

# WORLDWIDE PATTERNS IN SPECIES RICHNESS OF FALCONIFORMES: ANALYTICAL NULL MODELS, GEOMETRIC CONSTRAINTS, AND THE MID-DOMAIN EFFECT

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## ABSTRACT

Recently, the hypothesis that the geographic distribution of species could be influenced by the shape of the domain edges, the so-called Mid-Domain Effect (MDE), has been included as one of the five credible hypotheses for explaining spatial gradients in species richness, despite all the unsuccessful current attempts to prove empirically the validity of MDE. We used data on spatial worldwide distributions of Falconiformes to evaluate the validity of MDE assumptions, incorporated into two different sorts of null models at a global level and separately across five domains/landmasses. Species richness values predicted by the null models of the MDE and those values predicted by Net Primary Productivity, a surrogate variable expressing the effect of available energy, were compared in order to evaluate which hypothesis better predicts the observed values. Our tests showed that MDE continues to lack empirical support, regardless of its current acceptability, and so, does not deserve to be classified as one possible explanation of species richness gradients.

*Key words:* species richness, spatial patterns, richness gradients, net primary productivity, mid-domain effect, null models, Falconiformes.

## RESUMO

### **Padrões mundiais de riqueza de espécies de Falconiformes: modelos nulos analíticos, restrições geométricas e o efeito do domínio médio**

Recentemente, a hipótese de que a distribuição geográfica das espécies poderia ser influenciada pela forma das bordas continentais, conhecida como Efeito do Domínio Médio (EDM), foi incluída como uma das cinco hipóteses prováveis para explicar os gradientes espaciais de riqueza de espécies, apesar das últimas tentativas infrutíferas de prová-la empiricamente. Usamos os dados globais de distribuição espacial dos Falconiformes para avaliar os pressupostos do EDM, por meio de dois tipos de modelos nulos, em uma análise global e, também, separadamente por cinco domínios/continentes. Os valores de riqueza de espécies preditos pelos modelos nulos do EDM e pela produtividade primária líquida, uma variável substitutiva para expressar o efeito da energia disponível, foram comparados para avaliar qual hipótese prediz melhor os valores observados. Nossos testes mostraram que o EDM permanece sem suporte empírico, apesar da corrente notoriedade, não merecendo, portanto, ser classificado como uma das explicações possíveis para os gradientes de riqueza de espécies.

*Palavras-chave:* riqueza de espécies, padrões espaciais, gradientes de riqueza, produtividade primária líquida, efeito do domínio médio, modelos nulos, Falconiformes.

## INTRODUCTION

The causes of the gradients in species richness were always controversial, and ecologists and biogeographers are still looking for strong and concise explanations for this long known and very well documented biological phenomenon (Rohde, 1992; Whittaker *et al.*, 2001). Attempts to identify potential mechanisms that operate in macro-scale patterns in geographic distributions of species richness date back almost two centuries (von Humboldt, 1807), and within just the past two decades, more than 100 explanatory hypotheses have been considered.

Currently, there are about 30 considered hypotheses, with five groups of them have recently been classified as the "most credible": energy availability, evolutionary time, habitat heterogeneity, area, and geometric constraints (Rahbek & Graves, 2001). Although it is still necessary to define the best hypothesis among them, a useful reduction has already been made in relation to various hypotheses previously proposed.

One of these hypotheses is the mid-domain effect (MDE), which argues that, at macro-scales, the gradient in spatial patterns of richness is geometrically constrained by how and where ranges can be placed within the hard of domain boundaries to which the species is confined. Independently of all evolutionary and environmental features, higher richness would be in the middle of the domain, as expected by chance alone, as a consequence of "the increasing of the overlap of species ranges towards the center of a shared geographic domain, due to geometric boundary constraints in relation to the distribution of species' range sizes and midpoints" (Colwell & Lees, 2000).

