described by the power function model ($R^2 = 0.64$, $P << 0.001$) with a slope of $z = 0.18 \pm 0.02$ (Fig. 1A). It predicts a species density S_0 of about two species per km^{-2}. For comparison, we also tested the logarithmic SAR model ($S = S_0 + z\ln(A)$) and found its fit worse ($R^2 = 0.48$, $P < 0.001$). Moreover, this model was unable to predict a realistic species density ($S_0 = -6.7$). This regression model (Fig. 1A) excludes five apparent outliners. Svalbard and Jan Mayen apparently lack any bat species and are not shown. On Iceland, the other isolated island far in the north, only stray (most likely ship-assisted) individuals of *Pipistrellus nathusii* were recorded. On the Azores only two species occur (*Myotis myotis*, *Nyctalus azoreum*) and from the Cycladic Islands only the typical Mediterranean species *Hypsugo savii* is reported.

A plot of the residuals of the vespertilionid SAR against latitude showed a distinct peak in area corrected species richness at 46°N. Switzerland, Slovenia and Croatia appear to have the highest latitude and area corrected number of vespertilionid species. These three countries have about 10 species
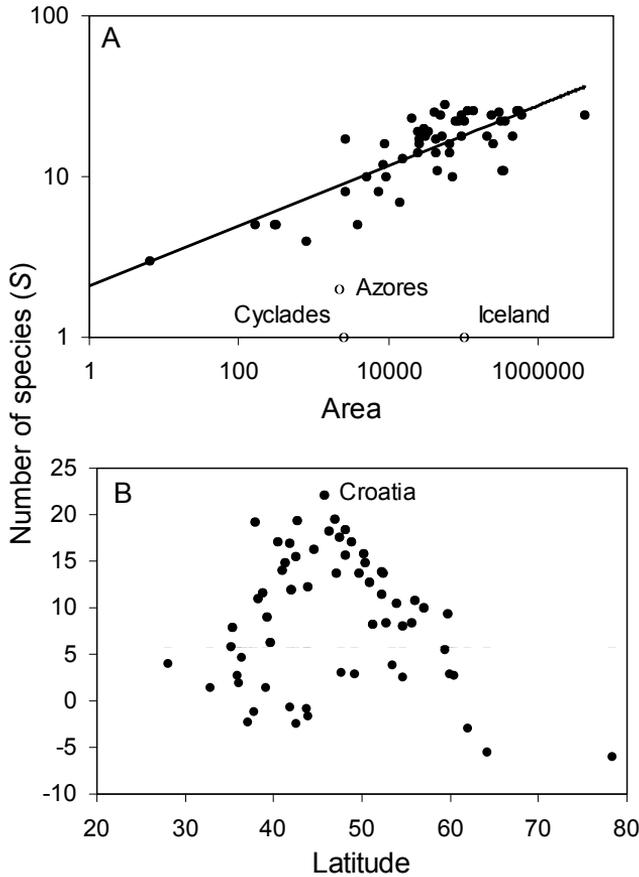
FIG. 1. A: The simple SAR of the European Vespertilionidae is well fitted by a power function model of the form $S = 0.73A^{0.19 \pm 0.02}$; $R^2 = 0.64$, $P(t) < 0.001$. Three distinct outliners (open circles) are not included in the regression; B: The residuals of the Vespertilionidae SAR have a distinct peak at about 46°N. Croatia has the highest area corrected number of species

more than expected from area and latitude alone.

We next included the other environmental variables that might influence vespertilionid species richness S_V: the distance from Turkey D, the mean number of days below 0°C $N_{T<0}$, the mean yearly temperature difference ΔT, and landscape heterogeneity H. We first fitted an additive non-linear model of the form:

$$S_v = A^2 + b_1\Delta L + b_2 D + b_3 H + b_4 \Delta T + b_5 N_{T<0} \text{ [eq. 2]}$$

where ΔL denotes the latitudinal distance from 46°N according to Fig. 2: $\Delta L = |L - 46°N|$.

