Contributions to Zoology, 76 (3) 197-204 (2007)

Low predictive power of mid-domain effect to explain geographic species richness patterns in Palearctic songbirds

M. Aliabadian[1, 2], C. S. Roselaar[1], R. Sluys[1], V. Nijman[1]
[1]*Institute for Biodiversity and Ecosystem Dynamics and Zoological Museum, University of Amsterdam, P.O.Box 94766, 1090 GT Amsterdam, The Netherlands;* [2] *Faculty of Science, Department of Biology, Ferdowsi University of Mashhad, Mashhad, Iran*

Key words: Aves, Passeriformes, Palearctic, mid-domain effect, species richness, geographic range size.

Abstract

In the study of diversity patterns, the Mid-domain effect (MDE), which explains gradients in diversity solely on the basis of geometric constraints, has emerged as a null-model against which other hypotheses can be tested. The effectiveness, measured by its predictive power, of these MDE models appears to depend on the size of the study area and the range-sizes of the taxa considered. Here we test the predictive power of MDE on the species richness patterns of birds and assess its effectiveness for a variety of species range sizes. We digitised distribution maps of 889 species of songbird endemic to the Palearctic, and analysed the emergent biogeographic patterns with WORLDMAP software. MDE had a predictive power of 20% when all songbirds were included. Major hotspots were located south of the area where MDE predicted the highest species-richness, and some of the observed coldspots were in the centre of the Palearctic, contradicting the predictions of the MDE. MDE had little explanatory power (3-19%) for all but the largest range sizes, whereas MDE performed equal or better for the large-ranged species (20-34%) compared to the overall model. Overall MDE did not accurate explain species-richness patterns in Palearctic songbirds. Subsets of larger-range species did not always have a larger predictive power than smaller-range species or the overall model. Despite their low predictive power, MDE models can have a role to play in explaining biogeographic patterns but other variables need to be included in the model as well.

Contents

Introduction

Species are not evenly distributed on the surface of earth. Although this knowledge dates back centuries (e.g., Wallace, 1878), explaining and identifying the patterns of geographical distribution of species diversity both in space and time remains a fruitful area of research (e.g. Veith *et al.*, 2006; van Weers, 2005). Over the last decades more than 30 evolutionary and ecological hypotheses (Hawkins *et al.*, 2003) have been postulated to account for diversity gradients and species richness, of which Rahbek and Graves (2001) and Whittaker *et al.* (2001) identified five as "credible hypotheses", centring on: (1) gradients in the effect of energy availability (Wright, 1983; Currie 1991), (2) habitat heterogeneity (Rahbek and Graves, 2001), (3) area *per se* (Schoener 1976; Rosenzweig 1995), (4) evolutionary time (Ricklefs *et al.*, 1999), and (5) geometric constraints (Colwell and Hurtt, 1994; Willing and Lyons, 1998; Colwell and Lees, 2000; Brehm *et al.*, 2007; McClain *et al.*, 2007).

As the most prominent representative of the fifth category above, the mid-domain effect (MDE) provides explanations of gradients in species diversity based solely on geometric constraint on species ranges, without the incorporation of underlying biological mechanisms, and thus can serve as a null-model against which other hypotheses can be tested. Under the MDE model, a mid-domain peak in richness is generated in the centre of the domain purely by chance, as this is the area where there is an increasing overlap in species ranges. The initial models of the mid-domain effect were constructed in uni-dimensional space and in the context of a latitudinal gradient in diversity (and associated Rapoport effect, i.e., a decrease in species range sizes towards the equator). Bokma and Monkkonen (2000) extended this analytical model to cover the distribution of species by taking account of both latitudinal and longitudinal dimensions. As such, these bi-dimensional models have been tested with different taxa and in different continental and inter-continental settings with varying degrees of success (reviewed by Colwell *et al.*, 2004).

MDE model predictions depend critically on the range size frequency distribution of individual species within the domain. In general, the range overlap produces a pattern of increasing species richness from the boundaries toward the centre of the domain, and if the ratio of maximum attainable range size to domain size increases the MDE increases and tends to converge towards a parabolic pattern (Colwell and Hurtt, 1994; Lees *et al.,* 1999; Zapata *et al.*, 2003). Large-ranged species necessarily overlap in the middle of the domain whereas small-ranged species are unobstructed by geometric constraints and are free to occur virtually anywhere within the domain (Colwell *et al.*, 2004). Thus, MDE are hypothesised to explain a larger proportion of the observed variation for large-ranged species than small-ranged species. Hence, when large-ranged species are excluded from analysis, it is hypothesised that the MDE models will be a weak predictor for the observed pattern of species richness in the remaining (small-ranged) species (Colwell and Lees, 2000).

