



# Climate and regional beta-diversity gradients in spiders: dispersal capacity has nothing to say?

ALBERTO JIMÉNEZ-VALVERDE,<sup>1</sup> ANDRÉS BASELGA,<sup>2</sup> ANTONIO MELIC<sup>3</sup> and NAYRA TXASKO<sup>4</sup> <sup>1</sup>Natural History Museum and Biodiversity Research Center, The University of Kansas, Lawrence, KS, USA, <sup>2</sup>Departamento de Zoología, Facultad de Biología, Universidad de Santiago de Compostela, Santiago de Compostela, Spain, <sup>3</sup>Sociedad Entomológica Aragonesa, Zaragoza, Spain and <sup>4</sup>Departamento de Biología Animal-Artrópodos, Facultad de Biología, Universidad de Barcelona, Barcelona, Spain

**Abstract.** 1. The importance of dispersal capacity in structuring beta-diversity gradients has been pointed out in a number of recent studies, making geographical distance (GD) an important predictor of the composition of assemblages apart from environment. In this study, we analyse the relative importance of climate, habitat complexity and GD in four spider families with different dispersal tendencies in the centre of the Iberian Peninsula.

2. Regional beta-diversity was calculated for the four families and values were bootstrapped to test for significant difference between groups. Mantel tests assessed the explanatory capacity of four potential predictors – climatic similarity, similarity of vegetation complexity, GD and cost distance (CD) considering topography – on faunistic similarity. Simple regressions were used to compare decay rates, and bootstrapping tested for significant differences in coefficients.

3. Regional beta-diversity values were higher in less vagile families. Climatic distance was strongly correlated with faunistic dissimilarity in the four families, whereas GD had no explanatory power. Except in one family, CD was correlated with faunistic dissimilarity but its independent association was negligible when controlling for climate.

4. Both the pattern of regional beta-diversity among families and the pattern of variation in species composition explained by climate are consistent with the hypothesis that dispersion capacity influences the composition of the assemblages. However, climate distance was the main factor determining species sorting in space while GD had a weak effect. Differences in the degree of specialisation or nonlinear relationships between species composition and space may obscure the signal of GD at the scale of work.

**Key words.** Araneae, beta-diversity, dispersal, environmental gradient, geographical distance.

## Introduction

In contrast to species richness, little work has been devoted to the understanding of patterns of beta-diversity, i.e. variation in species composition across space (Harrison *et al.*, 1992; McKnight *et al.*, 2007). Gradients in species composition were firstly tied to environmental gradients (Whittaker, 1960), based on the assumption that the more similar the environmental conditions, the more similar the assemblages will be. However, several studies have shown that current environmental patterns are not enough to explain compositional patterns (e.g. Condit *et al.*,

2002; Duivenvoorden *et al.*, 2002; Tuomisto *et al.*, 2003; Cottenie, 2005; Qian *et al.*, 2005; Baselga, 2008).

Spatial autocorrelation is an inevitability of the natural world making ecological variables more similar the nearer they are measured along spatial gradients (spatial autocorrelation; Legendre, 1993); species composition is not an exception. The niche difference model (*sensu* Nekola & White, 1999) explains how species with different physiological tolerances are sorted along environmental gradients, replacing each other and causing species similarity to decrease as environmental dissimilarity increases with distance. Thus, taxa with broad environmental tolerances are expected to show lower rates of similarity decay (Nekola & White, 1999). However, several dynamic biotic and historical processes also contribute to the spatial configuration of species assemblages, such as spatial aggregation, speciation, extinction and stochastic events (Condit *et al.*, 2002; Genner *et al.*, 2004;

Correspondence: Alberto Jiménez-Valverde, Natural History Museum and Biodiversity Research Center, The University of Kansas, Lawrence, KS 66045, USA. E-mail: ajvalv@ku.edu

Veech, 2005; Graham *et al.*, 2006; Steinitz *et al.*, 2006; Baselga & Jiménez-Valverde, 2007; Baselga, 2008). These factors will increase the decay of species similarity with geographical distance (GD), but their effects will depend on spatial configuration of the suitable habitats and on the dispersal capacity of the species. Habitat patchiness promotes assemblages differentiation through extinction-colonisation, with its effect modulated by the degree of suitability of the matrix and the presence of corridors (Nekola & White, 1999; Hortal *et al.*, 2005; Vanschoenwinkel *et al.*, 2007). Nevertheless, in the long term, it is the dispersal capacity of taxa what determines the ability to reach environmentally suitable places. Thus, more vagile taxa should show lower values of beta-diversity and lower rates of similarity decay (Nekola & White, 1999; Seidler & Plotkin, 2006; Hulcr *et al.*, 2008). In fact, the neutral theory (Hubbell, 2001) predicts that communities of demographically similar species and with no adaptations to environmental niches can form spatial distribution patterns similar to those found in nature, so long as the species have a limited dispersal distance. The challenge is to be able to differentiate neutral from environmental sorting processes and to isolate the role of dispersion (and thus history) in structuring species assemblages (Gilbert & Lechowicz, 2004; Cottenie, 2005).

