Species diversity and endemism: testing the mid-domain effect on species richness patterns of songbirds in the Palearctic Region

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Abstract

Explanation of the spatial distribution patterns in species richness, and especially those of small-ranged species (endemics), bears relevance for studies on evolution and speciation, as well as for conservation management. We test a geometric constraint model, the mid-domain effect (MDE), as a possible explanation for spatial patterns of species richness in Palearctic songbirds (Passeriformes), with an emphasis on the patterns of small-ranged species. We calculated species richness based on digitised distribution maps of phylogenetic species of songbirds endemic to the Palearctic region. Data were plotted and analyzed over a one degree longitude equal area map of the Palearctic Region, with a grid cell area of 4062 km². The emergent biogeographic patterns were analysed with WORLDMAP software. Comparison of the observed richness pattern among 2401 phylogenetic taxa of songbirds in the Palearctic Region with the predictions of a fully stochastic bi-dimensional MDE model revealed that this model has limited empirical support for overall species richness of Palearctic songbirds. Major hotspots were located south of the area where MDE predicted the highest species-richness, while some of the observed coldspots were in the centre of the Palearctic Region. Although small-ranged species are often found in areas with the highest species richness, MDE models have a very restricted explanatory power for the observed species-richness pattern in small-ranged species. Regions with a high number of small-ranged species (endemism hotspots) may contain a unique set of environmental conditions, unrelated to the shape or size of the domain, allowing a multitude of species to co-exist.

Contents

Introduction

Biologists have long discussed the ecological and evolutionary mechanisms underlying large-scale spatial patterns in species richness, but so far there is little consensus (Chown and Gaston, 2000; Willig *et al.,* 2003). Numerous hypotheses have been put forward to explain the spatial structure and temporal variability of these patterns. These hypotheses focus on various factors, such as the amount of energy available in the local ecosystem, evolutionary time, habitat heterogeneity, area effect, and the mid-domain effect (MDE). Many have their merits, i.e. a relatively high explanatory power is present between the observed and expected patterns, yet few can be used as a general explanation (Rohde, 1992; Brayard *et al.,* 2005).

Here we focus on the mid-domain effect as an explanation for patterns of species richness and endemism in birds, building upon earlier work (Aliabadian *et al.,* 2005, 2007). The mid-domain effect model is a stochastic, range based model (SRB), with the mid-domain effect being a natural result when the model includes geometric constraints imposed by the physical boundaries of the area. SRB-models differ from many other hypotheses in that they attempt to explain the pattern of species richness without invoking any environmental or evolutionary factors. MDE-models are abiotic and

probabilistic hypotheses, based on the premises that the spatial distribution of species richness is constrained by the shape of landmasses and by species range size. Under these conditions, random placement of species ranges within a bounded domain creates an overlap of species ranges, and thus a peak of species richness, toward the center of the geographical domain (Colwell and Hurtt, 1994; Colwell and Lees, 2000). In a number of studies, the MDE has predicted the empirically observed pattern of species richness reasonably well (Lees *et al.,* 1999; Jetz and Rahbek, 2001, 2002; Bellwood *et al.,* 2005), but much less so in other analyses (Hawkins and Diniz-Filho, 2002; Aliabadian *et al.,* 2005; Kerr *et al.,* 2006).

As null models, mid-domain models constitute a major advance in our understanding of causal mechanisms for species richness gradients. Colwell and Hurtt (1994) first explored the random locating of range size in a bounded domain. Initially, it was implicitly assumed that in the absence of a bounded domain random placement of several species on a continent would produce a uniform pattern of variation in species richness. Once the domain is assumed to be bounded and the distribution of species along the gradient is limited at both ends by an impassable boundary, the mid-domain models showed that the pattern of species richness becomes parabolic or quasi-parabolic, with a peak of 0.5 times the total number of species at the centre of the domain (Colwell and Hurtt, 1994; Colwell and Lees, 2000).

