

# Determinants of local spider (*Araneidae* and *Thomisidae*) species richness on a regional scale: climate and altitude vs. habitat structure

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**Abstract.** 1. The habitat heterogeneity hypothesis states that the more complex the habitat, the higher the species richness. The present study analyzes the effect of local factors on regional spider (*Araneidae* and *Thomisidae*) richness. The main objective is to disentangle the relative importance of habitat structure and other environmental variables.

2. Fifteen territorial units of 1 km<sup>2</sup> were sampled to obtain reliable and comparable inventories of the two spider families. Richness values were modelled using general regression models and a set of climate, topographic and vegetation structure variables. Pure and joint effects were computed via variation partitioning.

3. The results highlight the great importance of vegetation complexity, especially of grass and sub-shrub cover, in determining spider species richness.

4. The maximum temperature is the only climate variable significantly related to species richness, although its effect is combined with that of spatial and vegetation structure variables.

5. These results support the habitat heterogeneity hypothesis, and highlight the importance of taking vegetation complexity into account when managing habitats and where spider conservation is desired.

**Key words.** *Araneae*, *Araneidae*, general regression models, species richness, *Thomisidae*, variation partitioning, vegetation structure. *Volero odolobortio cortion*

## Introduction

About 40 000 spider species are presently known (Platnick, 2005), although estimations of their total number vary from 60 000 to 170 000 (Coddington & Levi, 1991). Spiders are generalist predators colonising almost all habitats, and are quite abundant and diverse in natural systems (density values are usually around 150 individuals/m<sup>2</sup>; Nyffeler, 2000). They develop a great variety of life histories, behaviour, and morphologic, physiological and ecological adaptations (Turnbull, 1973; Wise, 1993; Foelix, 1996). Because of their diverse relationships with the environment and their impact on prey populations (Nyffeler, 2000), spiders have been proposed as very suitable for pest limitation and bioindication (Clausen, 1986; Marc *et al.*, 1999).

*Araneidae*, one of the most successful spider families (approximately 2600 species; Foelix, 1996), are relatively easy to detect because of their size, colouration, and their orb webs. Unlike the araneids, *Thomisidae* (crab spiders) do not use webs to capture prey, and instead ambush prey from flowers or leaves, where their cryptic colouration allows them to go unnoticed. Some genera, like *Xysticus* Koch (1835) and *Ozyptila* Simon (1864), live primarily among leaf litter and herbaceous vegetation.

The habitat heterogeneity hypothesis states that the more complex the habitat, the more niches are available, and therefore the higher the species richness (Tews *et al.*, 2004). Habitat structure and, more precisely, vegetation complexity, has been consistently recognised as one of the most important factors in determining the presence of spider species, as well as their species richness and composition (Colebourn, 1974; Hatley & Macmahon, 1980; Robinson, 1981; Urones & Puerto, 1988; Döbel *et al.*, 1990; Uetz, 1991; Wise, 1993; Downie *et al.*, 1995; Balfour & Rypstra, 1998; Downie *et al.*, 2000; Borges & Brown, 2001). Thus, despite the absence of strong spider association with host plants,

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vegetation type can be an important factor in determining spider assemblages because of their relationship with vegetation structure (Urones & Puerto, 1988). Additionally, other climate and topographic factors have been highlighted as relevant for spiders: humidity (Coulson & Butterfield, 1986; Rushton *et al.*, 1987; Rushton & Eyre, 1992; Bonte *et al.*, 2002), temperature (Rypstra, 1986), and altitude (Urones & Puerto, 1988; Rushton & Eyre, 1992; Chatzaki *et al.*, 2005). However, the relative importance of these factors has scarcely been investigated. Greenstone (1984) noticed that web-building spider diversity along altitude transects, in both tropical and temperate localities, were mainly determined by vegetation structure, whereas elevation and climate differences between localities had no important consequences. On the other hand, Rypstra (1986) measured web-building spider richness in temperate, subtropical and tropical localities within an area of three hectares, stating that spider diversity was also mainly determined by the vegetation structure of each locality, followed by prey availability and environmental temperature, whereas relative humidity had no effect.