Some mathematical models were created to test the fit of real data to this hypothesis, which initially focused only on latitudinal gradients (Willig & Lyons, 1998; Colwell & Lees, 2000; Koleff & Gaston, 2001). However, since these models ignore the fact that ranges are bi-dimensionally spread over a space, new models were created taking into account not only latitudinal dimension, but also the longitudinal dimension (Bokma & Mönkkönen, 2000). To date, Bokma *et al.* (2001), Jetz & Rahbek (2001), Diniz-Filho *et al.* (2002), and Hawkins & Diniz-Filho (2002) have carried out unsuccessful attempts to prove empirically the validity of the mid-domain

effect. In all cases, the coefficients of determination were very low, revealing a weak relationship between the predicted and observed richness. The first attempt, in analyzing the New World mammals an  $r^2$  was found of 8.5% (Bokma *et al.*, 2001); in the second, with Afrotropical birds, the  $r^2$  found was about 26% (Jetz & Rahbek, 2001); the third, with South American birds of prey, showed an  $r^2$  of less than 5% (Diniz-Filho *et al.*, 2002); and the last found an  $r^2$  of less than 24% with Nearctic bird richness (Hawkins & Diniz-Filho, 2002).

Alternatively, environment is usually a much better explanation for gradients in species richness. In general, there are many environmental factors driving richness patterns, such as climate (e.g. precipitation and temperature; Schall & Pianka, 1977, 1978), energy (e.g. sunlight incidence; Turner *et al.*, 1987, 1988), topography (Rahbek & Graves, 2001; Blackburn & Ruggiero, 2001), water availability (Currie, 1991), and area (Ruggiero, 1999; for an opposite position, see Hawkins & Porter, 2001). Probably the most successful environmental explanation for biotic richness is the "energy hypothesis" which, in summary, predicts that energy is converted by the physiological metabolism of plants to energy available to the food web, perhaps causing the observed richness, abundance, and biodiversity patterns at wide scales (habitat heterogeneity and biomass types) (Wright, 1983; Turner *et al.*, 1987, 1988; Brown & Lomolino, 1998; Rahbek & Graves, 2001; for habitat heterogeneity, see Rosenzweig, 1995; Ruggiero, 1999).

One of the best predictors of available biotic energy is net primary productivity (NPP), which is an important environmental measurement of the rate of production of biomass per unit of surface area, which is directly dependent on the rate that solar energy is converted to plant tissues, in addition to nutrient and water availability (Brown & Lomolino, 1998; Guégan, 1998).

The primary scope of the present work is to test the MDE, mathematically synthesized in bidimensional analytical null models, by correlating observed and expected spatial patterns of the species richness of Falconiformes on a worldwide scale and for the five "isolated" domains (Eurasia, Africa, Australia, Neotropics, and Nearctic). Subsequently we compare and discuss the explanatory power of MDE in relation to the effect of a general environmental factor: net primary productivity (NPP).

## MATERIALS AND METHODS

### *Empirical data*

We generated the observed richness patterns overlaying the geographic distribution maps of 307 of each species of Falconiformes (Del Hoyo *et al.*, 1994), over a world map covered with a regular standardized grid system. We used a map with Lambert equal area projection, with a total of 1430 grid points, distant approximately 350 km from each other, based on the grid of the WORLDMAP computer program (Williams, 2000). In one single point, the species richness (i.e., diversity) is simply the sum of the number of species occurrences at that point. Fifty-three species, present only on islands (such as Madagascar and the Oceanic islands) were excluded from the analysis since those islands were not used to define the domain.

The MDE works better for endemic species only, because their ranges are entirely confined and constrained by the same shared hard boundaries (Colwell & Hurt, 1994; Jetz & Rahbek, 2001; but see Diniz-Filho *et al.*, 2002). Therefore, we arbitrarily divided the global map into five macro-regions or domains (Africa, Eurasia, Australia, Neotropic, and Nearctic). The species with breeding range restricted to within only one of these domains/landmass were considered as endemic. Analyses were therefore based on overall species as well as endemic species only.

### *Null models*

Willig & Lyons (1998) proposed a computationally simple null model to isolate and test the influence of the continental shapes over spatial patterns of species richness. In this model extended to bi-dimensional space (Bokma & Mönkkönen, 2000), the final species richness prediction at a point (P) is given by  $4pqstS$ , where p, q, s, and t are the relative distances from each point to the northern, southern, eastern, and western continental boundaries, respectively, and S is the number of species in the overall species pool to be assumed in this case, relative to each domain, in such a way that S is the total number of species taken into account (whole pool and endemics only). The prediction of the model is directly dependent on continent shape, and the maximum number of species (a quarter of the total pool), as MDE assumes, is found at the center of each land area. Henceforward, this model, created

by Willig & Lyons (1998), will be called "WL2D null model".