Willig and Lyons (1998), Colwell and Lees (2000) followed up with uni-dimensional analytical models, while Bokma *et al.* (2001), Jetz and Rahbek (2001), Hawkins and Diniz-Filho (2002) developed bi-dimensional models in which a similar peak in species richness, with a maximum value of 0.25 times the total number of species, appears in the centre of two-dimensional models. A bounded domain in bi-dimensional models is defined by latitude and a longitude axes.

Because the domain is bounded at both ends, the MDE model predictions depend crucially on the frequency distribution of range size, as small-ranged species can be freely located nearly anywhere within the domain, in contrast to species with large ranges, which are forced to be closer to the center or mid-domain (Colwell and Hurtt, 1994; Lees *et al.,* 1999). Based on analytical models, Lees *et al.* (1999), hypothesized that geometric constraints are expected

to affect the distribution of species with large ranges more than species with small ranges.

Here we focus on the distribution patterns of restricted range species or centres of endemism, as these are important from a conservation perspective (e.g., Stattersfield *et al.,* 1998; Mittermeier *et al.,* 1999; Meijaard and Nijman, 2003) and also from evolutionary and biogeographical perspectives (Jetz *et al.,* 2004; Orme *et al.,* 2005). Several authors (Endler, 1982; Haffer, 1982; Prance, 1982) have postulated that richness patterns of small-ranged species should be spatially concentrated in regions with an already high overall species richness, the so-called hotspots. Furthermore, species richness of both small-ranged and large-ranged species is predicted to be higher in these hotspots (Endler, 1982; Jetz *et al.,* 2004; Roselaar *et al.,* 2007).

We use a fully stochastic uni- and bi-dimensional MDE model in order (a) to test the role of MDE in explaining the species richness pattern of all passerine birds endemic to the Palearctic Region, and (b) to evaluate the distributional pattern of small-ranged species richness relative to the overall species richness pattern.

Methods

Delimitation of the Palearctic region

During the advent of the discipline of analytical biogeography, Sclater (1858) was the first to recognize the Palearctic as an area characterized by the presence of unique faunal components with geographic ranges restricted to this biogeographic region. Sclater based his regional biogeographical system on the distribution of passerine birds, but analyses of other groups of terrestrial animals by subsequent workers, notably Wallace (1876), supported and also expanded Sclater's scheme. The Palearctic Region as proposed by Wallace (1876) is currently widely accepted as a natural subdivision of the biosphere (cf. Schmidt, 1954), comprising a large section of the globe; it extends from Iceland to Kamchatka, with its southernmost border approximately located at the Tropic of Cancer (23.5°N). However, it should be noted that particularly the southern part of the Palearctic is not defined by a sharp faunal boundary separating it from the Ethiopian and Indian and Oriental Regions. Regional biogeographic boundaries are sub-

ject to limited latitudinal shifts, depending on the taxa analyzed by different biogeographers (cf. Müller, 1974, fig. 33). It should be noted also that floristic regions may differ from the zoogeographically based Sclater-Wallace system (cf. Good, 1974; Cox, 2001). Notably, the boundary of the floristic Holarctic or Boreal Kingdom is drawn by Good (1974) along the northern edge of the Sahara desert, while zoologists have generally positioned the boundary across the middle of the Sahara. Recently, also Cox (2001) argued that the southern border of the Palearctic Region should be drawn along the southern edge of the Mediterranean Region, i.e. within Africa but close to the Mediterranean coast and along the northern edge of the Sahara, but now encompasing the entire Arabian Peninsula, contrasting with the traditional boundary across the peninsula. In contrast, Takhtajan (1978) locates the southern border of his Holarctic Floristic Kingdom again along the southern edge of the Sahara, along the foot of the Himalayas and through southern China.

Within each of his major biogeographical regions, Wallace (1876) distinguished between four subregions. For the Palearctic he recognized a Northern European, Southern European, Siberian, and Manchourian subregion. However, it had already been pointed out by contemporary workers that Wallace's separation of the European and Siberian subregions, for example, was based on insufficient data and that the criteria used were more geographic than faunistic (Udvardy, 1969). Nevertheless, in later years Wallace's boundary between the European and Siberian subregions, running along the Ural Mountains and the Caspian Sea, has been used to demarcate western subsections of the Palearctic Region (cf. Voous, 1960; Cramp *et al.,* 1977-1994).