In this paper, we analyse beta-diversity patterns in spiders at the regional scale, comparing four families with different ecological strategies, and assessing the relative roles of environment and GD as determinants of the observed patterns. Spiders are generalist predators abundant in most terrestrial ecosystems (Wise, 1993). This makes spiders ideal subjects to avoid the influence of the underlying beta-diversity patterns of other taxa (e.g. hosts; Novotny & Weiblen, 2005; Beck & Khen, 2007) in determining the geographical distribution of spider assemblages. In general, spiders have great dispersal capacities due to the passive air dispersal using silk threads (ballooning). Due to this, they can be found in the air at high altitudes (Freeman, 1946) and are among the first colonisers of islands (Edwards & Thornton, 2001). However, spiders have a variety of body sizes and ecological strategies across families and the propensity to balloon differs among them (Platnick, 1976; Dean & Sterling, 1985; Bishop, 1990; Bishop & Riechert, 1990; Suter, 1999; Richardson *et al.*, 2006). Thus, assuming that ballooning is the primary method of long-distance dispersal in spiders (Bishop & Riechert, 1990; Thomas *et al.*, 1990, 2003), different families should have different patterns of beta-diversity, and the relative roles of environment and space will vary as well. The latter is based in the assumption that distributions of the more vagile species will be in a higher degree of equilibrium with environmental gradients because they are able to reach all the habitats with favourable environmental conditions. On the contrary, species with poor dispersal abilities are not able to colonise all the habitats in which they could survive, and thus their distributions are not in equilibrium with environmental gradients but constrained by spatial limitations (Araújo & Pearson, 2005; Steinitz *et al.*, 2006). Therefore, our main goals are to test the following three predictions:

- 1 The more vagile the spider family, the lower the regional beta-diversity should be.
- 2 Similarity in species composition should decrease with environmental and GD.

- 3 The more vagile the spider family, the higher the importance of environmental distance and/or the less the importance of GD should be in explaining beta-diversity.

## Material and methods

### *Spider families selected*

Four spider families were selected for this study: Araneidae, Thomisidae, Salticidae and Gnaphosidae. Araneidae (orb-web spiders) build orb webs to capture prey, whereas thomisids (crab spiders) ambush prey from flowers or leaves. Some thomisid genera, like *Xysticus* and *Ozyptila*, are largely edaphic, capturing prey among leaf litter and herbaceous vegetation. Salticids (jumping spiders) are very active diurnal stalking spiders, creeping and finally jumping on their prey; they occupy nearly all possible habitat strata. On the contrary, gnaphosids are predominately ground-dwelling nocturnal wandering spiders (Wise, 1993; Uetz *et al.*, 1999). As thomisids, neither salticids nor gnaphosids use silk to capture prey.

We assume that ballooning is the main long-distance dispersal method employed by spiders. A higher ballooning propensity is expected under (i) a greater silk production and (ii) a stronger dependence on tall vegetation (Platnick, 1976; Bonte *et al.*, 2003). Thus, based on published data on the relative abundance in aerial samples (Dean & Sterling, 1985; Greenstone *et al.*, 1987; Bishop, 1990; Pearce *et al.*, 2005) and to their known ecology (Platnick, 1976; Richman & Jackson, 1992; Wise, 1993; Foelix, 1996; Richardson *et al.*, 2006), we assume the following sorting of the four families along a dispersal capacity gradient (see Table 1): Araneidae (high vagility) – Thomisidae and Salticidae (medium vagility) – Gnaphosidae (low vagility). Despite the paucity of quantitative information for ballooning activity of different families of spiders, the simplicity of the suggested three-class gradient makes it more robust and reflects what can be supposed based on the available data, i.e. that Araneidae and Gnaphosidae are at opposite extremes of the dispersal gradient.

### *Study area*

The autonomous Spanish region of Madrid, with approximately 8028 km<sup>2</sup>, is located in Central Iberia (Fig. 1). Its heterogeneous topography, with altitude ranging from 2430 m.a.s.l. in the Central System mountain range to 434 m.a.s.l. in the Alberche Valley, generates a clear northwest–southeast environmental gradient comprising Mesomediterranean, Supramediterranean, Oromediterranean and Crioromediterranean bioclimate divisions (Rivas-Martínez, 1987).