As noted by Hawkins & Diniz-Filho (2002), due to the relative distances used by the previous model, high species richness could be predicted in the center of small peninsular areas, small islands, and narrows. Therefore, they proposed a second version of the model, which takes into account the maximum distance in each direction, rather than the relative distance of the originally proposed. From this new point of view, the expected richness in a point is given by the northern, southern, eastern, and western distances from this point to the nearest continent all boundary, divided by the maximum distance of the considered area of each direction, giving the values p, q, s, t, of the standard formulae. We used the maximum distance of each domain to calculate the values of the variables. According to Hawkins & Diniz-Filho (2002), this model, here labeled as the AC-WL2D model (area correct version of Willig & Lyons' (1998) original null model).

Coefficients of determination ( $r^2$ ) of linear regressions were used to evaluate the relationship between observed richness (all species and endemics only) and the prediction obtained by the null models. Regressions were performed globally, using all points of the grid system, and also for each domain, which identifies where and which MDE's null model yields the best prediction.

### *Spatial analysis*

As is well known, geographic data (i.e., species richness) measured in a grid system is usually strongly autocorrelated (Bini *et al.*, 2000; Rahbek & Graves, 2001; Diniz-Filho *et al.*, 2002), in such a way that significance levels of regression coefficients are biased. In this paper, we initially used spatial correlograms, defined by Moran's I coefficients at distinct distance classes, to describe and examine spatial autocorrelation in the patterns of species richness in each domain. Moran's I coefficient is given by the following formula:

$$I = \left( \frac{n}{K} \right) \left[ \frac{\sum_i \sum_j (y_i - \bar{y})(y_j - \bar{y}) w_{ij}}{\sum_i (y_i - \bar{y})^2} \right]$$

where  $n$  is the number of points in the grid,  $y_i$  and  $y_j$  are the values of the variable (i.e., species richness) in the points  $i$  and  $j$ ,  $\bar{y}$  is the average of  $y$ ,  $w_{ij}$  is an element of the matrix  $W$ , which assumes a value of 1 if the pair  $i, j$  of points is within the geographic distance class interval.  $K$  is given by the count of these connections among points in  $W$  for each class interval. The value expected under the null hypothesis of no autocorrelation is given as  $-1/(n-1)$  (see Legendre & Legendre, 1998, for further details).

Also, we used the correlograms to reduce the number of degrees of freedom to test regression coefficients, as suggested by Dutilleul (1993). The basic idea is that, under strongly positive autocorrelation at short distances (as expected for richness data), the number of degrees of freedom is overestimated, making the statistical tests too liberal, therefore, spatial autocorrelation is used to provide a conservative number of degrees of freedom for statistical testing. For the worldwide analyses, the number of degrees of freedom was set as the sum of reduced degrees of freedom for each domain, since there is no sense in performing autocorrelation analyses among different landmasses. This approach used the program MODTTEST of the R-Package, written by Legendre (2000) and freely available at

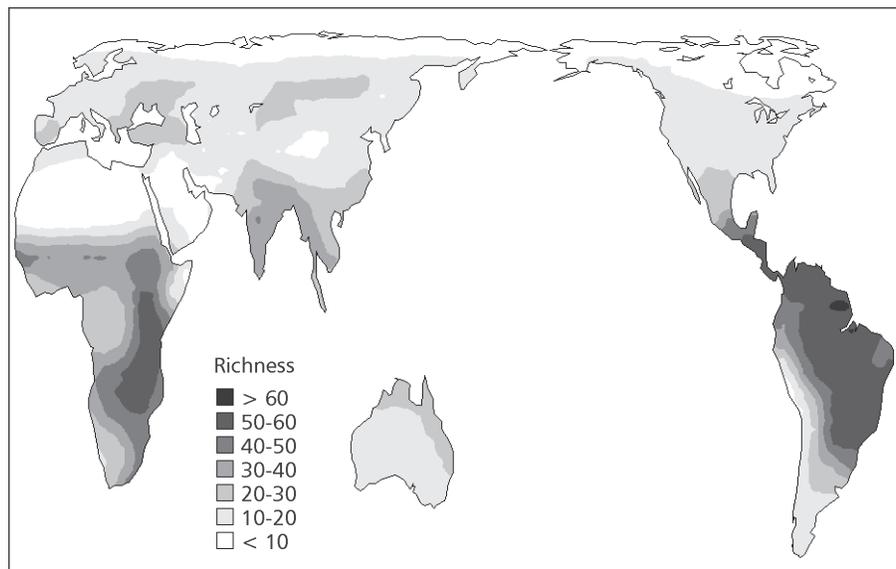
[http://www.fas.umontreal.ca/biol/casgrain/en/labo/mod\\_t\\_test.html](http://www.fas.umontreal.ca/biol/casgrain/en/labo/mod_t_test.html).