In this study we accept the Sclater-Wallace Palearctic Region as a biogeographically and a physical-geographically identifiable and informative subdivision of the biosphere. However, the boundaries of the Palearctic Region are subject to analysis and interpretation (see above and Storch *et al.,* 2006) and here we follow the geographic boundaries as recently proposed by Roselaar (2006).

Species concept and distributional data

The choice of species concept has proved to be important in the analysis of biogeographical patterns.

The spatial pattern of centres of endemism may (Meijaard and Nijman, 2003) or may not (Dillon and Fjeldså, 2005) differ between the application of different species concepts. Since our basic goal is the *taxic* description and analysis of biodiversity, we have chosen the phylogenetic species concept (sensu Cracraft, 1983) as our descriptor of species level diversity. For detailed discussion on species concepts and the appropriateness of a phylogenetic species concept in the taxic description of biodiversity and for further introduction to the literature, we refer to Sluys and Hazevoet (1999), Sangster *et al.* (1999), Agapow *et al.* (2004), and Agapow and Sluys (2005). Traditionally, ornithologists have applied the isolation or biological species concept and, as a consequence, have recognized a great number of subspecies. In practice, application of the phylogenetic species concept implies that many of these traditional subspecies will be elevated to the rank of full species (cf. Cracraft, 1992; Garnett and Christidis, 2007). Thus, our full database contains 3,036 maps, one for each taxon, i.e. phylogenetic species, contrasting with the c. 889 isolation or biological species of passeriforms that are traditionally recognized for the Palearctic (note that in Aliabadian *et al.* (2005, 2007), focussing on hybrid species, we followed the biological species concept). Our nomenclature and taxonomy follows Dickinson (2003) and in total we recognized 2,401 taxa that are endemic to the Palearctic Region.

For the current analysis we focus on birds that breed only in the Palearctic Region and as such are confined, endemic, to it. The distribution maps were generated by digitizing the breeding ranges of all phylogenetic species of passerines breeding in the Palearctic Region using WORLDMAP version 4.1 software (Williams, 2000), similar to Aliabadian *et al.* (2005) and Roselaar *et al.* (2007). Maps of species distribution were created interactively on an equal area map of the Palearctic (area: 30°W-170°W, 18°00'N-86°25'N; equivalent cylinder projection, equidistant on 55° parallel circle), overlaid by a 1° longitude grid (grid cell area: 4,062 km^2).

Ranges of species included in this study differ considerably (see results). What defines a small range species differs between studies, but in general it refers to species with a breeding range below a certain threshold, ranging for birds from 50,000 km^2 (Stattersfield *et al.,* 1998) to c. 960,000 km^2 (Dillon and Fjeldså, 2005). Following Aliabadian *et al.* (2007), small-ranged endemics are here defined

as species with a breeding range of <110,000 km², this being the threshold of the 25% smallest ranged species in our dataset.

For mapping the species richness patterns we have used the equal interval scale option in WORLD-MAP. For the equal interval scale, the different area extents of the various colours on the map show the frequency distribution of the scores as well as their spatial distribution, although this option may reduce discrimination among areas.

Range size frequency distribution

In order to explore the range size frequency distribution of endemic songbirds of the Palearctic Region (2,401 taxa), we analyzed the range size of each taxon along the latitude and longitude axes separately. Range sizes of taxa were represented with horizontal lines (corresponding to the range size) and midpoints indicate the position of the ranges along each axis. Overlap of range sizes and pattern of species richness observed along each axis was subsequently evaluated for evidence of MDE, using a uni-dimensional null model.