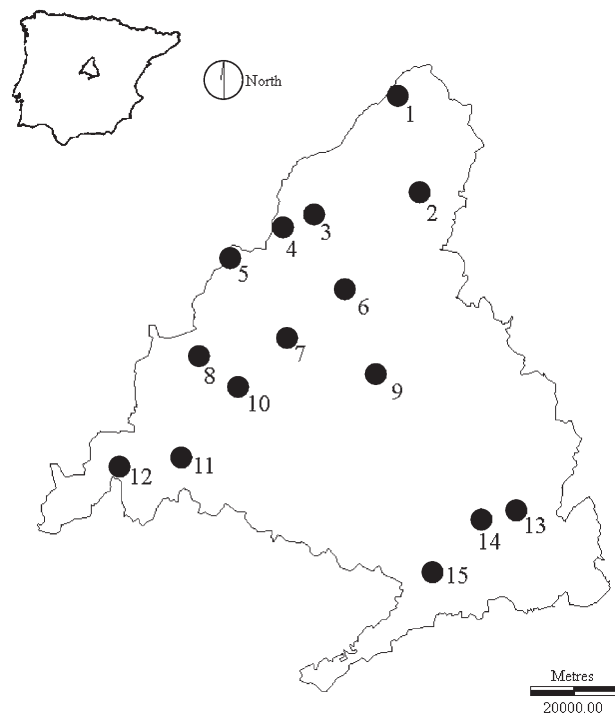
The main problem with these studies, based on correlations, is the unavoidable collinearity of explanatory variables, which limit regression analysis adequacy in finding appropriate causal variables (MacNally, 2000). As direct causal relationships are never known, because of the lack of detailed physiological and autoecological studies, variables widely considered to be influential on species diversity, and introduced to regression analysis, are not necessarily causally related, even when correlated with species richness (Legendre & Legendre, 1998; MacNally, 2000). Results from the search of causality are further degraded by collinearity affecting the automatic variable selection methods. Additionally, although statisticians emphasise that a model without proper validation has no merit (Olden & Jackson, 2000), no validation of models is reported in any of these two formerly cited studies.

To preserve spider biodiversity, land management strategy design requires an understanding of the patterns of spider diversity on an appropriate regional scale (New, 1999). Thus, in an effort to overcome the previously mentioned drawbacks, the effect of local factors on regional spider richness (*Araneidae*, Simon, 1895; *Thomisidae*, Sundevall, 1833) has been analysed using variation partitioning techniques (Borcard *et al.*, 1992) to estimate the predictive capacity of each explanatory variable. The two families selected for this study have a well-established taxonomy, are collected in abundance in samplings, have a well-developed sampling protocol designed for them (Jiménez-Valverde & Lobo, 2005, 2006), and their habits lead us to presuppose a close relationship with vegetation structure. The main objective of this work is to estimate the relative importance of habitat structure and other environmental variables such as climate, altitude and lithology in determining *Araneidae* and *Thomisidae* species richness.

## Materials and methods

### The area of study

The Comunidad de Madrid, with approximately 8028 km<sup>2</sup>, is located in Central Iberia (Fig. 1). Although the mean altitude is



**Fig. 1.** Location of the 1-km<sup>2</sup> sampling plots in the Comunidad de Madrid, located in the Central Iberian peninsula. The plots were selected by a *k-means* procedure to maximize the environmental and spatial variation of the region (Jiménez-Valverde & Lobo, 2004). The site numbers correspond to the locality numbers in Table 2.

around 800 ma.s.l., the altitude ranges from 2430 ma.s.l. in the Sistema Central mountain range to 434 ma.s.l. in the Alberche Valley. The heterogeneous lithology of the area includes acid-rock mountains (granite and gneiss), a ramp of acidic and coarse-grained sands, many alluvial fine-grained soils in the lowlands, and a clay, limestone and gypsum soil plateau. The region has a continental climate with Mediterranean influence and the annual precipitation ranges from 350 mm to 2000 mm. The phytosociological characteristics of the Comunidad de Madrid include its location in the Mediterranean region, and its hosting of representatives of the Mesomediterranean, Supramediterranean, Oromediterranean and Crioromediterranean flora (Rivas-Martínez, 1987).

### Selection of the sampling territorial units

The geographic biodiversity pattern description requires reliable inventories that recover the maximum variation range of the focus taxa in the selected territory, so a good design of the sampling locations is essential. We have used the methodology proposed by Jiménez-Valverde and Lobo (2004), based on cluster analysis, which is designed to regionalize a territory and to maximize the field work that can be accomplished, while considering both the variables that *a priori* most affect the focus taxa and the spatial location of the sampling points. Sampling

effort has been previously defined, and is the initial realistic criterion that determines the number of sampling points to choose. Thus, this method maximizes the spatial–environmental variation recovered as a function of sampling effort (see Jiménez-Valverde & Lobo, 2004 for a detailed discussion of the method).