### **Environmental data**

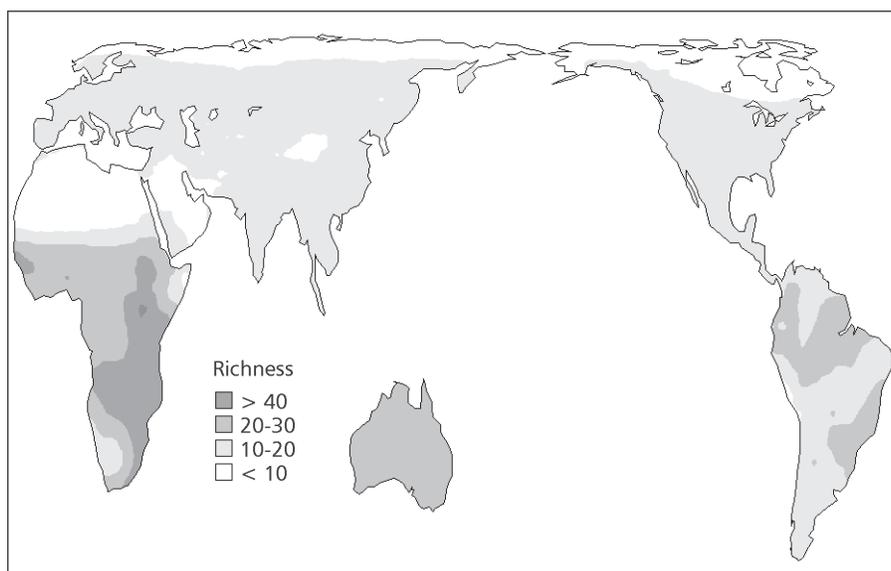
For purposes of comparison and in order to discuss how well the MDE explains the observed species richness data set, we also included in the analyses one environmental variable, net primary productivity (NPP) per area, defined by four classes (< 100, 100-400, 400-800, > 800) of grams of carbon per  $m^{-2}yr^{-1}$ , taken from Brown & Lomolino (1998). Although a crude measure, NPP can be useful in comparing the relative explanatory power of these two alternative hypotheses (NPP as a surrogate for energy versus MDE) explaining richness.

## **RESULTS**

The species richness of Falconiformes around the world does not follow a simple latitudinal gradient in two dimensions, with complex variations within each continent, both for all species (Fig. 1) and species endemic to each domain (Fig. 2). In general, the higher diversities are at lower latitudes near the Equator; at higher latitudes, species richness tends to be lower.



**Fig. 1** — World map illustrating spatial patterns of diversity of all Falconiformes.



**Fig. 2** — World map illustrating spatial patterns of diversity of endemic Falconiformes for each considered domain.

High diversities of all species of Falconiformes are in the northeastern Neotropics and in central-eastern sub-Saharan Africa, while the lower ones are in the higher latitudes of the northern hemisphere, and in Saharan Africa (Fig. 1). A high richness of endemic Falconiformes is also found in central-eastern sub-Saharan Africa (Fig. 2). Spatial patterns of species richness for all species and endemics are only slightly similar around the world ( $r^2 = 0.5140$ ), with highest similarities in Africa and Australia ( $r^2 = 0.9254$ ) and lowest in the Neotropics ( $r^2 = 0.3136$ ).