Mid-domain effect and analysis

We evaluated the mid-domain effect on the empirical data of Palearctic passerines using the 'area corrected' version of the Willig and Lyons (1998) model (Bokma *et al.,* 2001; Hawkins and Diniz-Filho, 2002; Aliabadian *et al.,* 2005, 2007). Under this pure stochastic process, the species richness for each point in the domain is defined by considering its position relative to the maximum boundaries across north (p), south (q), east (t), and west (r) axes of the Palearctic Region. Expected species richness at point P in the uni-dimensional (latitude and longitude) domain than equals $2pqS,$ where S is the total species richness at the domain; for the bi-dimensional situation it is than given by $4pqrt.$ Values were only estimated for the 14,715 grid cells that included one or more species. This approach is conservative because any MDE prediction of the presence of species in other grid cells would lower the fit of the model.

In order to test whether centres of endemism have an unexpectedly greater number of species than other areas, we excluded small-ranged endemics from the analysis and compared the new pattern of species richness with the original pattern.

Statistical analysis

Biogeographical data tend to be strongly spatially autocorrelated (Diniz-Filho *et al.,* 2002, 2003; Legendre *et al.,* 2002), which may lead to an overestimation of the degrees of freedom, and consequently to type I errors in statistical analyses. Therefore, significance tests generally tend to be too liberal (Diniz-Filho *et al.,* 2003). In order to correct for spatial autocorrelation in regression residuals, the effective number of degrees of freedom were calculated according to Dutilleul's method (Dutilleul, 1993; Brehm *et al.,* 2007), and adjusted P-values (P_{adj} for R^2) were considered, based on the effective degrees of freedom. The MDE predictions were compared with the observed species richness patterns for the same subsets of taxa using Coefficients of determination (R^2) of linear regression.

Results

Range-size distribution and species richness patterns

The average range size is almost 100,000 km². However, many species have small ranges, whereas only relatively few possess very large ranges (Fig. 1).

Figure 2 presents the observed species richness pattern of Palearctic passerines along latitude and longitude axes. Species richness along the latitudinal axis increases gradually from north to the equator (25° to 35°) and then decreases again gradually towards the south (Fig. 2a). Along longitude and from east to west, the species number increases
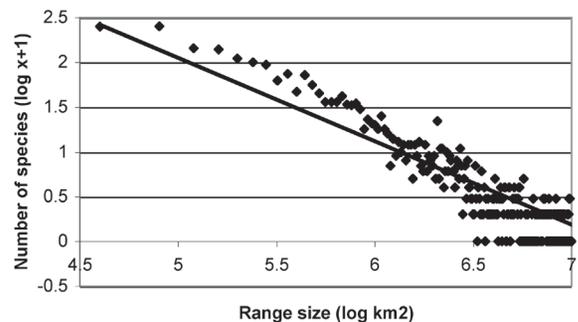