Using a Geographic Information System (Idrisi 32; Clark Laboratories, 2000a), five environmental layers were created, namely vegetation structure, precipitation, temperature, altitude, and lithology, as these are widely recognized factors affecting spider distribution (see the Introduction). The Corine Land Cover map (European Environment Agency, 1996) was reclassified in three broad categories, representing structural complexity: grasslands, scrublands, and forests. The mean annual temperature and total annual precipitation data were supplied courtesy of the Spanish Instituto Nacional de Meteorología (Madrid, Spain). The mean altitude was obtained from a global digital elevation model (Clark Laboratories, 2000b). A lithologic map (ITGE, 1988) was digitized and reclassified into basic and acidic soils. The sampling territorial units with a dominance of either urban or agricultural land use, of bare rock, of bodies of water or of sand were not included. If sub-regions were delimited using only environmental variables, locations that were environmentally similar but separated in space were grouped together. These locations may have dissimilar species composition and richness as a result of unique historical events. So, to generate homogeneous sub-regions from an environmental as well as from a spatial point of view, the central latitude and longitude of each 1-km<sup>2</sup> sampling territorial unit must be included in the analysis. All variables were standardised to 0 mean and 1 standard deviation. These seven variables were used to divide the Comunidad de Madrid territory into 15 sub-regions by a *k-means* cluster analysis, maximizing the initial distance among the initial centroids (Statsoft, 2001). The area of each sub-region was composed by localities ordered along a spatial–environmental gradient, some of which were located closer to the mean values of each sub-region than others. These mean values are represented by the centroids of each cluster. In order to select the final 15 sampling territory units (Fig. 1), two hierarchic criteria were used: (1) the distance to the cluster centroid (such that the smaller the distance, the better the spatial–environmental representation of the sub-region), and (2) the ease of access.

#### Sampling method

The sampling protocol developed by Jiménez-Valverde and Lobo (2005) was employed because it yields reliable inventories of both families (*Araneidae* and *Thomisidae*) in 1-km<sup>2</sup> sampling plots. Each 1-km<sup>2</sup> sampling territorial unit (or sampling plot) was divided into 2500 sub-plots of 400 m<sup>2</sup>; 20 of these sub-plots were chosen at random, and a sampling effort unit carried out in each. A sampling effort unit was defined as the combined effort of the following sampling methods.

- 1 A one-person sweep of the herbaceous vegetation and shrub over a period of 15 min.
- 2 A one-person beating of bushes and small trees and branches with a heavy stick over a period of 15 min; the specimens fell

on a 1.25 m × 1.25 m white sheet. In cases where the structure of the vegetation made the use of the sheet difficult, a 41 cm × 29 cm plastic pail was employed.

- 3 Four open pitfall traps were run for 48 h. These traps were 11.5-cm wide and of 1 l in volume, and were positioned 10-m apart to avoid interference effects and to maximize their efficacy. Traps were filled with water, and a few drops of detergent were added to break the surface tension so as to prevent the spiders from escaping.

Additionally, in places where, because of special habitat structure, araneids tended to concentrate in particular habitat patches, a one-person visual search from knee level to as high as one can reach over a period of 15 min was also added to the sampling protocol.

Sampling was always performed by the same person (A.J.-V) in order to avoid possible differences attributed to the collector (see Jiménez-Valverde & Lobo, 2005 for a detailed description of the protocol).

#### Sampling-related considerations

Juveniles are usually discarded in spider biodiversity studies (e.g. Jerardino *et al.*, 1991; Toti *et al.*, 2000; Sørensen *et al.*, 2002) because of the difficulty in identification (Coddington *et al.*, 1996; Dobyns, 1997). However, their inclusion is necessary to obtain reliable estimates of species richness (Jiménez-Valverde & Lobo, 2006). Thus, in this study juveniles that could be identified to the species level were included in the analysis. This was possible for many araneid and some thomisid species, which have a distinguishing, characteristic colour pattern, and for some genera represented by only one species in the Iberian Peninsula (i.e. *Mangora acalypha*, Walckenaer, 1802; *Runcinia grammica*, Koch, 1837; *Synaema globosum*, Fabricius, 1775).

Unfortunately, long-term intensive sampling is not often affordable in biodiversity surveys, especially in those with multiple sampling points. So, in each sampling plot, one exhaustive sampling protocol as detailed above was performed in spring (April–June; Jiménez-Valverde & Lobo, 2006). Southern localities were surveyed first in order to account for phenological differences. This strategy yields reasonable estimates of the entire spring fauna, enabling sites to be effectively compared, as spring inventories are a good representation both of the annual species richness and faunistic composition (Jiménez-Valverde & Lobo, 2006). Moreover, short intensive samplings avoid the effects of immigration, and thus enabling a more robust comparative analysis (Samu & Lövei, 1995; Sørensen, 2004). As it was impossible to sample the 15 localities during the same spring period, sampling was prolonged during the years 2002–2004.