Analyzing the predictions of the different null models used (Figs. 3 and 4), we can easily note their underlying differences. The WL2D always predicts high richness in the middle of domains, regardless of their range, and the estimated values decrease in a regular gradient toward the borders (Fig. 3). On the other hand, in the AC-WL2D there are only isolated peaks in the center of the domains (Fig. 4).

The coefficients of determination of the linear regressions between observed and expected richness under the null models were always very low (Tables 1 and 2). However, the spatial correlograms usually indicated a significant autocorrelation for species richness in the different regions. There are usually strong positive autocorrelations at small spatial scales (first distance classes), followed by a monotonic decay of autocorrelation with distance, with a

reversal of the gradient in the last distance classes (Fig. 5).

When considering all species, coefficients of determination were usually low, and except for the whole world (WL2D:  $r^2 = 0.0729$ ;  $p = 0.0001$  and AC-WL2D:  $r^2 = 0.0605$ ;  $p = 0.0114$ ), none was significant at 5% level (Table 1). However, it is important to note that the degrees of freedom for the entire world were defined by summing the degrees of freedom for the different regions, since a world-scale autocorrelation analysis is meaningless. This while this number of degrees of freedom may still be overestimated, the most important fact is the very low  $r^2$  for both models (less than 10%)

Using only endemic species, the coefficients are slight larger, and only coefficients for the whole world (WL2D:  $r^2 = 0.1089$ ;  $p = 0.0001$  and AC-WL2D:  $r^2 = 0.1030$ ;  $p = 0.0027$ ), Eurasia (WL2D:  $r^2 = 0.1127$ ;  $p = 0.0161$ ), and Nearctic (WL2D:  $r^2 = 0.1050$ ;  $p = 0.0307$ ) were significant at the 5% level (Table 2).

The NPP is usually higher at lower latitudes, in a conspicuous latitudinal gradient, with the maximums close to the Equator, in tropical climates (see Brown & Lomolino, 1998). The highest production of biomass per surface area is in the Amazon, western and central sub-Saharan Africa, and southwestern India, while the lowest values is in the

deserts, northern Africa, the center of Asia and Australia, and also in cold zones, such as northern North America and northern Asia. The NPP was a much better predictor of richness of Falconiformes around the world ( $r^2 = 0.5027$ ;  $p = 0.0001$  for all species and  $r^2 = 0.3352$ ;  $p = 0.0001$  for endemics only), with most coefficients being significant at the 5% level. The higher  $r^2$  were obtained in Australia, when analyzing all species ( $r^2 = 0.5640$ ;  $p = 0.0167$ ),

and also with endemics only ( $r^2 = 0.5595$ ;  $p = 0.0160$ ). The weakest and non-significant coefficients were for endemic species in the Neotropics ( $r^2 = 0.1239$ ;  $p = 0.1310$ ) and in Eurasia ( $r^2 = 0.1529$ ;  $p = 0.0726$ ) (Table 3). Since NPP is independent of the two MDE measures, partial correlations between richness and WL2D and WL2D-AC (keeping NPP constant) remain qualitatively unchanged.

TABLE 1

Coefficients of determination ( $r^2$ ) of species richness regressed against predicted diversity by each null model, for all species of Falconiformes worldwide and for each domain separately. The number of points in the grid is “ $n$  pts”, while the number of species in each domain is “ $n$  spp”. The degrees of freedom ( $D.F.$ ) were given by taking into account the spatial autocorrelation in data, as suggested by Dutilleul (1993), giving a more appropriate estimate of Type I error of regression coefficient ( $p$ ).

Domain	n spp	n pts	WL2D null model			AC-WL2D null model		
			$r^2$	D. F.	p	$r^2$	D. F.	p
Worldwide	254	1430	0.0729	211.7	0.0001	0.0605	103.1	0.0114
Eurasia	82	576	0.0097	103.1	0.3160	0.0017	45.9	0.7775
Africa	91	340	0.0363	23.0	0.3607	0.0150	16.1	0.6260
Australia	25	88	0.1887	15.3	0.0785	0.1644	12.5	0.1420
Neotropic	91	227	0.0924	24.0	0.1314	0.0560	15.2	0.3573
Nearctic	39	199	0.0977	46.3	0.0510	0.1502	13.4	0.1466