In birds, theoretical and empirical evidence for MDE has been obtained for a variety of taxa on different continents (Jetz and Rahbek, 2001; 2002; Hawkins and Diniz-Filho 2002; Diniz-Filho *et al.*, 2003; Colwell *et al.*, 2004). These analyses have shown that, at least for birds, the predictive power of bi-dimensional MDE models explains less than a quarter of the observed variation, whereas models that invoke environmental factors typically explain over three-quarters of the observed variation (Balmford *et al.*, 2001; Boone and Krohn, 2000; Hawkins and Diniz-Filho, 2002).

Here we test a bi-dimensional MDE model on the geographic pattern of species richness of songbirds (Passeriformes) in the Palearctic Region. Its large size, heterogeneous environment and the large number of songbirds occurring in the Palearctic Region make it an interesting test-case to assess the predictive power of the MDE models. MDE models are predicted to perform best in homogenous, single-biome domains in which a substantial proportion of the species have ranges more than half the size of the domain (Lees *et al.*, 1999; Colwell *et al.*, 2004, 2005). The Palearctic Region is arguably the most climatically and topographically diverse heterogeneous landmass on the planet, with relatively few birds having large distribution ranges, making it an excellent case for testing the performance of MDE models. Furthermore, we test the effect of species-range sizes on how well the MDE performs using two different approaches.

Materials and methods

The data set

The full database consists of breeding distribution maps for all 1108 traditional biological or isolation species (3032 taxa in total, i.e. species and subspecies) of songbirds in the Palearctic Region (Europe, N. Africa and Asia: 30º-170ºW, 86º-18ºN), which have been digitized using WORLDMAP software (Williams, 2000), identical to that in Aliabadian *et al.* (2005) and Roselaar *et al.* (2007). The geographic distributions were plotted over a one degree longitude equal area map (grid-cell area: 4062 km^2) of the Palearctic Region. The distribution data were compiled from standard reference works, supplemented by data obtained from numerous zoological collections (see Roselaar *et al.*, 2007). Nomenclature and taxonomy follows Roselaar and Shirihai (in press).

The empirical diversity gradient was generated by recording whenever a grid cell was within the reported range of a species. Since the logic of the MDE hypothesis assumes that species ranges are found entirely within the domain we limited our analysis to those taxa whose breeding ranges are confined to the Palearctic Region, the so-called Palearctic endemics. This data set contains 889 biological species comprising 680,586 presence records across 14,714 grid-cells.

To explore the role of range size frequency distribution on geometric constraints we applied the following two approaches that have been used previously, i.e. by Diniz-Filho and colleagues and by Jetz and Rahbek.

(1) Hawkins and Diniz-Filho (2002) and Rangel and Diniz-Filho (2003) classified species ranges into three classes based on the percentage of all sample points occupied by individual species, i.e. small (<25% of all sample points), medium (26-50%), and large (>50%). Following this approach we classified the 680,586 species presence records of breeding songbirds across 14,714 grid cells into small-range species (n = 846), medium-range species (n = 36), and large-range species (n = 7).

(2) Jetz and Rahbek (2001; see also Rahbek *et al.*, 2007) classified species into one of four equal-interval

classes. Following these quartile range sizes, Palearctic songbirds were classified from first to fourth quartile range sizes, each containing about 222 species with <81, 82-235, 236-767, and >768 grid-cells range sizes per quartile, respectively.