Fig. 1. Relationship between range size (grouped in classes of c. 40,000 km², up to 7,000,000 km²) and species frequency (number of species within each range size class, N = 2,401 taxa), showing many species with small ranges and few species with large ranges.
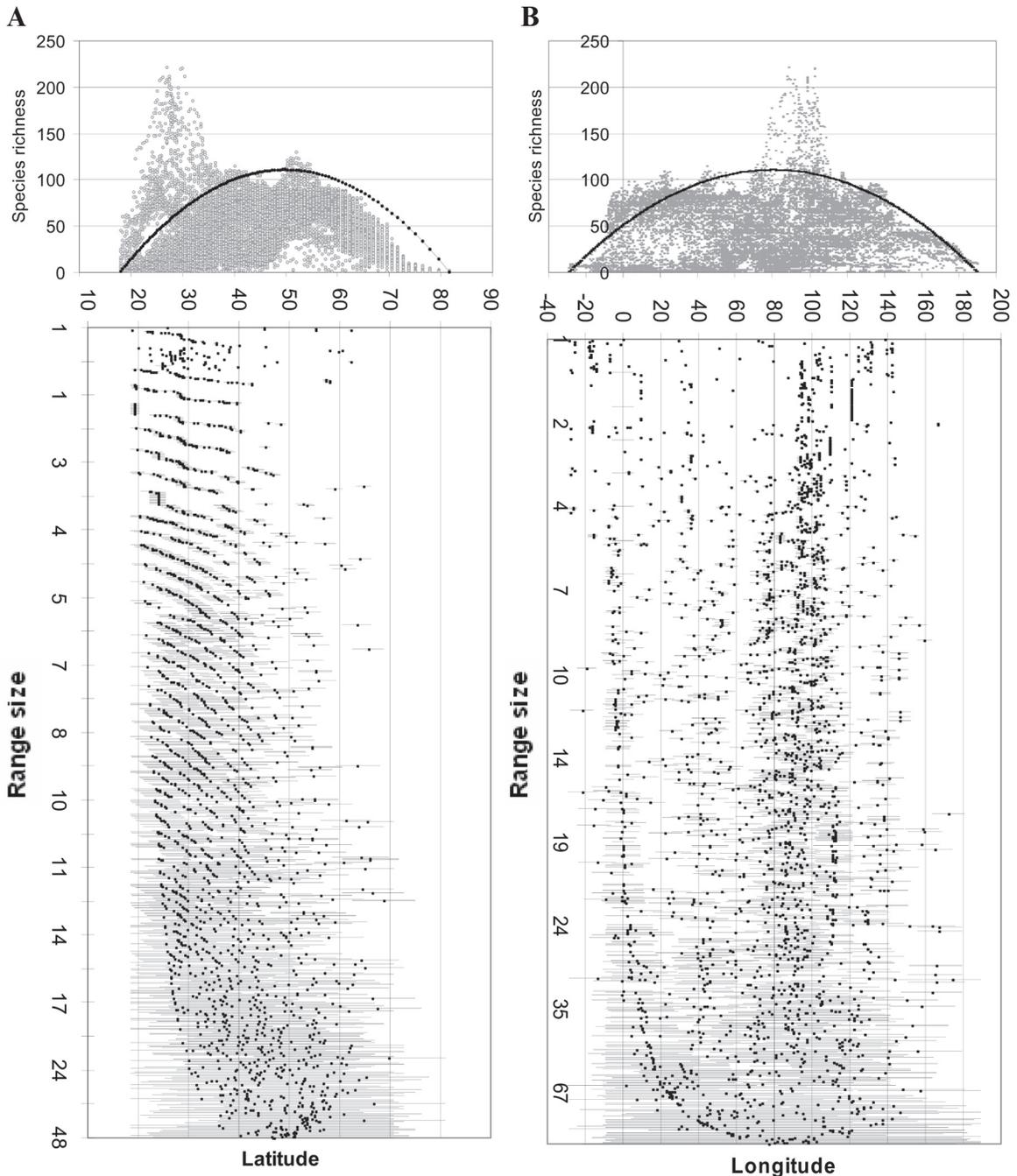
Fig. 2. Frequency distribution of range size of 2401 endemic songbirds of the Palearctic along the (A) latitude and (B) longitude axes. Horizontal lines indicate range sizes and midpoints indicate the position of the ranges along the latitude or longitude axes. Overlap among ranges on the bottom panels produces the pattern of species richness observed on the upper panels (grey dots). The MDE predictions are indicated by curved solid lines.

gradually towards the centre of the domain (100° Himalayan and central Siberia), then decreases gradually and shows a plateau in the eastern parts (Fig. 2b). Relatively few taxa have very large ranges