This model explained 78% of the total variance in S_V (Table 2). The entrance order of the predictor variables did not affect the result. Further, the predictors were only weakly correlated with each other. All pairwise coefficients of correlation were below 0.6 except for the $N_{T<0}$ and ΔT with $r = 0.72$. Particularly, latitude was not significantly correlated with area ($r = 0.20$, $P(t) = 0.11$). Leaving out $N_{T<0}$ or ΔT left the significance levels of the other predictors unaffected. Hence, multicollinearity should not influence the estimates. The model identified area, latitude, length of winter and maximum temperature difference as
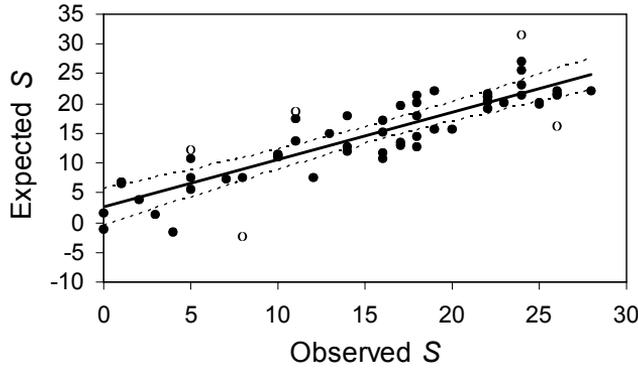
FIG. 2. Predicted vespertilionid species numbers [eq. 3] in relation to the observed number of species. Given are also the regression line (slope = 0.76 ± 0.05) and the associated 99% confidence limits. The five most pronounced outliners (North Aegean islands, Canary Islands, Finland, Greek mainland, and the European part of Russia: residuals > |7| species) are marked by open dots

being highly significant predictors of S_V. The distance from Turkey and landscape heterogeneity, however, did not explain significant parts of the variability in S_V ($P(t) > 0.1$) (Table 2).

A stepwise procedure using the Akaike model choice criterion pointed to A, ΔL, and ΔT, as being the main predictors of vespertilionid species richness:

$$S_V = A^{0.20 \pm 0.01} - (0.63 \pm 0.11)\Delta L + (0.64 \pm 0.08)\Delta T \text{ [eq. 3]}$$

This model explained 70% of the total variance in S_V. It points to a latitude and temperature corrected SAR slope z of 0.20. The model further predicts that the yearly temperature range correlates positively with species richness. Judged from the squared semi-partial correlations (R_{sp}^2) of the equivalent multiple regression model (using ln S and ln area) latitude was the most important predictor ($R_{sp}^2 = 0.17$), followed by area ($R_{sp}^2 = 0.13$), and temperature range ($R_{sp}^2 = 0.03$).

In the next step, we looked at whether islands and mainlands differ in patterns of species richness. According to the model of eq. 3, latitude and temperature corrected species numbers [corr. $S = S_V - (-0.63\Delta L + 0.64\Delta T)$] should scale to area by an exponent of 0.20. This was

indeed the case. Residual species numbers scaled to area by 0.18 ± 0.02 after exclusion of a group of small islands (Channel Islands, Cycladic Islands, and North Aegean Islands) and one mainland country (Liechtenstein) with slightly negative corrected species numbers. A plot of expected [eq. 3] against observed vespertilionid species numbers (Fig. 2) shows how well the model works. Notable exceptions are the North Aegean Islands (5 species observed, 12 expected). The overestimation can probably be attributed to an insufficient survey work. For four island groups the model predicts a lack of vespertilionid bats (exp. S < 1). These are Svalbard and Jan Mayen (no species recorded), the Faroe Islands (no