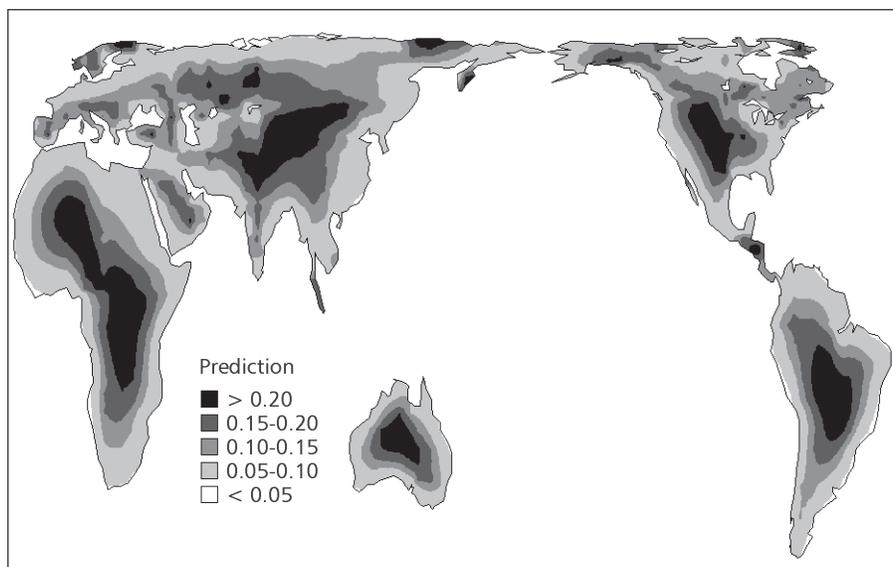


Fig. 3 — World map illustrating the prediction of diversity by the WL2D null model.

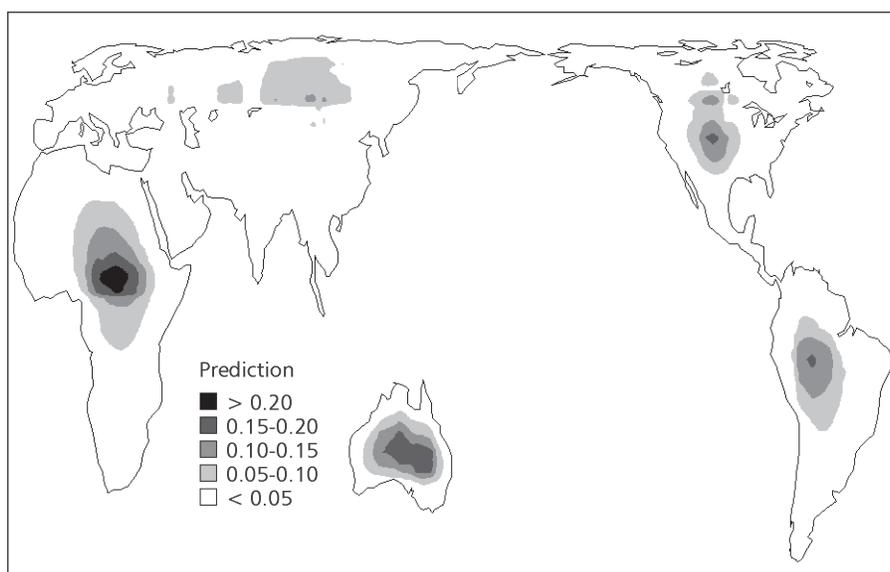


Fig. 4 — World map illustrating the prediction of diversity by the AC-WL2D null model.