spanning the entire Palearctic Region, which has a strong effect on the average range size (Fig. 2a, b). The range-size frequency distributions are highly right-skewed, particularly along the latitude axis.
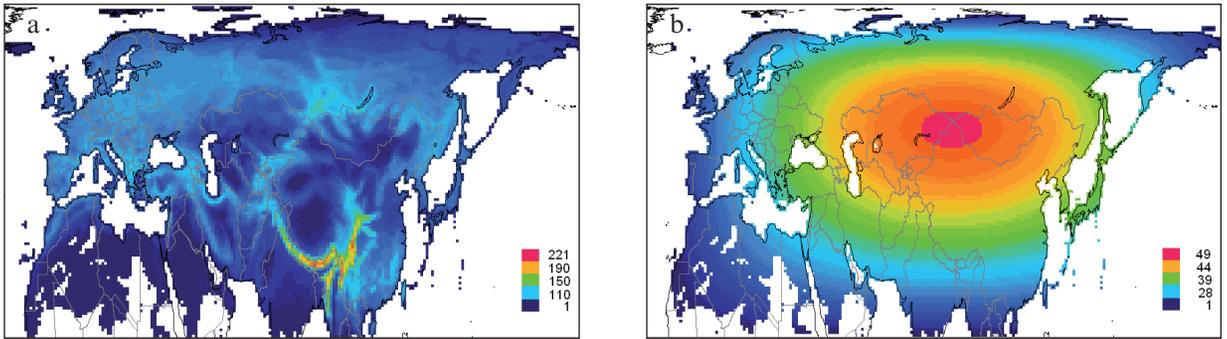
Fig. 3. Species richness patterns of songbird species endemic to the Palearctic (N = 2,401 taxa), showing (a) the observed pattern and (b) the simulated pattern, following a fully stochastic bi-dimensional mid-domain effect model.
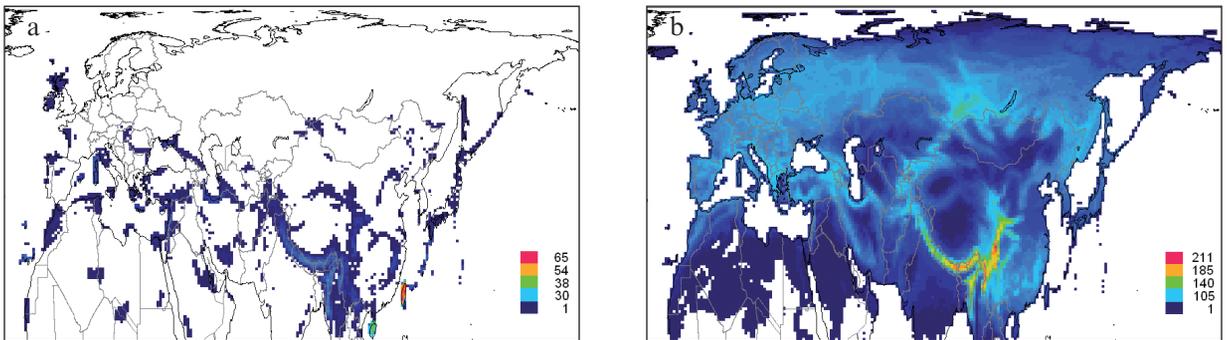

Fig. 4. Species richness patterns of songbird species endemic to the Palearctic, showing (a) the observed pattern of small-ranged endemics (N = 600 taxa), and (b) the observed pattern of all species, except the small-ranged endemics (N = 1,801 taxa).

Major geographic peaks of phylogenetic species richness are located in mountainous regions (Fig. 3a). Prominent peaks are located along the Himalayan, Pamir, Altai, and Tien Shan ranges. Other regions with high levels of richness are the Altai-Sayan mountain system, the Caucasus-Elburz system, and the Balkan Peninsula. The most prominent coldspot is located in the Gobi desert area in the central Palearctic.

The MDE predicts the lowest gradient along the longitude axis (R^2 = 3.1%) as compared to a much higher effect along the latitude axis (R^2 = 22.0%). However, effects along both gradients are statistically significant (Table 1).

A comparison of the songbirds' species empirical data with the prediction pattern of richness by bi-dimensional geometric constraints shows a coefficient of determination of 19.9% (Fig. 3b, Table 1). The observed pattern of species richness in small-ranged endemics is correlated strongly with overall species richness (r_s = 88) (Fig. 4a). The explanatory power of MDE, however, is at R^2 = 4.0%,

Table 1. Explanatory power of MDE null model predictions (estimated by coefficients of determination, R^2). The MDE prediction shows the lowest and highest gradient along longitudinal and latitudinal axes, respectively. When small-ranged endemics are excluded from the entire data set, MDE coefficients of determination are higher than when small-ranged species are included in the Palearctic endemics.