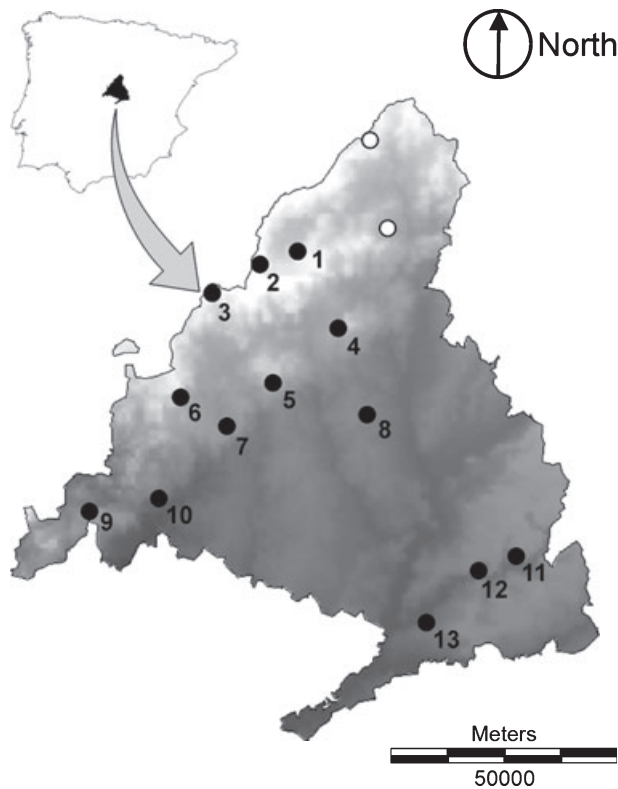
### *Sampling design*

Five environmental layers were used to characterise each of the 1 km<sup>2</sup> cells of the Universal Transverse Mercator (UTM)

**Table 1.** Evaluation of the dispersal capacity of the four families considering three criteria: 1, amount of silk production [araneids use silk for building the webs besides for other basic functions shared with the other three families (Foelix, 1996) and, so they score *high* while the other groups scored *medium* according to this criteria]; 2, Spatial strata occupied [araneids use the vegetation to attach their webs, while gnaphosids are ground-dwelling spiders (Foelix, 1996), so they represent the two extremes of the dispersal gradient according to this criteria. Thomisids and salticids have species that occupy both strata, so they are considered to show an intermediate dispersal capacity with respect to the other two families]; 3, abundance in aerial samples [based on Dean and Sterling (1985), Greenstone *et al.* (1987) and Pearce *et al.* (2005)].

Family	Criteria			Dispersal (ballooning) tendency
	Silk production	Strata	Abundance in aerial samples	
Araneidae	High	High	High	High
Thomisidae	Medium	Medium	Medium	Medium
Salticidae	Medium	Medium	Medium	Medium
Gnaphosidae	Medium	Low	Low	Low

grid covering the region: vegetation structure, precipitation, temperature, altitude and lithology. These are widely recognised factors affecting spider distribution (Rypstra, 1986; Balfour & Rypstra, 1998; Downie *et al.*, 2000; Borges & Brown, 2001; Bonte *et al.*, 2002; Chatzaki *et al.*, 2005). The Corine Land Cover map (European Environment Agency, 1996) was reclassi-



**Fig. 1.** Sampling locations selected using a k-means regionalisation procedure in the region of Madrid (Jiménez-Valverde & Lobo, 2004). White circles are localities not used in the analysis (see text). A Digital Elevation Model of the Madrid region is shown to illustrate the NW-SE environmental gradient of the region.

fied into three broad categories representing increasing structural complexity: grasslands, scrublands and forests. Mean annual temperature and total annual precipitation were courtesy of the Instituto Nacional de Meteorología (National Meteorological Institute). Mean altitude was obtained from a global digital elevation model (Clark Labs, 2000a). A lithologic map (ITGE, 1988) was digitised and reclassified into basic and acidic soils. Cells dominated by urban or agricultural land use, bare rock, bodies of water or sand were not included in the analysis.

These environmental variables were used to regionalise the territory of Madrid using k-means cluster analysis (Jiménez-Valverde & Lobo, 2004). Once the number of sampling locations that can be surveyed is fixed (according to the maximum sampling effort that can be invested), the method maximises the environmental variation recovered as a function of the sampling effort. However, if sub-regions are delimited using only environmental variables, locations environmentally similar but separated in space will be grouped together. These locations may have dissimilar species composition and richness due to unique historical events. Thus, central latitude and longitude of each 1 km<sup>2</sup> cell were included in the cluster analysis. All variables were standardised to 0 mean and 1 SD. The seven variables were used to divide the region into 15 clusters (the maximum number of locations that could be sampled based on the available resources). To select the final 15 sampling squares, two hierarchic criteria were chosen as follow: (i) distance to the cluster centroid (the smaller the distance, the better the spatial-environmental representation of the sub-region); (ii) ease of access (Fig. 1, note that two locations were discarded for subsequent analysis because of the loss of several samples during field work). See Jiménez-Valverde and Lobo (2004) for a detailed discussion of the method.