Null model

The predictions of the mid-domain effect have been tested by a variety of null models, including fully stochastic distribution and both range and midpoint–constrained models (Colwell *et al.*, 2004). To avoid an artificial reduction in dimensionality, which imposes a simplification of the patterns and a concomitant loss of information (Bokma *et al.*, 2001), we tested observed pattern of species richness with a bi-dimensional model. The species richness for each point of the grid cells (P) is estimated by a pure stochastic process, and is a function of its position relative to boundaries across northern (p), southern (q), western (r), and eastern (t) end points of a domain. The species richness expected at P is then given by 4pqstS, where S is the total species richness in the domain (Bokma *et al.*, 2001). Under this model some areas like peninsular regions, which do not contact the main body of the landmass, will show a large expected diversity because the value of p, q, r, and t are calculated from each point to the immediate boundaries and not the entire landmass. To reduce the peninsular diversity peaks, we followed the ‘area corrected’ version of Willing and Lyons (1998), taking the absolute distance of a point to the Palearctic border into account (Hawkins and Diniz-Filho, 2002). Then the p, q, r, and t proportions in the null model were estimated for each point of the grid based on the maximum N-S and E-W axes.

Statistical analysis

Biogeographical data, such as species richness, which are derived from geographical range maps, are not independent and tend to be strongly spatially auto-correlated (Diniz-Filho *et al.*, 2002; 2003; Legendre *et al.*, 2002). As such there is a serious overestimate of the degrees of freedom and therefore the significance levels of the regression coefficient are raised upward, in essence making significance tests too liberal (Diniz-Filho *et al.*, 2003). As to preclude this we restrict our comparisons to coefficient of determination (R^2) of linear regression (r_S), without presenting significance levels between observed and expected species richness at each grid cells of the Palearctic map (cf Jetz and Rahbek, 2001; Williams *et al.*, 2006). Following Aliabadian *et al.* (2005) values in the null model were only calculated for those grid cells that were actually occupied by one or more species in the real data set; this approach is conservative because any MDE prediction of the presence of species in other grid cells would lower the fit of the model.

Results

Species richness patterns of all breeding songbirds recorded within the boundaries of the Palearctic (n = 1108 species) and species endemic to the Palearctic (n = 889) are highly correlated (r_S = 91%). Since most of the extra-limital species occur in the Ethiopian and Oriental Regions, the Palearctic endemics dataset de-emphasizes the hotspot in Southeast Asia. In both analyses, major hotspots are located in the area from the Caspian Sea Basin extending northeastwards to Hindu-Kush, Pamir, Tien-Shan, and Altai, as well as in central Siberia. Smaller hotspots occur south of the Caspian Sea, curving northwestwards towards the Caucasus and the mountains of southern and eastern Turkey. In Western Europe, a hotspot occurs on the Balkan Peninsula (Fig. 1a; see also Roselaar *et al.*, 2007).