#### In situ structural variables

Vegetation complexity was measured in each sampling locality by employing a modified version of the method developed by Newsome and Catling (1979) (see also Coops & Catling, 1997a, b, 2000). Vegetation structure was visually assessed in each sub-sampling plot using seven habitat features (tree canopy cover, *TREE*; shrub canopy cover, *SHRUB*; sub-shrub canopy

cover, *SSHRUB*; ground herb cover, *GRASS*; soil moisture, *SMOIST*; amount of leaf litter, *LITTER*; amount of logs, rocks and debris, *LRD*), and scored between 0 and 3 using ordinal scales (see Table 1). Then, a mean score was calculated for each habitat feature in each 1-km<sup>2</sup> sampling unit, and a global score for vegetation complexity (*VEG*) was obtained by adding the seven partial values. From these seven values for each sampling unit, only *TREE* and *LITTER* were significantly correlated ( $r = 0.92$ , d.f. = 13,  $P = 0.000001$ ). This method has proved to be useful for predicting variations in species richness and the composition of ants (Lassau & Hochuli, 2004), wasps (Lassau & Hochuli, 2005) and beetles (Lassau *et al.*, 2005b).

#### Statistical analyses

*The dependent variable.* As inventories are almost always incomplete, and because the degree of incompleteness is variable, it is necessary to reduce the survey bias to obtain data that is as accurate and comparable as possible (Hortal, 2004; Hortal *et al.*, 2004). For each location, species accumulation curves were drawn (Soberón & Llorente, 1993; Gotelli & Colwell, 2001; Jiménez-Valverde & Hortal, 2003) using sub-sampling plots as sampling effort units (Fig. 2). The order in which sampling effort units were added was randomized 500 times to build smoothed curves using ESTIMATES 7.5 software (Colwell, 2005). As completeness of inventories differed from location to location, no single non-parametric estimator performed well in all 15 sampling plots; the six calculated (Chao1 and 2, Jackknife1 and 2, ICE and ACE) produced meaningless estimations for different sampling plots (Brose *et al.*, 2003). Hortal *et al.* (2004), using the Clench estimation as a dependent variable in their analysis of butterfly species richness in mainland Portugal, produced more consistent models with fewer residual errors in the prediction than by using observed species richness directly. Therefore, it was decided to estimate the asymptotic value of the accumulation curves using the Clench equation (Soberón & Llorente, 1993; Colwell & Coddington, 1994; León-Cortés *et al.*, 1998; Peterson & Slade, 1998). The models were fitted to the data through nonlinear regression using the Simplex and Quasi-Newton algorithm (StatSoft, 2001). Although other

more complex models have been recommended (Flather, 1996; Jiménez-Valverde *et al.*, 2006), meaningless predicted species richness values discouraged their use (Jiménez-Valverde *et al.*, 2006). The estimated species richness values of the Clench model were considered as the dependent variable in subsequent analysis.

*The modelling process* Multiple relationships between species richness and the explanatory variables were analysed using general regression models (*GRM*) (STATISTICA; StatSoft Inc., Tulsa, OK, USA). The continuous variables selected are as follows: mean altitude (*ALT*), annual precipitation (*PRECP*), precipitation of the least rainy month (precipitation of August; *PAUG*), precipitation of the most rainy month (precipitation of April; *PAP*), mean annual temperature (*TEMP*), maximum and minimum annual temperature (*TMAX* and *TMIN*, respectively), insolation (*INS*), lithology (basic and acid soils; *LIT*), land use following Corine (reclassified in grasslands, shrubland and forests; *LUU*), and vegetation structure scores (partial and global) (all climate variables were provided by the Spanish Instituto Nacional de Meteorología). Continuous variables were standardised to 0 mean and 1 standard deviation to avoid scale effects. As a first step, categorical variables and linear and quadratic functions of the continuous variables were regressed independently against the response variable in order to determine significant predictors. Then, significant terms were sequentially introduced in the model, according to their change in deviance, and selected by a backward stepwise procedure. Spatial variables were included in the model after environmental variables to account for effects caused by other unaccounted-for historic, biotic or environmental variables, and also to eliminate the probable spatial autocorrelation in the residuals (Legendre & Legendre, 1998). The terms of the third-degree polynomial equation of the central latitude (*LAT*) and longitude (*LON*) of each square ( $\beta_1LAT + \beta_2LON + \beta_3LAT^2 + \beta_4LAT \cdot LON + \beta_5LON^2 + \beta_6LAT^3 + \beta_7LAT^2 \cdot LON + \beta_8LAT \cdot LON^2 + \beta_9LON^3$ ) were independently tested for significance. The significant spatial terms were added to the model and subjected to a backward stepwise procedure together with environmental predictors.

The reliability of the final model was checked using a Jackknife procedure, in which 15 models were recalculated leaving out one sampling plot in turn, and then calculating the

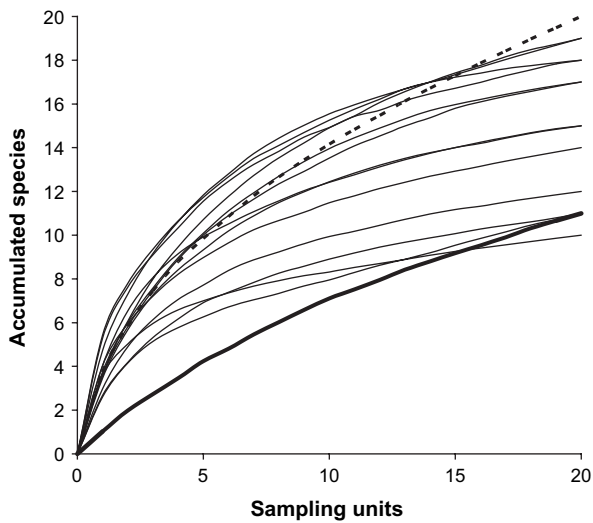
**Table 1.** Visual scoring of vegetation structure features in each sub-sampling plot (adapted from Coops & Catling, 1997b).