Each 1 km<sup>2</sup> sampling location was divided into 2500 subplots of 20 × 20 m; 20 of these subplots were chosen at random, and the following sampling methods were applied (by the same person, A. J.-V., to avoid possible differences due to the effect of the collector) in each one: (i) a one-person sweep of the herbaceous vegetation and shrub for 15 min. (ii) A one-person beating of bushes and small trees and branches for 15 min with a heavy stick; the specimens fell on a 1.25 × 1.25 m white sheet. In cases

where the use of the sheet was impossible or very difficult due to vegetation structure, a 41 × 29 cm plastic pail was employed. (iii) The running of four open pitfall traps for 48 h. The traps were 11.5 cm wide and 1 l in volume, each 10 m apart to avoid interference effects and to maximise their efficacy. Additionally, in places where, due to special vegetation patchiness, spiders tend to concentrate in certain areas, a one-person visual search from knee level to as high as could be reached for 15 min was also added to the sampling protocol. Sampling was carried out in spring (April–June, 2002–2004), and southern localities were surveyed first each year to account for phenological differences. This strategy yields reasonable estimates of the entire spring fauna, enabling sites to be compared, since spring inventories are a good representation both of the annual species richness and faunistic composition (Jiménez-Valverde & Lobo, 2006; Cardoso *et al.*, 2007). Juveniles that could be identified with certainty were included in the analysis (Jiménez-Valverde & Lobo, 2006).

#### *Vegetation structural variables*

Vegetation structure was visually assessed in each subplot using four habitat features (shrub canopy cover, sub-shrub canopy cover, ground herb cover and amount of leaf litter), scored between zero and three using ordinal scales (Table 2, see Newsome & Catling, 1979; Coops & Catling, 1997, 2000). Then, a mean score was calculated for each habitat feature in each 1 km<sup>2</sup> sampling location. These variables are known to highly influence spider species richness and composition of assemblages (Uetz, 1991; Jiménez-Valverde & Lobo, 2007).

#### *Data analysis*

The nonparametric estimator of species richness Jackknife1 (Jack1) was calculated – as recommended by Hortal *et al.* (2006) and Jiménez-Valverde and Lobo (2006) – for each inventory to assess their reliability (completeness = [observed species richness/estimated species richness] × 100). EstimateS (version 8.0.0; Colwell, 2006) was used for computations.

Regional beta-diversity for each family were estimated using the multiple-site similarity measure based on the Simpson similarity index  $M_{Sim}$  (Baselga *et al.*, 2007):

$$M_{Sim} = \frac{\sum_i S_i - S_T}{\left[ \sum_{i < j} \min(b_{ij}, b_{ji}) \right] + \left[ \sum_i S_i - S_T \right]}$$

where  $S_i$  is the total number of species in site  $i$ ,  $S_T$  is the total number of species in all sites considered together, and the term  $\left[ \sum_{i < j} \min(b_{ij}, b_{ji}) \right]$  is the sum of minimum values of species not shared between each pair of sites. This multiple-site measure avoids the loss of information for the number of species shared among three or more sites – that occurs when the average of pair-wise comparisons is computed – and accounts for spatial turnover only, avoiding the effect of nestedness patterns in the beta-diversity measure (Baselga *et al.*, 2007; Baselga, 2009). The dispersion of  $M_{Sim}$  values was estimated for each family by bootstrapping to detect significant differences between families. Thousand resamples were run, and the probability of obtaining by chance lower  $M_{Sim}$  values for the most vagile family in pair-wise comparisons was calculated empirically. Computations were run in R (R Development Core Team, 2005) using the boot package (version 1.2–30) and the R code provided in Baselga *et al.* (2007) for  $M_{Sim}$ .

In a second analysis, we tested whether the relative importance of environmental distance (compared with that of GD) as a determinant of the decay of similarity increases in the more vagile families. As our analyses are concerned with variation in beta-diversity (level three *sensu* Tuomisto & Ruokolainen, 2006), Mantel tests and regressions on distance matrices are appropriate methods for testing dependence between variables (see Tuomisto & Ruokolainen, 2006 for a thoughtful discussion). Eight distance matrices were built (four faunistic matrices – dependent variables – and four predictor matrices – independent variables):

- 1 Faunistic matrices. The Simpson dissimilarity index ( $\beta_{Sim}$ ) (Koleff *et al.*, 2003) between samples was used to calculate a faunistic distance matrix for each spider family (four faunistic matrices).  $\beta_{Sim}$  was selected because it measures differences in species composition (species turnover) independent of richness gradients (nestedness) (Koleff *et al.*, 2003; Baselga, 2007).
- 2 Predictor matrices. (i) Geographical distance: a spatial distance matrix was built using the GD between the centroids of the 1 km UTM cells surveyed. (ii) Cost

**Table 2.** Visual scoring of vegetation structure features in each subplot.

Structure	Score			
	0	1	2	3
Shrub canopy cover (% cover)	0	< 30	30–70	> 70
Sub-shrub canopy cover (% cover)	0	< 30	30–70	> 70
Ground flora (height in m)	(< 0.5)*	(> 0.5)*	(< 0.5)**	(> 0.5)**
Leaf litter (% cover)	0	< 30	30–70	> 70

\*Sparse ground flora: grasses covering < 50% of the subsampling plot. \*\*Dense ground flora: grasses covering > 50% of the subsampling plot (adapted from Coops & Catling, 1997).



**Table 3.** Sampling locations (numbers in brackets correspond with numbers in Fig. 1) with the number of observed species (Obs), the number of estimated species ( $\pm$ SD) using the Jackknife1 nonparametric estimator (Jack1), and percentage of completeness of the inventories (Obs/Jack1  $\times$  100).