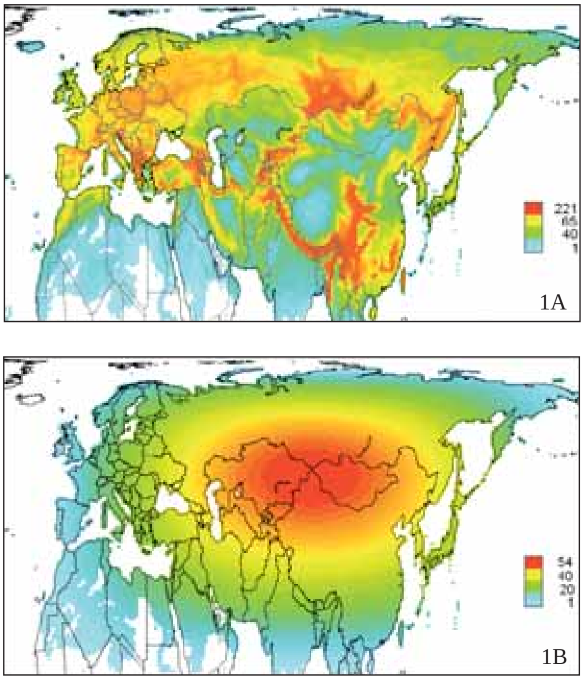
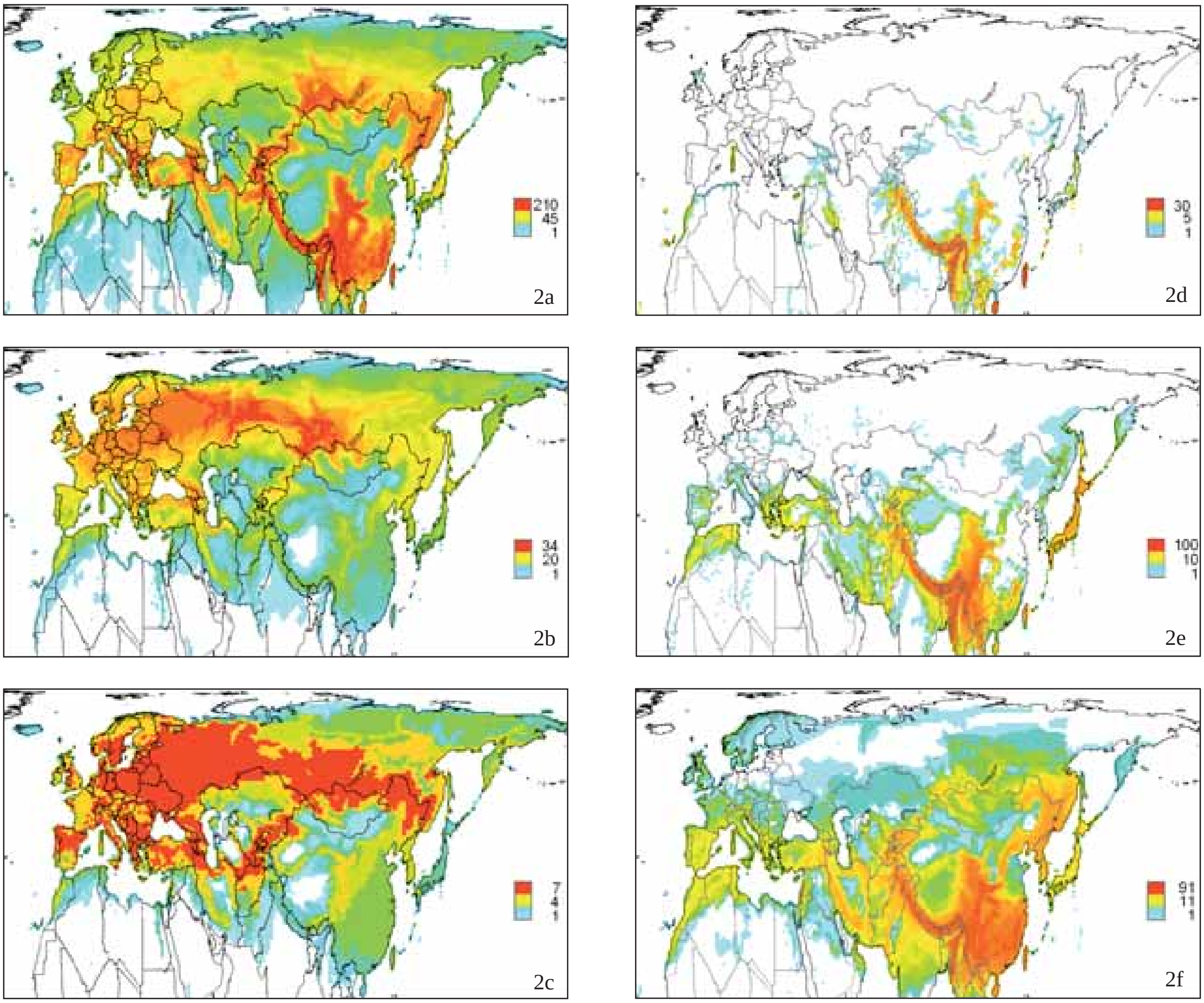


Fig. 1. Observed (A) and simulated (B) patterns of species richness for all Palearctic endemic songbirds (for further explanation, see text).



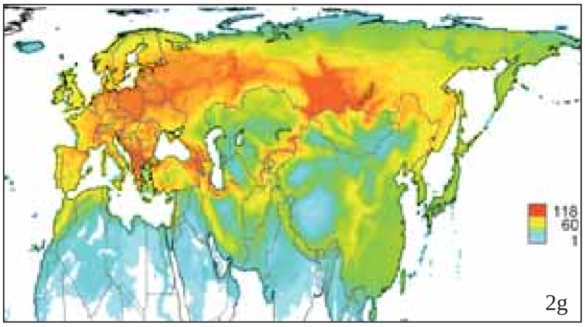


Fig. 2. Species richness pattern of the Palearctic endemic songbirds. a) small-range species (n=846, 67.5% records); b) medium-range species (n=36, 24.2% records); c) large-range species (n=7, 8.4% records); d) first quartile range species (n=223, 1.1% records); e) second quartile range species (n=222, 4.8% records); f) third quartile range species (n=222, 14.3% records); g) fourth quartile range species (n=222, 79.86% records).