TABLE 2. Regression model [eq. 2] to predict vespertilionid species richness S from area (A), latitudinal distance from 46° (ΔL), distance from Turkey (Ankara) (D), geographical heterogeneity (H), mean temperature range (ΔT), and mean number of days below 0°C ($N_{T<0}$). The model explains 76% of total variance in S ($F_{58, 6} = 139.5$, $P < 0.001$)

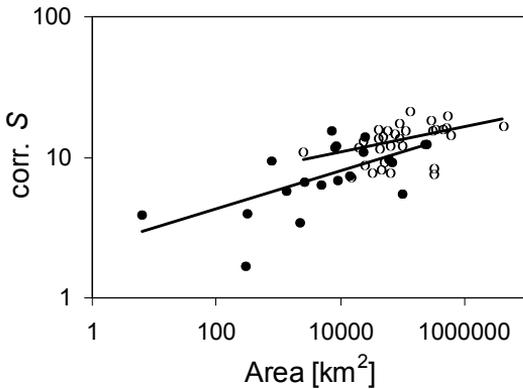| Parameter	$\bar{x} \pm SE$	t(45)	$P(t)$
A	0.21 ± 0.01	18.28	< 0.001
ΔL	-0.79 ± 0.12	-6.51	< 0.001
D	0.0007 ± 0.0005	1.59	0.12
H	-0.04 ± 0.05	-0.67	0.51
ΔT	0.83 ± 0.09	9.55	< 0.001
$N_{T<0}$	-0.05 ± 0.01	-3.94	< 0.001

FIG. 3. Temperature- and latitude-corrected vespertilionid species richness, corr. S [eq. 3] of mainlands (open squares) and islands (black dots) depending on area. Mainlands: $S = (4.74 \pm 1.70)A^{0.09 \pm 0.03}$; $R^2 = 0.20$, $F_{36, 2} = 239.3$, $P < 0.001$; islands: $S = (1.19 \pm 1.26)A^{0.15 \pm 0.06}$; $R^2 = 0.26$, $F_{20, 2} = 33.4$, $P < 0.001$

species recorded), Madeira (4 species), and the Canary Islands (5 species). Of the mainland countries, the Greek mainland most deviates in having 26 species while 16 are expected. In turn, for the European part of Russia the model expects 32 species whereas 24 have been recorded.

The latitude and temperature corrected SARs of the vespertilionid species differed in slope when separately constructed for islands and mainlands. As predicted from current theory the island slope ($z = 0.15$) was significantly higher ($P(t) < 0.001$) than the mainland slope ($z = 0.09$ — Fig. 3). Further, the model predicts species densities S_0 of islands to be significantly ($P(t) < 0.001$) lower ($S_0 = 2.16$) than that of mainlands ($S_0 = 4.74$).

Only eight non-vespertilionid bats occur in Europe (Appendix) and a similar regression analysis as above is prone to all sorts of Poisson errors. We were therefore surprised to see that despite this low number 'of species strong signals of latitude and area appeared. The peak in European non-vespertilionid species richness is at 41°N as inferred from the intercept of the two linear

regressions of the ascending and descending parts of Fig. 4A. However, Cyprus (35°N) is colonised by all eight European non-vespertilionid bats. The residuals from these two regressions resulted in a highly significant SAR that explained 28% of the total variance in S ($P < 0.001$ — Fig. 4B). Cyprus and Russia were more species rich than expected; the Azores were depauperated.

The model of eq. 3 pointed for the non-vespertilionid bats to area, latitude, and temperature range as significant predictors (Table 3). These variables explained 64% of the total variance in S. Distance from Turkey, topographical heterogeneity, and winter length instead explained only small parts (< 10%) of total variance.