Locality	Obs (Araneidae–Thomisidae–Salticidae–Gnaphosidae)	Jack1	% Completeness
Cerro Cardoso, Rascafría (1)	25 (3–7–7–8)	41 $\pm$ 3.32	61
Sillada de Garcisancho, Rascafría (2)	23 (7–6–3–7)	29 $\pm$ 2.40	79
Cercedilla (3)	23 (8–7–4–4)	31 $\pm$ 2.70	74
Dehesa de Navalvillar, Colmenar Viejo (4)	26 (8–5–5–8)	34 $\pm$ 2.76	76
Hoyo de Manzanares (5)	32 (7–8–8–9)	38 $\pm$ 2.42	84
La Herrería, El Escorial (6)	27 (7–10–7–3)	40 $\pm$ 3.43	67
Valdemorillo (7)	16 (4–5–2–5)	22 $\pm$ 2.34	73
Monte de Valdelatas, Madrid (8)	33 (7–9–6–11)	42 $\pm$ 2.93	79
Pelayos de la Presa (9)	11 (5–3–1–2)	17 $\pm$ 2.35	65
Chapinería (10)	22 (6–8–2–6)	28 $\pm$ 2.42	79
Tielmes (11)	18 (4–5–2–7)	24 $\pm$ 2.39	75
Perales de Tajuña (12)	22 (3–5–7–7)	30 $\pm$ 2.77	73
Chinchón (13)	29 (7–6–7–9)	40 $\pm$ 3.24	72

distance (CD): another spatial matrix was built but considering the distance over the terrain, i.e. the real distance that a cursorial organism would have to cover. The digital elevation model was used to build a slope map and this was included as the friction surface in a CD analysis in Idrisi32 (Clark Labs, 2000b). The resultant cost maps for each sampling location were used to calculate the CD matrix. These CDs are expected to have more importance in determining the species composition of less vagile families than GD, while no difference is expected in the case of more vagile families. (iii) Climate: six climatic variables were used to characterise each UTM cell sampled (annual precipitation, precipitation of the least rainy month, precipitation of the most rainy month, mean annual temperature, maximum and minimum annual temperature (Instituto Nacional de Meteorología)). They were standardised and the Euclidean distance (with equal weights for all the variables) between squares was used to compute the climate distance matrix. (iv) Habitat structure: each sampling square was characterised by the mean of each one of the four indices of vegetation structure measured in the field and the Euclidean distance was used to built a distance matrix reflecting differences in habitat complexity between 1 km squares.

Regression and partial regression tests between each faunistic matrix and the predictor matrices were run, and *P*-values calculated using Mantel tests, permuting 1000 times the response variables (Legendre & Legendre, 1998). Mantel tests were computed with the vegan package (Oksanen *et al.*, 2005) for R. Significance of differences between slopes (decay rates) was assessed by bootstrapping (1000 resamples) and was calculated empirically by comparing the estimated distributions in pair-wise comparisons.

## Results

Most of the inventories had a high degree of completeness, between 72% and 84% (Table 3), except three in which the

Jack1 estimator yielded values between 61% and 67%. The Multiple-site Simpson-based similarity index ( $M_{\text{Sim}}$ ) was higher for the most vagile spider family, Araneidae, followed by Thomisidae and Gnaphosidae; Salticidae had the lowest  $M_{\text{Sim}}$  (Table 4). Significant differences were found in the pair-wise comparisons of Araneidae with Salticidae and Gnaphosidae ( $P = 0.004$  and  $0.045$ , respectively), and Thomisidae with Salticidae ( $P = 0.030$ ).

Mantel tests indicated that, although climate and GD were correlated (Pearson's  $r = 0.326$ ,  $P = 0.023$ ), similarity in species composition in the four families decays significantly with climate differences but not with GD, for which no significant relationships were found (Table 5). The variation explained by climate was higher in the more vagile family (Araneidae) and lower in Salticidae (Table 5, Fig. 2), following the same gradient as  $M_{\text{Sim}}$ . Climate and habitat structure were also weakly correlated ( $r = 0.194$ ,  $P = 0.046$ ), but composition similarity decays significantly with the differences in vegetation complexity only in Araneidae and Thomisidae. Partial mantel tests showed that there is no independent association with habitat structure, so the variation explained by this variable cannot be disentangled from the effect of climate. Contrary to GD, CD shows a higher correlation with climatic distance ( $r = 0.814$ ,  $P < 0.001$ ) and similarity of species composition in the four families decays significantly with CD (Table 5). However, CD had no independent association and most of the variation was still explained by

**Table 4.** Multiple-site Simpson-based similarity ( $M_{\text{Sim}}$ ) scores for the four spider families, bias and standard error of the bootstrapped values. Superscripts show pairs with significantly different  $M_{\text{Sim}}$  values ( $P < 0.05$ ; families with the same number show significant differences).