The observed pattern of songbirds' richness clearly varied from that predicted by geometric constraints (Fig. 1b), which placed the highest species richness in the centre of the Palearctic, corresponding to the Gobi desert, Altai and Tien-Shan systems, with a gradual decrease when departing from the midpoint of the Palearctic. For all Palearctic endemics MDE explains 20.0% of variation in species richness.

The predictive power of the MDE decreases with smaller range sizes, ranging from 20.0% for large-range species to 18.9 and 9.1% for medium-range and small-range species, respectively (Table 1; Figure 2a,

Subdivision	**Species (n)**	**Gridcells occupied (%)**	**Correlation with Palearctic endemics (r_s)**	**Mid-Domain Effect (R^2)**
Palearctic endemics	889	100	1	19.95
Small-range species	846	67.46	0.97	9.07
Medium-range species	36	24.18	0.84	18.87
Large-range species	7	8.35	0.87	19.66
First quartile species	223	1.07	0.39	3.45
Second quartile species	222	4.78	0.46	3.66
Third quartile species	222	14.29	0.62	3.40
Forth quartile species	222	79.86	0.90	34.33

Table 1. Results of linear regressions of observed species richness in songbirds, using distinct parts of the species pool (n), against the proportion of the species pool expected under area-corrected bi-dimensional MDE model. Subdivisions into small-, medium- and large range species, and first to forth quartile species follow Hawkins and Diniz-Filho (2002) and Jetz and Rahbek (2001), respectively.

b, c). The observed pattern of species richness for all Palearctic endemics is most strongly correlated with that of the small-range species, and less so for medium-range and large-range species (Table 1). Hotspot patterns for the small-range and medium-range species differ qualitatively from the large-range species, with an increasing emphasis on northern and western regions.

Partitioning the songbirds into range size quartiles, it is clear that the pattern of species richness for the fourth-quartile species (i.e. those with the largest ranges) (Fig. 2g) differ qualitatively from that of the first-, second- and third–quartile species (Figs 2d, e, f). For the latter species, hotspots are located mainly in Southeast Asia and gradually move northwestwards from the first-, to the third–quartile species. The fourth-quartile species, in contrast, do not show a hotspot in Southeast Asia but only in central Siberia and Europe. The predictive power of MDE is low for the first-, second- and third-quartile range species, whereas MDE explains about a third of the observed variation in the fourth-quartile species (Table 1). The observed pattern of species richness for all Palearctic endemics is weakly correlated with that of the first-quartile species, and increases progressively with increasing range-sizes (Table 1).

Discussion

Under a geographic constraint model such as MDE, species richness is expected to be highest in the central Palearctic with a gradual decrease towards the continental edges. Our data of the songbirds, however, shows that hotspots of species richness are not only located in the central parts of the Palearctic but also in southwestern Asia, southern Europe, and especially Southeast Asia. Within these regions especially mountain areas contain high numbers of species, with hotspots clearly following the main mountain ranges (cf. Roselaar *et al.*, 2007; Aliabadian *et al.*, 2005). Moreover, some of the coldspots observed in the songbird distribution are in the centre of the Palearctic and as such contradict the predictions from the MDE model. Overall, the MDE had a low explanatory power of around 20% for almost 900 species of songbirds endemic to the Palearctic Region.

Geometric constraints are expected to affect the distribution of large-ranged species more than they affect small-ranged species as species with small ranges are free to occur (or not to occur) virtually anywhere within the domain, whereas range centres of large-ranged species must cluster near mid-domain (Colwell *et al.*, 2004). In other words, the strength of the MDE decreases and tends to converge towards a uniform pattern as the ratio of maximum attainable range size to domain size decreases (Zapata *et al.*, 2003).