TABLE 2

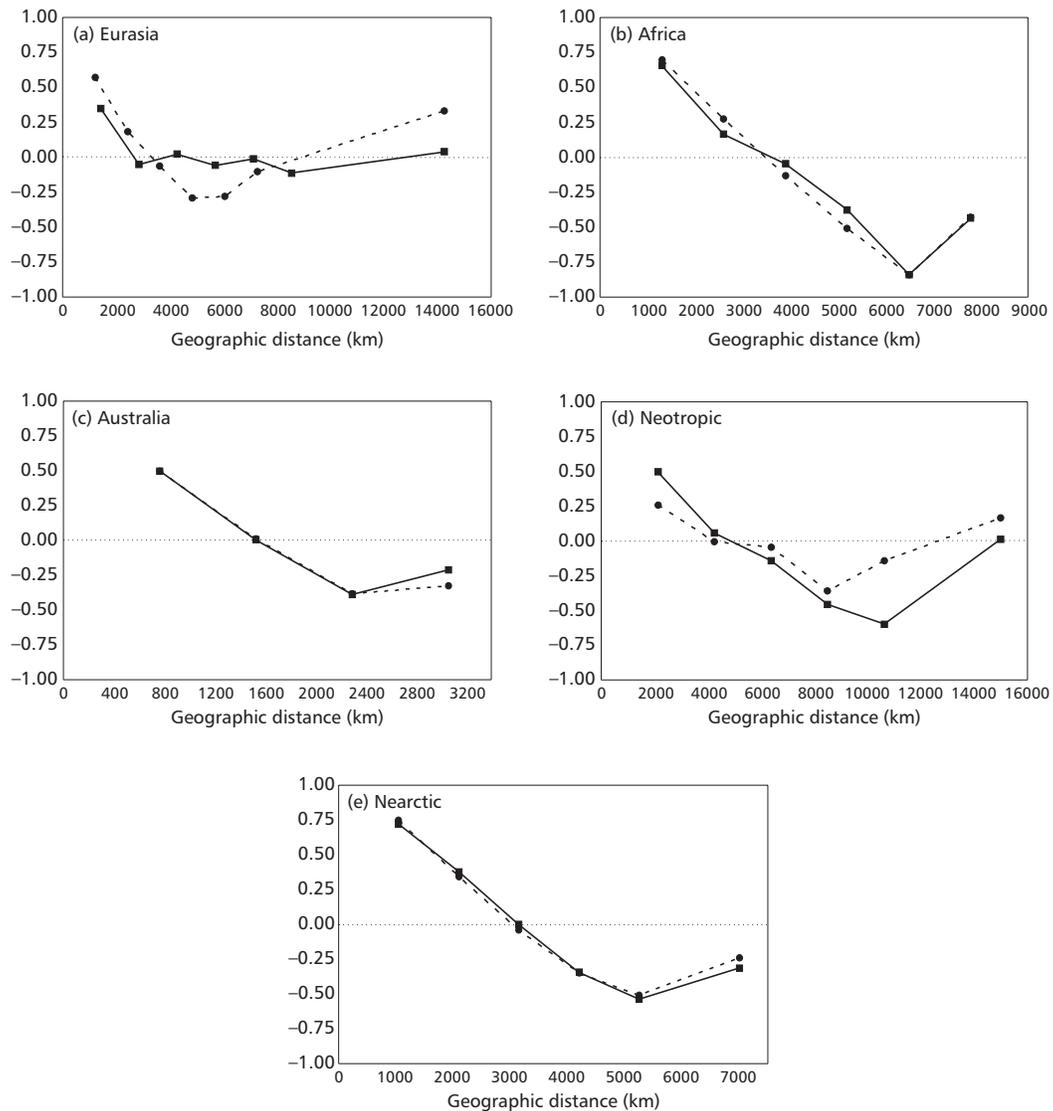
Coefficients of determination ( $r^2$ ) of species richness regressed against predicted diversity by each null model, for worldwide endemic species of Falconiformes and for each domain separately. The number of points in the grid is “ $n$  pts”, while the number of species in each domain is “ $n$  spp”. The degrees of freedom ( $D.F.$ ) were given by taking into account the spatial autocorrelation in the data, as suggested by Dutilleul (1993), giving a more appropriate estimate of Type I error of regression coefficient ( $p$ ).

Domain	n spp	n pts	WL2D null model			AC-WL2D null model		
			$r^2$	D. F.	p	$r^2$	D. F.	p
Worldwide	189	1430	0.1089	169.6	0.0001	0.1030	82.6	0.0027
Eurasia	41	576	0.1127	48.8	0.0161	0.0559	16.8	0.3311
Africa	56	340	0.0541	22.7	0.2707	0.0123	14.8	0.6731
Australia	19	88	0.1174	16.6	0.1556	0.1077	13.5	0.2215
Neotropic	65	227	0.0298	39.0	0.2799	0.0712	24.8	0.2163
Nearctic	8	199	0.1050	42.5	0.0307	0.2150	12.7	0.0849

TABLE 3

Coefficients of determination ( $r^2$ ), between the net primary productivity (NPP) against diversities of Falconiformes. The number of points in the grid is “ $n$  pts”, while “ $n$  spp” is the number of species.