Structure	Score			
	0	1	2	3
Tree canopy cover (% cover)	0	<30	30–70	>70
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)**
Logs, rocks and debris (% cover)	0	<30	30–70	>70
Soil moisture	Dry	Moist	Water†	Water-logged
Leaf litter (% cover)	0	<30	30–70	>70

\*Sparse ground flora, grasses covering < 50% of the sub-sampling plot;

\*\*dense ground flora, grasses covering > 50% of the sub-sampling plot;

†water permanently adjacent to site.



**Fig. 2.** Accumulation curves for the 15 inventories (bold line, Cerro Cardoso; dashed line, La Herrería; see also Table 2).

estimated species richness for each plot (Hortal *et al.*, 2001). The predictive error (*ME*) of the final model was calculated as the mean of:

$$E_i = [(|O_i - P_i|)/O_i] \times 100,$$

where  $E_i$  is the predictive error in plot  $i$ ,  $O_i$  is the observed species in each plot and  $P_i$  is the predicted value (Pascual & Iribarne, 1993). The predictive power of the model is calculated as  $100 - ME$ . Outliers were identified as the observations in which the residual absolute value is greater than the standard deviation of the predicted values (Nicholls, 1989). Outliers were checked to determine if they were caused by either erroneous data or to unique environmental conditions; although the former must be discarded, the latter should be included in the analysis to account for such special environmental conditions (Hortal *et al.*, 2001). After removing outliers, models were fitted again.

Finally, the variation partitioning of significant explanatory variables was used to quantify the relative importance of the effect of each determinant alone, and its respective shared influences (Legendre & Legendre, 1998). After rejecting variables that were not related with the dependent variable, the total variation was decomposed among three groups of variables (the most important ones): *EV*, environment variables (maximum annual temperature); *SV*, spatial variables (latitude); *VEGS*, vegetation structure variables (sub-shrub cover, grassland cover). The percentage of explained deviance was also calculated for eight different components:  $a$ , sole effect of *EV* alone;  $b$ , sole effect of *SV* alone;  $c$ , sole effect of *VEGS* alone;  $d$ , combined variation as a result of the joint effect of *EV* and *SV*;  $e$ , combined variation as a result of the joint effect of *EV* and *VEGS*;  $f$ , combined variation as a result of the joint effect of *SV* and *VEGS*;  $g$ , combined variation as a result of the joint effect of the three components;  $U$ , variation not explained by the independent variables included in the analysis. The decomposition of the variation in species richness into the three sets of explanatory variables was carried out by means of a partial regression analy-

sis (Legendre & Legendre, 1998). Such an approach allows one to deal with dependent explanatory variables, as it is explicitly designed to identify the portions of explained variability that are shared by different factors, and to identify those that are independent (Heikkinen *et al.*, 2004; Lobo *et al.*, 2004). In the process of variation decomposition, species richness ( $y$ ) was regressed with the three types of variables together (*EV*, *SV*, and *VEGS*), which represent the total explained variation in the data set ( $a + b + c + d + e + f + g$ ). Regressing  $y$  with each one of the explanatory variables yields the variation separately attributable to *EV* ( $a + d + e + g$ ), *SV* ( $b + d + f + g$ ), and *VEGS* ( $c + e + f + g$ ). Subsequently, residuals of the regression of *EV* against *SV* + *VEGS* variables were calculated, and  $y$  was regressed with these residuals to estimate the sole effect of *EV* variation ( $a$ ). Fractions  $b$  and  $c$  were estimated in the same way after computing the regression residuals of *SV* against *EV* + *VEGS*, and the regression residuals of *VEGS* against *EV* + *SV*, respectively. The remaining variation fractions were computed according to two sets of equations (Borcard *et al.*, 1992), where:

$$d + e + g = EV - a$$

$$d + f + g = SV - b$$

$$e + f + g = VEGS - c \text{ and}$$

$$d = (EV - SV) - (e + f + g) - (a + b);$$

$$e = (EV + VEGS) - (d + f + g) - (a + c);$$

$$f = (SV + VEGS) - (d + e + g) - (b + c);$$

$$g = (d + e + g) - d - e = (d + f + g) - d - f = (e + f + g) - e - f.$$

## Results

The accumulation curves of the 15 inventories indicate quite complete inventories, as almost all of them approach the asymptote (Fig. 2) with low slopes at the end of the fitted Clench function (Table 2). The most notable exceptions were La Herrería and Cerro Cardoso (the dashed and bold lines in Fig. 2, respectively), which end while still rising with the highest slope values. The latter is especially striking as it rises quite slowly, indicating an extremely slow addition of the species to the inventory. Clench estimations indicate that between 71 and 92% of the fauna have been collected, except in Cerro Cardoso where the estimation of the function is quite high and yields a value of completeness of 47% (Table 2).