We assessed the effects of species range sizes on the MDE by creating different range-size classes, one based on number of occupied grid-cells and one based on range-size quartiles. In the first approach, small-ranged species show a species-richness pattern similar to that of all Palearctic songbirds but the explanatory power of MDE was halved. The medium- and large ranged species made up only a small part of the overall species pool, and although the explanatory power of MDE was better than that of the small-ranged species, unlike Hawkins and Diniz-Filho's analysis (2002), it did not perform better than when all endemic Palearctic songbirds were included. Following a second approach, based on range-size quartiles, similar to Jetz and Rahbek (2002) we found that although MDE had little explanatory power for the first- to third-quartile species, MDE performed well for the fourth-quartile range sizes. In fact, it clearly outperformed the all endemic Palearctic songbirds dataset, and confirms the notion that MDE performs best for species with large ranges (Colwell and Hurtt, 1994; Lees *et al.*, 1999). As such the two approaches led to different results suggesting that how large or small range species are defined is an important factor when testing the MDE. As noted by Lees *et al.* (1999) and Colwell *et al.* (2004, 2005), MDE models are predicted to perform best in homogenous, single-biome domains in which a substantial proportion of the species have ranges more than half the size of the domain, and this is clearly not the case with songbirds in the Palearctic (with many species with narrow ranges and geographically great climatic and topographic variability).

Much attention has been paid to 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) or from an evolutionary and biogeographical perspective (Jetz *et al.*, 2004; Orme *et al.*, 2005). What defines a restricted range species differs between studies, but in general it refers to species that have a distribution or breeding range below a certain threshold, ranging from 50,000 km^2 (Stattersfield *et al.*, 1998) to c. 960,000 km^2 (Dillon and Fjeldså, 2005). For Palearctic songbirds, the distribution pattern of first-quartile range species (with a breeding range of <325,000 km^2) can thus be considered the distribution pattern of centres of endemism.

In interpreting patterns of species distributions these centres of endemism have repeatedly been regarded as areas where the overall species richness is higher than elsewhere, regardless of the particular restricted range species within them (Jetz *et al.*, 2004). Jetz *et al.*, (2004) found supportive evidence for the hypothesis that centres of endemism indeed do contain an unexpectedly greater number of species than other regions in Sub-Saharan African birds and found that environmental factors such as productivity are a better predictor for the observed patterns than MDE. We showed that MDE is a poor predictor for patterns of restricted range species (Table 1). In the Palearctic, all restricted range species hotspots are also hotspots of overall species richness (compare Figs 2d with 1a). Subtracting the restricted range species from the overall species pool does not alter the pattern of species richness (Fig. 3), confirming the observation that centres of endemism indeed do contain a larger than average number of species.

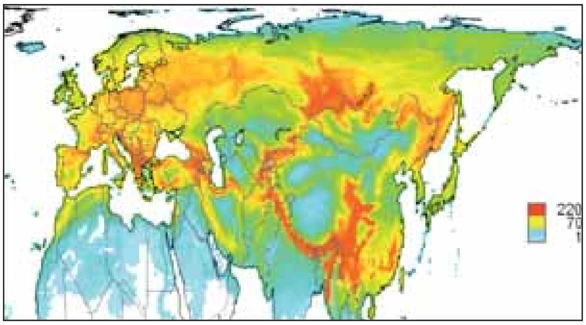


Fig. 3. Observed pattern of species richness of Palearctic songbirds excluding restricted-range species, showing that restricted-range species hotspots are also disproportional rich in non-restricted-range species (see text for details).

Our analysis revealed a distinctly uneven geographical distribution of songbirds in the Palearctic region, irrespective of the range size classes included or excluded. This may be related to its large climatic and topographic heterogeneity. In general MDE failed to explain a significant proportion of the observed variation, although for selected subsets of large-range species the explanatory power was larger than in other subsets. However, not even in the best subset MDE did not explain more than 35% of the variance. Hawkins and Diniz-Filho (2002) and Zapata *et al.* (2003) concluded that (1) there were both theoretical and empirical arguments undermining the validity of the hypothesis behind the MDE, (2) MDE models had failed to predict the observed patterns of species richness in a variety of taxa, and (3) that the practical usefulness of MDE models were limited. Despite these conclusions, we agree with Colwell *et al.*, (2005), that process-based models (e.g., Connolly, 2005; Davies *et al.*, 2005; Rangel and Diniz-Filho, 2005) that mechanistically integrate geometric constraints with environmental gradients and/or evolutionary processes in bounded domains offer a way forward from the correlative approaches of both classic MDE analyses and conventional, regression-based analyses of richness in relation to environmental variables.