Discussion

The major aim of the present work was to test six basic hypotheses concerning the influence of geographical variables on the species richness of European bats. First, vespertilionid and non-vespertilionid bats follow pronounced SARs after correcting for effects of latitude and temperature. The resulting vespertilionid slopes (0.15 and 0.09 for islands and mainlands, respectively) are similar to those of other mammals and birds (Reichholf, 1980; Rosenzweig,

TABLE 3. Regression model [eq. 2] to predict non-vespertilionid species numbers (S) from area (A), latitudinal distance from 46° (ΔL), distance from Turkey (Ankara) (D), geographical heterogeneity (H), mean temperature range (ΔT), and mean number of days below 0°C ($N_{T<0}$). The model explains 64% of the total variance in S ($F_{58, 6} = 48.3$, $P < 0.001$)

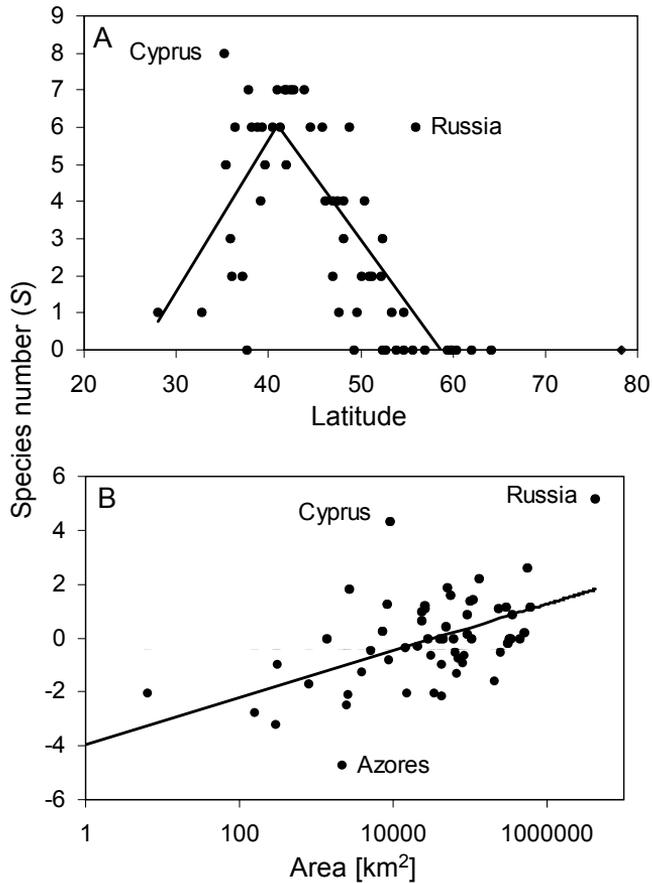| Parameter	$\bar{x} \pm SE$	t(45)	P(t)
A	0.12 ± 0.02	6.25	< 0.0001
ΔL	-0.24 ± 0.05	-4.36	<0.0001
D	-0.0002 ± 0.0002	-0.85	0.40
H	0.01 ± 0.03	0.41	0.68
ΔT	0.16 ± 0.05	3.34	0.002
$N_{T<0}$	-0.01 ± 0.007	-1.62	0.11

FIG. 4. A: The species number-latitude relationship of non-vespertilionid bats is distinctly peaked at about 41°N. Given are also linear fits of the ascendant and descendant branches; B: The residuals from the linear regressions of the ascendant and descendant parts in A in dependence of area is well fitted by a logarithmic function: $\Delta S = (0.37 \pm 0.08) \ln(A) - (3.9 \pm 0.9)$; $R^2 = 0.28$, $P < 0.001$

1995; Ricklefs and Lovette, 1999; Brook *et al.*, 2003; Michalak and Ulrich, 2006). These results contradict to a certain degree claims that bats do not exhibit pronounced SARs (Willig and Selcer, 1989; Kaufman and Willig, 1998; Lyons and Willig, 1999; Willig *et al.*, 2003*a*). On the other hand, Ricklefs and Lovette (1999) reported a habitat diversity corrected allometric SAR slope of $z = 0.38 \pm 0.15$ for the bats of the Lesser Antillean Islands. The interprovincial area and species richness data of Willig and Bloch (2006) point also to a strong area signal within provinces. A multiple regression using ln-transformed area and species

richness data of their Table 1 gave a significant positive SAR slope ($z = 0.23$, $P(t) < 0.001$) and the negative latitudinal signal ($P(t) < 0.001$) reported by Willig and Bloch. These contrasting results point to a general problem in the constructing of SARs. To uncover the area per se effect (McGuinness, 1984; Rosenzeig, 1995) we have to control for covariates like habitat diversity, latitudinal trends in species richness, climatic variability, or differences in productivity. Otherwise SAR patterns, even if significant, cannot be compared directly.