Only two of the 10 environmental variables tested were significantly related to species richness: *TMAX* (as a quadratic function, see Fig. 3) and *LIT* (Table 3a). Only *TMAX* remains when submitted with *LIT* to a backward stepwise selection procedure. Of the eight *in situ* structural variables, only *VEG*, *GRASS* and *SSHURUB* accounted for a significant explained variance, showing a positive relationship with species richness, and only the latter two remained in a complete model with structural variables. *LONG* (as a quadratic function) and *LAT* were the only spatial variables significantly related with the dependent variable, but only *LAT* remains after a backward stepwise selection. The final complete model, built with all formerly significant

**Table 2.** Sampling localities (numbers in brackets correspond with the site numbers in Fig. 1), observed number of species, estimated number of species according to the Clench function, percentage of completeness [(observed/predicted) × 100], percentage of explained variance of the Clench model ( $R^2$ ), and slope at the end of the fitted Clench curve.

	Locality	OSR*	ESR**	C† (%)	R <sup>2</sup> (%)	Final slope
(1)	La Acebeda	17	21.9	77.6	99.8	0.19
(2)	El Berruoco	19	22.4	84.8	98.7	0.16
(3)	Cerro Cardoso, Rascafr'a	11	23.5	46.8	99.9	0.29
(4)	Sillada de Garcisancho, Rascafr'a	15	17.4	86.2	99.3	0.11
(5)	Cercedilla	18	25.2	71.4	99.9	0.24
(6)	Dehesa de Navalvillar, Colmenar Viejo	15	18.4	81.5	99.9	0.14
(7)	Hoyo de Manzanares	18	21.8	82.6	99.9	0.15
(8)	La Herrería, El Escorial	20	25.5	78.4	99.0	0.31
(9)	Monte de Valdelatas, Madrid	17	21.8	78.0	99.8	0.19
(10)	Valdemorillo	12	14.2	84.5	99.7	0.10
(11)	Chapinería	18	21.2	84.9	99.1	0.15
(12)	Pelayos de la Presa	11	13.1	84.0	96.5	0.11
(13)	Tielmes	11	13.2	83.3	99.6	0.10
(14)	Perales de Tajuña	10	10.8	92.6	97.7	0.05
(15)	Chinchón	14	16.3	85.9	99.0	0.11

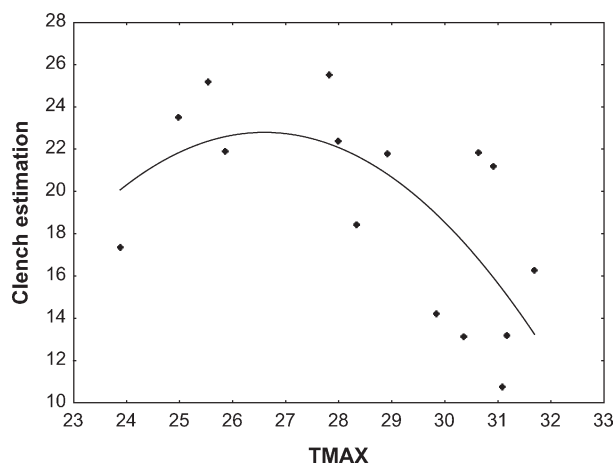
\*OSR, observed species richness;

\*\*ESR, estimated species richness (Clench model);

†C, completeness.

variables, only retained *GRASS* and *SSHRUB*, accounting for 61% of the total variability in species richness. The jackknife procedure yields a predictive power of 86.2%, and Cerro Cardoso and Perales de Tajuña were identified as possible outliers. The first sampling plot had the greatest absolute residual value and so was analyzed first. It was recognized as a true outlier, because the addition of species to the inventory was so slow (see Fig. 2) making the estimation of the Clench function highly unreliable. Therefore Cerro Cardoso was eliminated from the matrix and the models were fitted again.

After removing the outlier, the variables significantly related to species richness were the same as before except for *LONG*, which was no longer included (Table 3b). Variance explained

**Fig. 3.** Relationship between species richness (Clench estimation) and the maximum temperature (TMAX °C).

varied little, with *GRASS* and *SSHRUB* the variables which most increased. In fact, the complete model retains only these two structural variables that explain 81% of the variability of the dependent variable. The predictive power increased to 88.6%, and no outlier was identified.