Acknowledgements

We are grateful to Peter Mekenkamp for generating the equal area map, and Paul Williams for implementing it in the WORLDMAP programme, and to Fred Schram and Miguel Vences for help and advice. Funding was provided by the Ministry of Science, Research and Technology of the Islamic Republic of Iran, the P.A. Hens Memorial Fund, and SYNTHESYS (SE-TAF-639, DK-TAF-849, DE-TAF-796, GB-TAF-826). We thank the two anonymous reviewers whose comments improved the clarity of our writing.

References

Aliabadian M, Roselaar CS, Nijman V, Sluys R, Vences M. 2005. Identifying contact zone hotspots of passerine birds in the Palaearctic Region. *Biological Letters* 1: 21-23.

Balmford A, Moore JL, Brooks T, Burgess N, Hansen LA. Williams P, Rahbek C. 2001. Conservation conflicts across Africa. *Science* 291: 2616-2629.

Bokma F, Monkkonen M. 2000. The mid-domain effect and the longitudinal dimension of continent. *Trends in Ecology and Evolution* 15, 288-289.

Bokma F, Bokma J, Monkkonen M. 2001. Random processes and geographic species richness patterns: why so few species in the north? *Ecography* 24, 43-49.

Boone RB, Krohn WB. 2000. Partitioning sources of variation in vertebrate species richness. *Journal of Biogeog*raphy 27: 457-470.

Brehm G, Colwell RK, Kluge J. 2007. The role of environment and mid-domain effect on moth species richness along a tropical elevational gradient. *Global Ecology and Biogeography* 16: 205-219.

Colwell RK, Hurtt GC. 1994. Nonbiological gradients in species richness and a spurious Rapoport effect. *American Naturalist* 144: 570-595.

Colwell RK, Lees DC. 2000. The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology and Evolution* 15, 70-76.

Colwell RK, Rahbek C, Gotelli NJ. 2004. The mid-domain effect and species richness patterns: what have we learned so far? *American Naturalist* 163, E1-E23.

Colwell RK, Rahbek C, Gotelli NJ. 2005. The mid-domain effect: There's a baby in the bathwater. *American Naturalist* 166: E149-E154.

Connolly SR. 2005. Process-based models of species distributions and the mid-domain effect. *American Naturalist* 166: 1-11.

Currie DJ. 1991. Energy and large-scale patterns of animal-species and plant-species. *American Naturalist* 137: 27-49.

Davies TJ, Grenyer R, Gittleman JL. 2005. Phylogeny can make the mid-domain effect an inappropriate null model. *Biological Letters* 1: 143-146.

Dillon S, Fjeldså J. 2005. The implication of different species concepts for describing biodiversity patterns and assessing conservation needs for African birds. *Ecography* 28: 682-692.

Diniz-Filho JAF, Ramos de Sant'Ana CE, de Souza MC, Rangel TFLVB. 2002. Null models and spatial patterns of species richness in South American birds of prey. *Ecology Letters* 5: 47-55.

Diniz-Filho JAF, Bini LM, Hawkins BA. 2003. Spatial autocorrection and red herrings in geographical ecology. *Global Ecology and Biogeography* 12: 53-64.

Hawkins BA, Diniz-Filho JAF. 2002. The mid-domain effect cannot explain the diversity gradient of Nearctic birds. *Global Ecology and Biogeography* 11: 419-426.

Hawkins BA, Field R, Cornell HV, Currie DJ, Guegan JF, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, Porter EE, Turner JRG. 2003. Energy, water, and broad-scale geographic patterns of species richness. *Ecology* 84: 3105-3117.

Jetz W, Rahbek C. 2001. Geometric constraints explain much of the species richness pattern in African birds. *Proceedings of the National Academy of Science USA* 98: 5661-5666.

Jetz W, Rahbek C. 2002. Geographic range size and determinants of avian species richness. *Science* 297: 1548-1551.

Jetz W, Rahbek C, Colwell RK. 2004. The coincidence of rarity and richness and the potential signature of history in centres of endemism. *Ecology Letters* 7: 1180-1191.

Legendre P, Dale MRT, Fortin MJ, Gurevitch J, Hohn M, Myers D. 2002. The consequence of spatial structure for the design and analysis of ecological field survey. *Ecography* 25: 601-615.