The area effect on species richness might depend on latitude. This possibility

led Lyons and Willig (1999) to use an additive non-linear interaction model to uncover the potential covariance of area and latitude. To test for this possibility we modified our basic model of eq. 3 according to the Lyons and Willig model and obtained:

$$S_V = A^{0.19 \pm 0.01} - (0.52 \pm 0.09)\Delta L +$$
$$+ (0.30 \pm 0.08)\Delta T + A^{0.19}\Delta L^{(-0.16 \pm 0.07)} \text{ [eq. 4]}$$

This model is qualitatively identical to eq. 3 and explained 78% of the total variance. Hence, although the additional interaction term is statistically significant ($P = 0.02$) it explained only about 1% of the residual variance of the basic model [eq. 3]. The Akaike criterion also pointed to the basic model as being superior ($AIC_{eq. 3} = 6.63$, $AIC_{eq. 4} = 8.50$). Therefore, we conclude that area and latitude act largely independently as found by Lyons and Willig (1999). Both results also show that simple additive models are appropriate for modelling species richness.

Second, our analysis strongly points to latitude as a main explanatory variable of the variables included in our analysis. Horáček *et al.* (2000) have already shown that total bat species richness of the Palaearctic Region peaks between 40–50°N. Our results confirm this view and show that this hump-shaped pattern of species richness is stable after controlling for major covariates. Latitude itself is believed to be a surrogate variable that correlates with other, mainly climatic variables to which species respond (Hawkins and Diniz-Filho, 2004; Patten, 2004). These are temperature, productivity, precipitation, day length, or the length of the seasons. Patten (2004) showed that the latitudinal trends in North American vespertilionid species richness vanish after controlling for mean January temperatures and topographic heterogeneity (estimated as in the present study). To test for this hypothesis, we fitted the model of eq. 3 leaving out the latitudinal effect (Table 4). This

TABLE 4. Regression model to predict vespertilionid species numbers (*S*) [eq. 3] without the latitude variable (ΔL). The model explains 58% of the total variance in *S* ($F_{58, 5} = 123.8$, $P < 0.001$)

Parameter	$\bar{x} \pm SE$	t(45)	P(t)
A	0.20 ± 0.02	11.50	< 0.001
D	-0.001 ± 0.0005	-2.01	0.05
H	-0.04 ± 0.08	-0.46	0.64
ΔT	0.74 ± 0.12	6.16	<0.001
$N_{T<0}$	-0.04 ± 0.02	-2.06	0.04

new model identifies the distance from Turkey as significant variable because ΔL and D are correlated significantly ($R^2 = 0.27$, $P(t) < 0.001$). However, the explanatory power of the model without ΔL was less ($R^2 = 0.58$) than that of the model including ΔL ($R^2 = 0.76$; Table 2). From this, we conclude that other variables that correlate with latitude explain a major part of European vespertilionid species richness. Further, Patten (2004) used simple latitude whereas we used the latitudinal difference from the area corrected peak in species richness. Because the species richness–latitude relationship in the Vespertilionidae is hump-shaped this difference in modelling might in part explain the contrasting results.