Family	Original $M_{\text{Sim}}$	Bias	SE
Araneidae <sup>1,2</sup>	0.298	0.032	0.044
Thomisidae <sup>3</sup>	0.244	0.029	0.032
Salticidae <sup>1,3</sup>	0.152	0.036	0.028
Gnaphosidae <sup>2</sup>	0.209	0.028	0.034

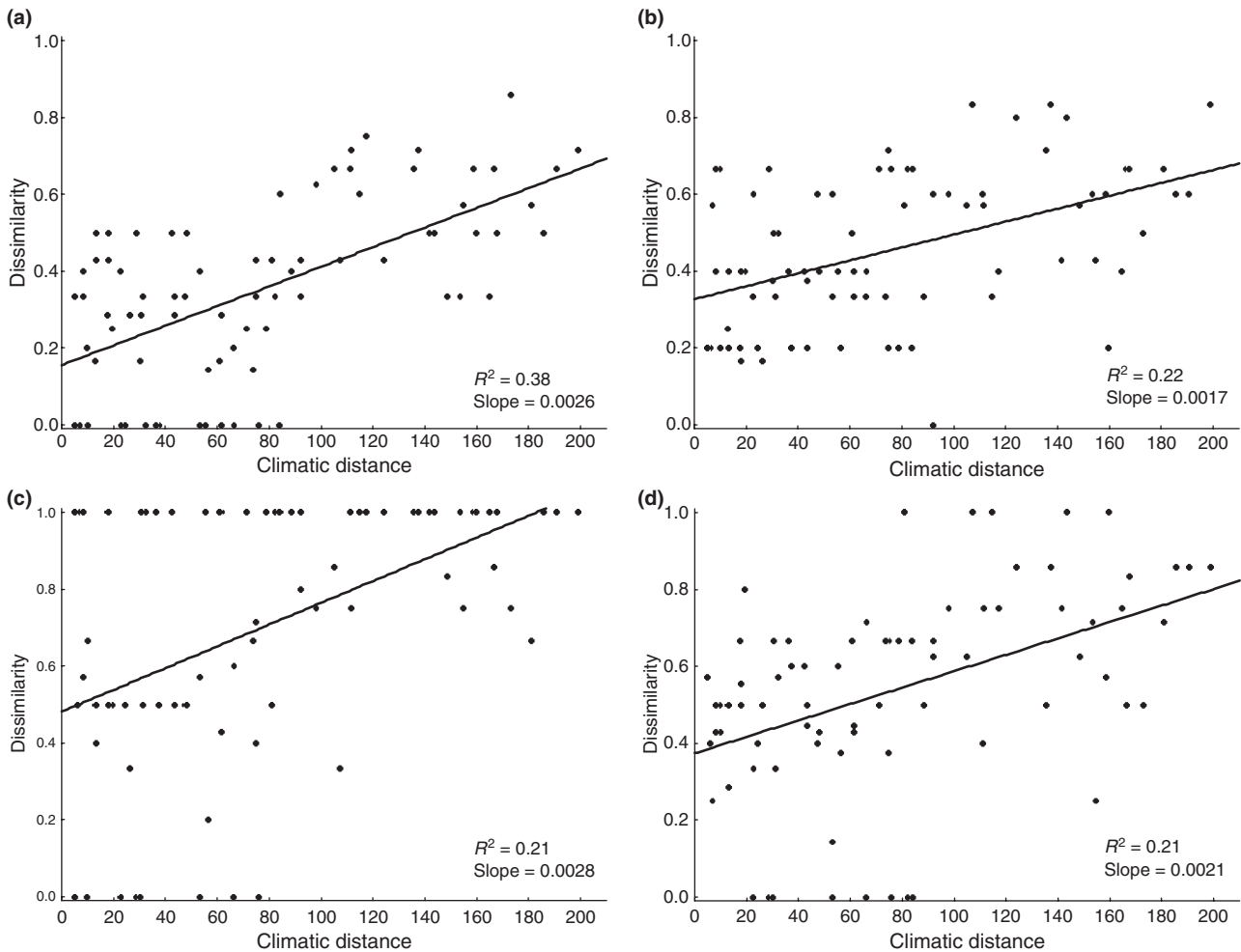
**Table 5.** Mantel tests between each faunistic matrix and the four predictor matrices. Partial mantel tests were used to isolate the pure effects of climate and cost distance.

Family	Pearson <i>r</i>					
	Climate	Vegetation structure	Geographical distance	Cost distance		
				Cost distance	Pure climate	Pure cost distance
Araneidae	0.614***	0.210*	0.173	0.480***	0.439**	-0.043
Thomisidae	0.519**	0.207*	0.112	0.584***	0.093	0.325**
Salticidae	0.476**	0.107	0.229	0.423**	0.250*	0.070
Gnaphosidae	0.505**	<0.001	-0.006	0.328*	0.434**	-0.166

*P*-values were calculated permuting 1000 times the response variables, \*\*\* < 0.001; \*\* < 0.01; \* < 0.05.

climate. Thomisidae was the exception showing the opposite pattern; climate lost all the explanatory capacity when controlling by CD (Table 5). Rates of similarity decay with climate

(slopes) were found only to be significantly lower in Thomisidae than in Salticidae ( $P = 0.037$ ) and Araneidae ( $P = 0.047$ ) (Fig. 2).