A considerable proportion of the variation in species richness results from the joint effect of the three types of variables considered, showing that around 30% of the total variability in species richness is not attributable to a single variable. However, variation partitioning highlights the important effect of vegetation structure alone (57%), and the lack of relevance of environmental and spatial variables by themselves (Fig. 4). Both environmental and spatial variables are important because of their joint effect (8.9%), indicating that spatially structured environmental factors seem to influence the variation in species richness slightly. Lastly, the negative signs of the interaction between vegetation structure with either environmental or spatial variables (−7.0 and −8.9%, respectively) suggests the probably moderate synergic effects of these variables (see Legendre & Legendre, 1998).

## Discussion

Despite habitat heterogeneity being a base hypothesis in the present ecology (Tews *et al.*, 2004), the bias (focus on vertebrates and on habitats under anthropogenic pressure) of studies dealing with this topic, together with the limited variety of spatial and temporal scales on which the effects of vegetation structure have been tested, impede comparisons and conclusive general results (McCoy & Bell, 1991; Tews *et al.*, 2004). Although studies on spiders are not free of temporal and spatial scale problems, habitat complexity has still been repeatedly indicated

**Table 3.** Statistically significant variables related to spider species richness and the models for each group of variables, respective regression coefficients, and percentage of explained variance [ $R^2$  (%)].  $f^2$  is the quadratic function of the variable considered: **A**, with the 15 sampling plots; **B**, deleting the outlier of Cerro Cardoso.

Variable	Function	$R^2$ (%)	$F$	$P$
<b>A</b>				
<i>TMAX</i>	Quadratic	36.40	5.01	0.026
<i>LIT</i>	–	34.58	8.40	0.012
<i>VEG</i>	Linear (+)	29.50	6.86	0.021
<i>GRASS</i>	Linear (+)	35.70	8.77	0.011
<i>SSHRUB</i>	Linear (+)	30.62	7.18	0.019
<i>LONG</i>	Quadratic	32.70	4.40	0.037
<i>LAT</i>	Linear (+)	34.65	8.42	0.012
Model for <i>EV</i>	$f^2$ <i>TMAX</i>	36.40	5.01	0.026
Model for <i>SV</i>	<i>LAT</i>	34.65	8.42	0.012
Model for <i>VEGS</i>	<i>GRASS</i> + <i>SSHRUB</i>	61.19	12.04	0.001
Whole model	<i>GRASS</i> + <i>SSHRUB</i>	61.19	12.04	0.001
<b>B</b>				
<i>TMAX</i>	Quadratic	32.45	4.12	0.046
<i>LIT</i>	–	31.09	7.43	0.018
<i>VEG</i>	Linear (+)	26.92	5.79	0.033
<i>GRASS</i>	Linear (+)	42.48	10.60	0.007
<i>SSHRUB</i>	Linear (+)	42.84	10.74	0.007
<i>LAT</i>	Linear (+)	30.49	6.70	0.024
Model for <i>EV</i>	$f^2$ <i>TMAX</i>	32.45	4.12	0.046
Model for <i>SV</i>	<i>Lat</i>	30.49	6.70	0.024
Model for <i>VEGS</i>	<i>GRASS</i> + <i>SSHRUB</i>	81.03	28.76	< 0.001
Whole model	<i>GRASS</i> + <i>SSHRUB</i>	81.03	28.76	< 0.001

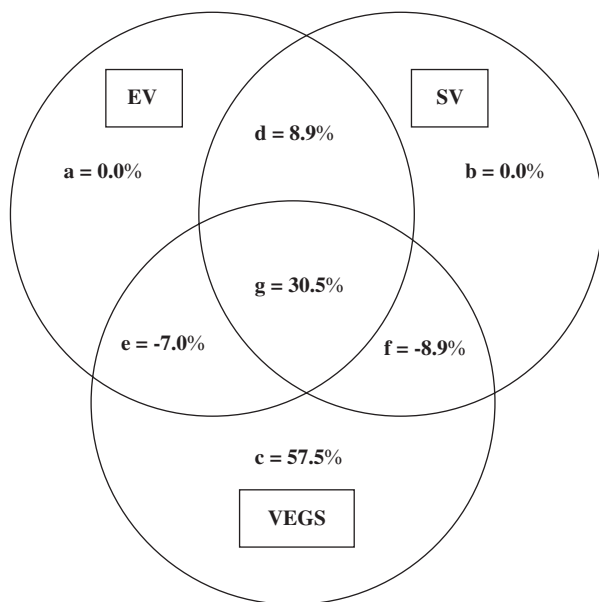
as the most important factor in determining spider distribution (Wise, 1993; Downie *et al.*, 1995; Balfour & Rypstra, 1998; Downie *et al.*, 2000; Borges & Brown, 2001). In this study, by employing a measure of habitat complexity in accordance with the spatial scale of analysis, vegetation complexity appears as a powerful predictor of local *Araneidae* and *Thomisidae* species richness on a regional scale. Of all the structural variables tested, only herbaceous and sub-shrub cover remains significant in the final model; their sole effect is considerable, reflecting the main range of height occupied by *Araneidae* and *Thomisidae* in natural habitats. Grill *et al.* (2005) reported that the cover of herbaceous vegetation is the main determining factor for web-building spider diversity on a local scale in the Mediterranean habitats of Sardinia. As thomisids live mainly on vegetation, with a great percentage of species living in the soil–grass interface (genus *Xysticus* and *Ozyptilla*), this variable is quite relevant for both families.