Lees DC, Kremen C, Andriamampianina L. 1999. A null model for species richness gradients: bounded range overlap of butterflies and other rainforest endemics in Madagascar. *Biological Journal of the Linnean Society* 67: 529-584.

McClain CR, White EP, Hurlbert AH. 2007. Challenges in the application of geometric constraint models. *Global Ecology and Biogeography* 16: 257-264

Mittermeier RA, Myers RAN, Gil PR, Mittermeier GC. 1999. Hotspots: Earth's biology richest and most endangered terrestrial ecosystems. CEMEX, Conservation International, and Agrupacion Sierra Madre, Mexico. 430 pp.

Orme CDL, Davies RG, Burgess M, Eigenbrod F, Pickup N, Olson, VA, Webster, AJ, Ding T, Rasmussen PC, Ridgley RS, Stattersfield AJ, Bennett PM, Blackburn TM, Gaston KJ, Owens IPF. 2005. Global hotspots of species richness are not congruent with endemism or threat. *Nature* 436:1016-1019.

Rahbek C, Graves GR. 2001. Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Science USA* 98: 4534-4539.

Rahbek C, Gotelli NJ, Colwell RK, Entsminger GL, Rangel TFLVB, Graves GR. 2007. Predicting continental-scale patterns of bird species richness with spatially explicit models. *Proceedings of the Royal Society of London series B* 274: 165-174

Rangel TFLVD, Diniz-Filho JAF. 2003. Spatial patterns in species richness and the geometric constraint simulation model: a global analysis of mid-domain effect in Falconiformes. *Acta Oecologica* 24: 203-207.

Rangel TFLVD, Diniz-Filho JAF. 2005. An evolutionary tolerance model explaining spatial patterns in species richness under environmental gradients and geometric constraints. *Ecography* 28: 253-267.

Ricklefs RE, Latham RE, Qian H. 1999. Global patterns of tree species richness in moist forests: distinguishing ecological influences and historical contingency. *Oikos* 86: 369-373.

Roselaar CS, Sluys R, Aliabadian M, Mekenkamp PGM. 2007. Geographic patterns in the distribution of Palearctic songbirds. *Journal of Ornithology* doi 10.1007/s10336-007-0129-1

Roselaar CS, Shirihai H. (in press) Handbook of geographical variation and distribution of Palearctic Birds, Vol. 1, Passerines. A & C Black, London.

Rosenzweig ML. 1995. Species Diversity in Space and Time. Cambridge Univ. Press, Cambridge, U.K.

Schoener TW. 1976. The species-area relation within archipelagos: models and evidence from island land birds. In Calaby JH (ed.), Proceedings of the XVI International Ornithological Congress. Australian Academy of Science: 629-642.

Stattersfield AJ, Crosby MJ, Long AJ, Wege DC. 1998. Endemic Bird Areas of the World: Priorities for Biodiversity Conservation. Birdlife International, Cambridge, UK.

Veith M, Fromhage L, Kosuch J, Vences M. 2006. Historical biogeography of Western Palaearctic pelobatid and pelodytid frogs: a molecular phylogenetic perspective. *Contributions to Zoology* 75: 109-120.

Wallace AR. 1878. Tropical nature and other essays. MacMillan, London.

Weers DJ van. 2005. A taxonomic revision of the Pleistocene *Hystrix* (Hystricidae, Rodentia) from Eurasia with notes on the evolution of the family. *Contributions to Zoology* 74: 301-312.

Whittaker RJ, Willis KJ, Field R. 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography* 28: 453-470.

Williams PH. 2000. WORLDMAP: Priority areas for biodiversity, Version 4.1. Privately distributed, London.

Williams P, Faith D, Manne L, Sechrest W, Preston C. 2006. Complementary analysis: mapping the performance of surrogates for biodiversity. *Biological Conservation* 128: 253-264.

Willing MR, Lyons SK. 1998. An analytical model of latitudinal gradients in species richness with an empirical test for marsupials and bats in the New World. *Oikos* 81: 93-98.

Wright DH. 1983. Species-energy theory: an extension of species-area theory. *Oikos* 41: 496-506.

Zapata FA, Gaston KJ, Chown SL. 2003. Mid-domain models of species richness gradients: assumptions, methods and evidence. *Journal of Animal Ecology* 72: 677-690.

Received: 12 June 2007
Accepted: 3 July 2007