What other environmental characteristics might underlie the latitudinal effect? We did not include the number of vascular plant species S_{VP} as a measure of vegetation variability in eq. 2 because only 41 countries and islands had reliable data. The number of vascular plants correlates significantly with ΔL ($R^2 = 0.36$, $P < 0.01$). However, the regression of residual species richness of the model defined by eq. 3 against S_{VP} explained only 11% of residual variance ($P = 0.04$). A regression of model residuals with variables that are highly correlated with the predictor variables of the model poses statistical problems for parameter estimation (Freckleton, 2002). We therefore added a power function term for S_{VP} to the model of eq. 3 and obtained (using the

Akaike criterion) for the Vespertilionidae of the subset of 41 countries and islands:

$$S_V = A^{0.23 \pm 0.01} + S_{VP}^{0.27 \pm 0.03}$$
$$- (0.76 \pm 0.13)\Delta L \text{ [eq. 5]}$$

This model returned highly significant parameter values for A, S_{VP}, and ΔL (all $P < 0.001$) and explained 64% of the total variance in S_V. The squared semi-partial correlations of the equivalent multiple regression model (using ln A and ln S_{VP}) pointed to area as being the most important predictor ($R_{sp}^2 = 0.12$), followed by latitude ($R_{sp}^2 = 0.11$) and plant species richness ($R_{sp}^2 = 0.06$). From this we conclude that latitude itself is a significant predictor of vespertilionid species richness in Europe, even after controlling for major covariates that we considered. Nevertheless, there may be additional covariates that might account for the variation in richness. Although significant, vascular plant species richness seems to be of only minor importance.

Our model does not contain longitude. Recently, Ruggiero and Hawkins (2006) advocated including longitude into spatial distribution model. In Europe some taxa show a pronounced longitudinal gradient in species richness (e.g., Aphodiidae: Lobo et al., 2004; Cynipidae: Atkinson et al., 2007). However, our study contains the postglacial immigration centre Turkey that is far in the east and therefore highly correlated with longitude. That the distance from Turkey did not enter our basic model does not point to a major effect of longitude.

As expected, islands and mainlands differed in their latitude- and temperature-corrected SAR slopes. In line with current theory (Rosenzweig, 1995; Lomolino and Weiser, 2001) the mainland slope was lower than the island slope (Fig. 3). Both SARs were well fitted by power functions. Recent claims state that SARs should be fitted by asymptotic or sigmoid models that imply an upper boundary of species richness

(Lomolino, 2000; Tjørve, 2003; Turner and Tjørve, 2005; but see Williamson et al., 2001). Unfortunately, no standard test identifies such a curvature (Lennon et al., 2002).

Our model confirms previous suggestions of a strong influence of climatic variables, in particular temperature, on bat species richness (Horáček et al., 2000; Patten, 2004). Temperature ranges and winter length proved to be significant as well as independent variables that act in an opposite manner. As expected, winter length correlated negatively with vespertilionid and non-vespertilionid species richness. However, the model predicts an increase of species richness with increasing temperature range ΔT. On the other hand, the model of Patten (2004) did not point to temperature range as a significant variable that explains part of the variance in vespertilionid species richness.

A critical point of the present paper is its relatively low spatial resolution. In order to infer the influence of area and climate, we use countries as our basic sampling units. There are more precise maps based on 100×100 km grids (Mitchell-Jones et al., 1999). However, such grid based richness maps do not allow inferring SARs and climatic influences simultaneously, and do not contain the many new records and 11 newly discovered species reported since 1999. Further, the higher the resolution is, the lower will be the precision of species lists because of the high faunal turnover and uneven sampling efforts. However, our results show that even a coarse resolution is able to identify basic influencing variables and to predict species numbers to a high accuracy. Hence, even coarse grained data might be sufficient to uncover basic macroecological patterns.

The present study uses both the classical concept of morphospecies and recently genetically discovered species but does not include one genetically defined species —

Myotis sp., for which data are available from only three countries (Ibáñez *et al.*, 2006; Mayer *et al.*, 2007). The spatial resolution of genetic studies is still low. At the moment for only a few European countries are sufficiently resolved data on cryptic species diversity available although it is very likely that several recently defined species have wider distributions than reported to date. Judged from our stepwise inclusion of new records into our basic models during model development [eqs. 3, 4, and 5] new genetically defined species will not significantly influence the model structure and the respective parameter values.