Data set partitions	taxa (n)	Correlation with Palearctic endemics (r_s)	Mid-Domain Effect (R^2)
Palearctic endemics	2,401	1	19.9 ***
Small-ranged endemics	619	25	4.3 ***
Palearctic endemics (excl. small ranged endemics)	1,782	99	21.4 **
Latitudinal gradient	2,401	-	22.0 ***
Longitudinal gradient	2,401	-	3.1 ***

which is considerably lower than that of the overall data set (Table 1).

The observed pattern of species richness in small-ranged endemics (Fig. 4a) reveals hotspots particularly in the southern and central parts of the Palearctic. This includes the Himalayas, Assam and Yunnan, the area south of the Caspian Sea, and the eastern parts of the Mediterranean. In addition, small-ranged endemics are found also in large numbers on islands such as Hainan, Taiwan, Corsica, Sardinia, and the Canary Islands.

When small-ranged endemics are excluded from the analysis, the observed pattern of species richness is similar to that when the small-ranged endemics are included (with $R^2=75.0\%$ in a linear regression model, Fig. 4b).

MDE in empirical data sets of birds

As compared to other groups of animals, birds have been more frequently assessed for the MDE models (more than one-third of published studies; cf. Table 2, Colwell *et al.,* 2004). To date, seventeen published studies (based on Web of Science, March 2008) have evaluated the role of MDE in explaining and predicting the empirical pattern of species richness in birds (Table 2).

Eight studies have focused on uni-dimensional MDE models to study the richness pattern for latitude, longitude, or two dimensions jointly (latitude and longitude or latitude and elevation), but most studies have used a bi-dimensional model (Table 2). Results from some of these studies show that MDE models explain much of the observed species richness patterns in birds (Lees *et al.,* 1999; Jetz and Rahbek, 2001, 2002; Koleff and Gaston, 2001). However, other authors have dismissed MDE models (Hawkins and Diniz-Filho, 2002; Rangel and Diniz-Filho, 2003). In general, the bi-dimension MDE predictions agree poorly with observed patterns of richness (Jetz and Rahbek, 2001; Zapata *et al.,* 2003; Colwell *et al.,* 2004).

Almost all studies that have partitioned ranges into range-size categories within the same data set have generally found stronger support for MDE among large-ranged species than among small-ranged species (Table 2), which is precisely as predicted by MDE theory.

Discussion

Our results indicate a poor correlation between species richness patterns of passerines in the Palearctic Region and the MDE geographic constraint model, particularly when this model is examined along the longitudinal axis. In contrast, the MDE predicts similar gradients in all directions (e.g., Jetz and Rahbek, 2001, Kerr *et al.,* 2006). Our study shows that Palearctic songbirds with small ranges relative

Table 2. Summary of sixteen empirical studies testing the Mid-domain effect on birds. Different values of R^2 refer to different subsets with different spatial resolution.

Reference	Domain	Taxa	Gradient	R² (%)
Aliabadian *et al.,* 2005	Palearctic	Songbird contact zones	bi-dimension	4
Aliabadian *et al.,* 2007	Palearctic	Songbirds	bi-dimension	4-34
Davies *et al.,* 2007	global	birds	bi-dimension	68-72
Diniz-Filho *et al.,* 2002	South America	birds of prey	bi-dimension	0-3
Hawkins and Diniz-Filho, 2002	North America	birds	bi-dimension	21
Herzog *et al.,* 2005	Bolivean Andes	birds	elevation	43
Jetz and Rahbek, 2001	sub-Saharan Africa	birds	latitude, longitude, and bi-dimension	21-66
Jetz and Rahbek, 2002	Sub-Saharan Africa	birds	bi-dimension	18
Kerr *et al.,* 2006	Madagascar	birds	latitude and bi-dimension	0-16
Koleff and Gaston, 2001	New World	Parrots and Woodpeckers	latitude	75-86
Lees *et al.,* 1999	Madagascar	birds	latitude	78-89
Rahbek, 1997	South America	birds	elevation	-
Rahbek *et al.,* 2007	South America	birds	bi-dimension	16
Rangel and Diniz-Filho, 2003	global	Falconiformes	bi-dimension	0-14
Romdal *et al.,* 2005	New World	birds	latitude	47
Storch *et al.,* 2006	global and biogeographical realms	birds	bi-dimension	2-60
Wisz *et al.,* 2007	sub-Saharan Africa	migratory Songbirds	latitude	5-15