The model developed would be more useful if it could be extrapolated to the entire region in order to map richness predictions that could be used in conservation planning. However, because *in situ* structural variables are not available for the whole territory, such a representation is impossible. Nevertheless, several authors have pointed out that the complexity measures used in this work can be recognized in airborne videographic data (Coops & Catling, 1997a, b). Moreover, Lassau *et al.* (2005a) found a good correlation between normalized difference vegetation index (*NDVI*) scores and these structural measures. *NDVI* provides a means of monitoring the density and vigour of green vegetation growth as Geographic Information System layers are available from a number of organizations (Pettorelli *et al.*, 2005);

thus, it is a widely used factor in studies of species-richness patterns and in predictive modelling (i.e. Egbert *et al.*, 2002; Suárez-Seoane *et al.*, 2002; Bailey *et al.*, 2004; Foody, 2004; Parra *et al.*, 2004; Roura-Pascual *et al.*, 2004; Ruggiero & Kitzberger, 2004). However, we tested correlations between our structural variables and the *NDVI* scores from a layer of 1-km<sup>2</sup> resolution, calculated as the mean maximum monthly value for April, May and June of the year 2001 (courtesy of the CREPAD, Instituto Nacional de Técnica Aeroespacial, Gran Canaria, Spain), and found no statistically significant correlations. Moreover, although *NDVI* was significantly related with species richness, it did not remain in any model, neither in the environmental nor in the final one. The lack of concordance between our results and those from Lassau *et al.* (2005a) may be caused by differences in resolution, and perhaps our greater plot size dilutes the relationship between both variables.

Although vegetation structure is widely recognized as one of the main determinants of spider community composition, the exact mechanism of its influence is unknown (Wise, 1993; Rypstra *et al.*, 1999). The availability of structures for attaching a web, and of ambush and refuge sites is probably the most direct effect of vegetation complexity, but other indirect effects may be related, such as, for example, microclimate, prey availability or reduced cannibalism (Uetz, 1991; Marc *et al.*, 1999). Many more field studies would be necessary to clarify this interesting and relevant question (Halaj *et al.*, 1998).

Maximum temperature seems to be a variable slightly related to species richness, although its effect is combined with the effects of spatial and vegetation structure variables. Species richness is maximized at intermediate values of this factor



**Fig. 4.** Variation partitioning in species richness between the statistically significant variables [EV, environment variables (maximum annual temperature); SV, spatial variables (latitude); VEGS, vegetation structure variables (sub-shrub cover, grassland cover)].

(~26.5 °C), diminishing at low and high values (see Fig. 3). Negative interaction effects between vegetation structure variables and either environmental or spatial ones suggest that both pairs of factors are able to explain more than the sum of their individual effects: i.e. more species richness can be observed either when the adequate vegetation structure occurs in a distinctive spatial location or under some characteristic climate conditions. It is interesting to note that low maximum temperatures generally occur in high altitudes and latitudes, and that the structure of the vegetation can acquire more relevance in this situation that in either lowland or warmer places.

*Araneidae* and *Thomisidae* are two families that have a high proportion of species with wide distributions. This fact may be related to their great dispersal potential, as *Araneidae* and *Thomisidae* are, after *Linyphiidae*, the two most numerous families of ballooning spiders (Dean & Sterling, 1985; Bishop, 1990). So, they are both species with broad environmental tolerance but with a great dependence on the physical structure of the environment because of their life histories. These facts highlight the importance of accounting for the preservation of vegetation complexity in management planning. Bell *et al.* (2001) reviewed how both intensity and type of management in grasslands and heathlands affect spider assemblages, and recommended preserving natural cover in conditions of intensive habitat pressure (grazing, cutting, etc.). The results of this study may probably be extrapolated to other epiphytic spider families such as, for example, either *Clubionidae* or *Philodromidae*. On the contrary, ground-dwelling families (for example, either *Gnaphosidae* or *Lycosidae*) may respond differently to environmental factors, and other variables such as humidity may constrain their diversity patterns (Grill *et al.*, 2005). Additional

research in this direction is necessary to make the reliable inclusion of spiders in management decisions possible.

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