The present results have implications for the identification of hot spots of bat diversity. A ranking of countries and islands using the residual vespertilionid species richness ($\Delta S = S_{observed} - S_{expected}$) of our basic model (eq. 3 — cf. Fig. 2) points to Croatia ($\Delta S = 7$), the Canary Islands ($\Delta S = 7$), Greece ($\Delta S = 6$), and Switzerland ($\Delta S = 6$) as exceptionally diverse. The North Aegean Islands ($\Delta S = -10$) and the Cycladic Islands ($\Delta S = -8$) are the most depauperate, although this may be due to insufficient field work. In the case of the non-vespertilionid species Cyprus ($\Delta S = 5$) and the Dodecanese Islands ($\Delta S = 4$) ranked highest. These high-ranking countries and islands might be targets for further biodiversity research (Ulrich, 2005; Ulrich and Buszko, 2005). Despite of low species richness the Azores, Madeira and Sardinia have one endemic species each (*Nyctalus azoreum*, *Pipistrellus maderensis*, and *Plecotus sardus*, respectively) and are of importance for European bat biodiversity.

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APPENDIX

The bat species of Europe

Family Molossidae — *Tadarida teniotis* (Rafinesque, 1814).

Family Miniopteridae — *Miniopterus schreibersii* (Kuhl, 1817).

Family Pteropodidae — *Rousettus aegyptiacus* (E. Geoffroy, 1810).

Family Rhinolophidae — *Rhinolophus blasii* Peters, 1866; *R. euryale* Blasius, 1853; *R. ferrumequinum* (Schreber, 1774); *R. hipposideros* (Bechstein, 1800); *R. mehelyi* Matschie, 1901.

Family Vespertilionidae — *Barbastella barbastellus* (Schreber, 1774); *Eptesicus anatolicus* Felten, 1971; *E.* cf. *isabellinus* (Temminck, 1840), *E. nilssonii* (Keyserling and Blasius, 1839); *E. serotinus* (Schreber, 1774); *Hypsugo* cf. *darwinii* (Tomes, 1859); *H. savii* (Bonaparte, 1837); *Myotis alcathoe* Helversen and Heller, 2001; *M. aurascens* Kusjakin, 1935; *M. bechsteinii* (Kuhl, 1817); *M. brandtii* (Eversmann, 1845); *M. capaccinii* (Bonaparte, 1837); *M. dasycneme* (Boie, 1825); *M. daubentonii* (Kuhl, 1817); *M. emarginatus* (E. Geoffroy, 1806); *M. escalerai* Cabrera, 1904; *M. myotis* (Borkhausen, 1797); *M. mystacinus* (Kuhl, 1817); *M. nattereri* (Kuhl, 1817); *M. oxygnathus* Monticelli, 1885; *M. punicus* Felten, 1977; *Nyctalus azoreum* (Thomas, 1901); *N. lasiopterus* (Schreber, 1780); *N. leisleri* (Kuhl, 1817); *N. noctula* (Schreber, 1774); *Pipistrellus kuhlii* (Kuhl, 1817); *P. maderensis* (Dobson, 1878); *P. nathusii* (Keyserling and Blasius, 1839); *P. pipistrellus* (Schreber, 1774); *P. pygmaeus* (Leach, 1825); *Plecotus auritus* (Linnaeus, 1758); *P. austriacus* (Fischer, 1829); *P. begognae* de Paz, 1994, *P. kolombatovici* Dulic, 1980; *P. macrobullaris* Kuzyakin, 1965; *P. sardus* Mucedda, Kiefer, Pidinchedda and Veith, 2002; *P. teneriffae* Barrett-Hamilton, 1907; *Vespertilio murinus* Linnaeus, 1758.