to the entire Palearctic Region, are less likely to be strongly affected by MDE theory (Aliabadian *et al.,* 2007), which is precisely as expected under this model. Patterns of Palearctic songbirds richness are more likely to be driven by environmental and/or historical factors and not so much by geometric constraints (Storch *et al.,* 2006; Davis et al, 2007). If the MDE would accurately predict patterns of species richness in Palearctic songbirds, we would expect the highest numbers of birds in the Gobi desert and environs, which in fact represents a coldspot. Furthermore, MDE does not predict the high species richness that is found in areas such as south-eastern Asia and parts of Europe. The bi-dimension MDE prediction pattern (Fig. 3) is in agreement with a recent study conducted by Storch *et al.,* (2006). In that study, however, the MDE model explained 60% of the variance in global scale of species richness, but the MDE prediction for the variation of species richness within Palearctic Region decreased to 14%.

MDE predictions depend critically on the relationship between maximum attainable range size and domain size (Colwell and Hurtt, 1994; Pineda and Caswell, 1998). In particular, the strength of the MDE decreases and converges to a uniform pattern as the ratio of maximum attainable range size to domain decreases (Colwell and Hurtt, 1994; Zapata *et al.,* 2003). Our results confirm that excluding wide-ranging species from analysis and considering only species with small ranges reduces the explanatory power of geometric constraints to very small values. This result is congruent with all other bi-dimensional analyses of the MDE (Bokma *et al.,* 2001; Jetz and Rahbek, 2001, 2002; Diniz-Filho *et al.,* 2002; Hawkins and Diniz-Filho, 2002). However, small-ranged taxa are less constrained by MDE. It was shown that in small-ranged species there are important environmental effects of which little influence could be detected in large-ranged species (cf. Dunn *et al.,* 2007). Most importantly, this means that studies that examine all species together, irrespective of their range size, i.e. without considering small-ranged species separately, often miss the diversity patterns of species of greatest conservation concern. This is due to the fact that the pattern of the small-ranged species is swamped by the MDE of large-ranged species. Furthermore, recent studies have concluded that richness patterns on different continents are influenced by many factors and cannot be attributed to one single factor (Hawkins *et*

al., 2007; Rahbek *et al.,* 2007; Symonds and Johnson, 2008). Therefore, MDE for species distribution is at best one of the possible explanations, among several others, for biodiversity patterns (Colwell and Lees, 2000; Colwell *et al.,* 2004).

Our results confirm the prediction that the centres of endemism of Palearctic songbirds show higher species richness than other areas, even when small-ranged species are excluded from the overall species richness pattern (Endler, 1982; Haffer, 1982; Prance, 1982). This high species richness within endemic areas may simply be caused by differences in environmental conditions that correlate with species richness (Anderson, 1994; Humphries *et al.,* 1999), or with historical processes (Lomolino *et al.,* 2005). Stable climates in these regions may have facilitated survival of small-ranged species during adverse times (Jetz *et al.,* 2004). Furthermore, these regions may exhibit a unique set of environmental conditions, allowing a multitude of small-ranged endemics to survive and co-exist. The question of why these hotspots of endemism are concentrated in areas already rich in species can be answered only by examining possible relationships between geographical distribution of habitat and topographic diversity on the one hand and the location of hotspots of small-ranged endemic species on the other.

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