**Fig. 2.** Relationship between species dissimilarity and climatic distance for the four spider families (A, Araneidae; B, Thomisidae; C, Salticidae; D, Gnaphosidae). Significance differences between slopes were estimated via bootstrapping (1000 resamples; in the four cases bias < 0.001 and error < 0.020); slopes were found to be significantly lower in Thomisidae than in Salticidae ( $P = 0.037$ ) and Araneidae ( $P = 0.047$ ).

## Discussion

### *Regional beta-diversity and the effect of climate distance*

Regional beta-diversity varies among spider families. As expected, the greater the dispersion capacity, the lower the species turnover among localities in the region. This result is concordant with that of Qian (2009) for plants at a much larger geographical scale.

Climate similarity shows a moderately strong correlation with compositional similarity, explaining between 25% and 38% of the variability, while vegetation structure has less explanatory power and no independent effect. This contrasts with the weak ability of climate to predict species richness, at least in the families Araneidae and Thomisidae, a biodiversity attribute that was better predicted by vegetation structure (Jiménez-Valverde & Lobo, 2007). Integrating both results, we argue that climatic conditions select which spider species can live in each locality but not how many, and habitat complexity is the main factor controlling the number of species that each locality can harbour, probably because complex habitats increase the availability of niches, although ultimate causes are unknown (Jiménez-Valverde & Lobo, 2007). Difference in vegetation complexity was also a significant determinant of composition similarity of Araneidae and Thomisidae, as expected due to their ecology, which makes them to interact more directly with vegetation than the other two families. Nevertheless, its importance was much less than climate and, further, its effects could not be disentangled from those of climate. Although our index of vegetation structure includes amount of leaf litter, which is relevant to ground-dwelling taxa such as Gnaphosidae (Uetz, 1991), its influence on species composition of this family was also negligible. The importance of environmental distance in explaining beta-diversity follows the same tendency as regional beta-diversity, i.e. higher in the most vagile family (Araneidae). As with  $M_{Sim}$ , Salticidae had the least variation explained by climatic distance, suggesting that its dispersal capacity could have been overestimated. Nevertheless, no significant differences were found between Salticidae and Gnaphosidae with respect to regional beta-diversity or to the similarity decay with climate, so its position along the dispersal gradient is difficult to ascertain.

### *The effect of geographical distance*

The influence of GD on compositional similarity has been observed in a variety of organisms and over diverse scales in a number of locations over the world (e.g. Condit *et al.*, 2002; Genner *et al.*, 2004; Qian *et al.*, 2005; Baselga & Jiménez-Valverde, 2007; Baselga, 2008). Several studies have found that the effect of GD is stronger in those taxa with lower dispersal capacities (e.g. Iberian Coleoptera, Lobo & Martín-Piera, 1999; birds and snails in Israel, Steinitz *et al.*, 2006; plants in western Amazonia and North America, Tuomisto *et al.*, 2003 and Nekola & White, 1999), supporting the hypothesis that dispersal capacity is an essential factor determining beta-diversity patterns (Bell, 2001; Hubbell, 2001). However, other studies failed to find these patterns (Harrison *et al.*, 1992; Poulin, 2003). In our

study, the lack of significant correlations between the compositional and geographical distance matrices (GD) suggests that dispersal limitation is not important in structuring spider assemblages at the scale of study. This is supported by the fact that, even when using CDs accounting for the relieve, the independent effect of CD is negligible both in the most and less vagile families (Araneidae and Gnaphosidae, respectively) and the independent effect of climate still accounts for most of the variation. However, in Thomisidae, the independent effect of CD accounts for most of the variation and no independent effect of climate is detected. Many species in Thomisidae are edaphic and, contrary to Gnaphosidae, which are well adapted ground dwellers, their cursorial capacity is limited. Thus, the dispersal capacity for Thomisidae may have been overestimated in the proposed gradient. In this family, dispersal limitation may be relevant for the structure of the assemblages at this regional scale.

The importance of factors in determining diversity patterns and, in particular, gradients of species composition varies with the spatial extent under consideration (Willis & Whittaker, 2002; Steinitz *et al.*, 2006). We expect the importance of GD to increase at coarser extents, where the effect of dispersal limitation and historical factors are maximised. Conversely, at very small (local) extents, the effect of factors such as aggregation of individuals would strengthen the weight of spatial distance (Gilbert & Lechowicz, 2004). At our regional extent of study, none of these factors may be significant enough to make GD a relevant determinant of similarity decay. Thus, in general, spiders might not have difficulty reaching suitable places despite their supposed differences in dispersal capacity. This fact may be enhanced by the clear northwest–southeastern environmental gradient of the region of Madrid (see Fig. 1), as it is expected that the more heterogeneous and patchy the environment, the greater the relevance of spatial distance (Harrison *et al.*, 1992; Nekola & White, 1999). However, Cottenie (2005) found extent to have a minor influence on the environmental versus spatial process structuring metacommunities, so it is unclear if the weak effect of GD in spiders is generalisable to other spatial scales, being an intrinsic property of the taxon. Maybe, despite the mean propensity for long-distance dispersal can vary among families, rare dispersal events could offset its effect on the composition of the assemblages.