Domain	n pts	All species				Endemic species			
		n spp	$r^2$	D. F.	p	n spp	$r^2$	D. F.	p
Worldwide	1430	254	0.5027	76.8	0.0001	189	0.3352	64.8	0.0001
Eurasia	576	82	0.4276	39.3	0.0001	41	0.1529	19.8	0.0726
Africa	340	91	0.4419	8.3	0.0315	56	0.5446	6.9	0.0238
Australia	88	25	0.5640	7.3	0.0167	19	0.5595	7.5	0.0160
Neotropic	227	91	0.5041	9.4	0.0122	65	0.1239	17.7	0.1310
Nearctic	199	39	0.4489	12.5	0.0073	8	0.3528	12.9	0.0199



**Fig. 5** — Correlograms of species diversity of Falconiformes for (a) Eurasia, (b) Africa, (c) Australia, (d) Neotropic, and (e) Nearctic. The continuous line with squares is the Moran's I estimated for the whole pool of species, while the dashed line with dots is for the endemic species only.

## DISCUSSION

The species richness of Falconiformes is strongly spatially patterned over the world, although these patterns cannot be expressed as simple bi-dimensional gradients within domains. Since the correspondence between observed and expected richness under bi-dimensional null models is very weak, richness patterns cannot be interpreted only as a function of continental edges, as predicted by

the mid-domain effect. Therefore, richness is not simply caused by a random overlap of constrained geographical ranges, and, thus, other environmental factors should be invoked to explain it. This result is congruent with all other bi-dimensional analyses of the mid-domain effect (Bokma *et al.*, 2001; Jetz & Rahbek, 2001; Diniz-Filho *et al.*, 2002; Hawkins & Diniz-Filho, 2002).

A null model, akin to these used here, is a statistical way to generate abstractive and imaginative

distribution patterns, based on chance alone, which allows testing isolated biological mechanisms (Gotteli, 2001). Thus, to test the MDE using a null model is to ask whether a randomized pattern can reproduce one based on real data, and excluding from the test any other important features (i.e., environment and specific characteristics).

Probably the most improper assumption of the MDE is about the underlying factors entailed by the definition of range per se. As pointed out by Brown *et al.* (1996), range is a "complex of spatial and temporal patterns in which individual organisms are dispersed over the earth" and includes various features, such as size, shape, boundaries, and internal structure. Each of these features is influenced by many variables (such as ecologically limiting factors, environmental sustainability), which restrict the variation in distribution over a given space and, consequently, the richness of species.

Actually, each species has a unique ecological niche resulting from a complex of interactions between environmental variables that determine the distribution of the specie over the domain. Only within a specific set of parameter values, survival and reproduction can occur. The niche variables, independently or not of any other set of variables, determine a local range boundary, and limit local or regional distribution at different locations around the periphery (Brown *et al.*, 1996). Hence, domains cannot be understood as homogeneous surfaces, without any internal boundaries or possible interactive features allowing species to easily spread over a space independently, and randomly across directions. There are actually many boundaries (so-called soft boundaries), e.g., environmental and ecological ones (Hawkins & Diniz-Filho, 2002).

In sum, the complex interactions between abiotic and biotic features cannot be isolated from geographic ranges, as MDE does, since geographic occurrence is not the primary cause of observed richness, but rather the result of various interactions between species and environment. Therefore, MDE, due to all of its spanned assumptions, does not reasonably fit the final richness in observed data. Even a crude measure of an environmental factor (i.e., NPP), as used here, explains much more of variance of richness across bi-dimensional space than does the mid-domain null model. Also, MDE does not explain even the residual variation in richness after taking into account the environment. Of course, a future step is to test

the response of the richness to NPP using better-quality data, at finer spatial scales.

Although the hypothesis that boundaries could constrain the spatial distribution of the ranges over a domain has recently reached generalized acceptance, it is based on mistaken assumptions about the definition of ranges and domains (Hawkins & Diniz-Filho, 2002).

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