As with spatial extent, grain size may be highly influential on the beta-diversity patterns observed and, consequently, on the relative importance of factors under consideration. Variation in faunal similarity among samples will decrease as grain size increase and *vice versa*, because coarse grain sizes imply homogenisation of the assemblages while small grain sizes imply a sample of a subset of the assemblages (Nekola & White, 1999; Mac Nally *et al.*, 2004). This may cause the artificial weakening or strengthening of the relationship between GD and composition similarity (Steinitz *et al.*, 2006). However, considering the home ranges usually reported for spiders (e.g. Turnbull, 1973; Hoefler & Jakob, 2006), we believe that a 1 km<sup>2</sup> resolution is suitable to avoid these resolution problems.

Insufficient sampling effort may also influence the observed results. If inventories are not reliable, then rare species may have been missed (Jiménez-Valverde *et al.*, 2006), homogenising the faunas. Absence of rare species from the inventories generates a

reduction in overall dissimilarity and a decrease in the amount of explained variability. On the other hand, if the completeness of the inventories is extremely low, then overall dissimilarity would be artificially increased because most of the species collected would be represented by single individuals (Hulcr *et al.*, 2008) and, as in the former case, the amount of explained variability would also decrease. Our inventories show high percentages of completeness and the regional beta-diversity values are high, indicating low homogenisation of the faunas, so we believe that undersampling is not affecting our results.

#### *The role of dispersal*

As also recently pointed out by Entling *et al.* (2007), our results strongly indicate that environmental requirements of the species are crucial in organising spider assemblages. In contrast to what we expected, GD was not influent on compositional similarity at this scale, suggesting a weak role of dispersal limitations at our spatial scale. This is consistent with the results of Cottenie (2005) who suggested that passive dispersion promotes the species-sorting dynamic along resource gradients. However, do these results mean that dispersal capacity is not conditioning the structure of the spider assemblages at the scale of study?

Higher regional beta-diversity values may be due to higher habitat specialisation which, for example, has been suggested to be strong in ground-dwelling spiders (Mallis & Hurd, 2005). The differences among slopes of the similarity decay with climate indicate, at least, differences in the degree of specialisation with respect to broad environmental conditions (i.e. higher slopes indicate narrower climatic niches). Greater specialisation also leads to more species turnover. However, a low propensity for ballooning (and thus lower dispersal capacity) has been found in specialist spiders because of the risk of landing in unsuitable locations (Bonte *et al.*, 2003), so environmental specialisation and dispersal capacity may be correlated and not easily separable. Another possibility is that the relationship between the composition of assemblages and space may not be linear (Gilbert & Lechowicz, 2004). For example, low vagility could be indirectly responsible of regional beta-diversity patterns by making colonisation difficult after extinction of species from local assemblages, which could follow a stochastic dynamic, and the signal of dispersion could be not reflected in spatial distance. This could be especially important in spiders, whose composition of assemblages is known to show large fluctuations in time (New, 1999). Thus, differences in vagility between families could be responsible, in the long term, of differences in regional beta-diversity and in its relationship with climate.

#### *Concluding remarks*

Our results indicate a strong environmental determination of spider assemblage composition at the regional scale and raise a number of interesting questions regarding the spatial structure of spider assemblages. It has been difficult to separate environmental (e.g. species sorting along environmental gradients due to niche differences) and spatial processes (e.g. aggregation due

to dispersal limitations) due to their unavoidable and usually high correlation, and most studies conclude that niche and neutral processes are acting in conjunction in natural systems (Cottenie, 2005; Gravel *et al.*, 2006). Our results add to the few studies that have found no or weak effect of GD on natural assemblages (e.g. Gilbert & Lechowicz, 2004). This must be assessed over other geographical extents to test its generalisation on spiders. Nevertheless, GDs without considering the topography may not make sense in terrestrial ecosystems, and our results show that when topography is considered results may change. This fact has to be considered in future studies dealing with beta-diversity gradients. However, this low importance of GD does not mean that dispersion has no influence on the structure of spider assemblages, but that it may be working in a complex heterogeneous world. Also, some families may show different patterns and so the results cannot be generalised to the whole order of Araneae. Techniques able to deal with complex relationships with space are necessary to detect complex spatial processes that are not detectable with the usually applied matrix correlation tests (Gilbert & Lechowicz, 2004). Moreover, as suggested by Morlon *et al.* (2008), several measures of beta-diversity (as used in our study, i.e. regional beta-diversity, explained variation of distance decay, decay slopes) must be studied to understand fully the patterns, as each one can reveal new and interesting properties. Finally, more studies on the dispersal capacity of spiders are necessary as the data available at present preclude a detailed quantitative evaluation.

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