

Spatio-temporal species aggregations do not rule out interspecific competition in tree hollow spider assemblages

LAS AGREGACIONES ESPACIOTEMPORALES ENTRE ESPECIES NO DESCARTAN LA COMPETENCIA INTERESPECÍFICA EN LOS ENSAMBLES DE ARAÑAS DE LAS OQUEDADES ARBÓREAS

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Abstract

1. A community's biological diversity reflects coexistence between species. This often depends, to some extent, on whether there is competition for resources and how it is dealt with.
2. The nature of old-growth tree hollows is confined and relatively isolated, which makes them ideal for investigating the competition phenomena between their inhabitants, such as Araneae.
3. The existence of interspecific competition in the structuring of tree hollow spider assemblages in Mediterranean forests was inferred by spatial co-occurrence pattern analyses with null models at both the community and pairwise levels. The analysis included 36 spider species collected monthly with emergence traps for 1 year. The distribution of four ecological traits, body size and phenology on the resulting pattern type was discussed.
4. The analyses showed spatial segregation at the community level and spatial aggregations between species with different traits predominated at the pairwise level. Hunting strategy and body size were the main differential traits to facilitate these aggregations. In addition, only the aggregations led by *Amaurobius scopolii*-*Scotophaeus scutulatus* and *Eratigena atrica*-*Liocranum majus* also showed an overlap during their main activity period.
5. Community segregation and spatio-temporal aggregations of species with differential traits suggest that interspecific competition is a very likely structuring factor of tree hollow spider assemblages. Instead, segregations at the pairwise level seem to result from other factors, for example, habitat preferences.

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KEYWORDS

Araneae, co-occurrence analysis, Mediterranean forest, niche differentiation, resource competition

INTRODUCTION

Knowledge of the mechanisms that explain species diversity and distribution is a main objective in ecology (Chesson, 2000; Davies et al., 2009). Coexistence between species with similar ecological requirements in the same space is key for understanding the processes by which communities are structured (Chesson, 2000; HilleRisLambers et al., 2012; Kraft et al., 2015). However, species have different competitive capacities insofar as weaker species are displaced by stronger ones when resources are scarce (Chase & Leibold, 2009; MacArthur & Levins, 1967). Consequently, species must employ a mechanism to reduce competition between them to coexist. Different coexistence mechanisms exist, such as resource partitioning, storage effect, host-specific natural enemies or relative non-linearity (Chesson, 2018; HilleRisLambers et al., 2012). Nevertheless, niche differentiation at the spatial, temporal and/or trophic level, that is, resource partitioning, is the commonest mechanism that allows species to coexist (Chesson, 2000).

The study of interspecific interactions in biological communities can be approached by different methodologies. Although it is true that in situ experimentation allows direct evidence for the existence of competition, it becomes more complicated as the number of involved species increases. Therefore, indirect methods are often used. The analysis of species' co-occurrence patterns with null models is one of the indirect methods used to study interspecific interactions in biological communities (Gotelli, 2000). It allows the identification of which species are found together more, less or as frequently as would be expected by chance and to focus on the factors responsible for such associations (Ulrich & Gotelli, 2007). In this way, non-random aggregation patterns are related to similar ecological requirements (Müller et al., 2022; Peres-Neto, 2004; Veech, 2006), mutualistic relationships (Holt, 1984; Sánchez-Galván et al., 2018) or predator-prey associations (Hughes & Grabowski, 2006). In contrast, non-random segregation patterns are attributed to competition phenomena (Camarota et al., 2016; Gotelli & Graves, 1996) or habitat filtering (Azeria et al., 2012; Oliveira-Junior et al., 2021). In addition, co-occurrence patterns can be studied at both the matrix (the whole community) and pairwise (species pairs) levels, although combining them is recommended because they provide different information (Lange et al., 2021; Oliveira-Junior et al., 2021; Sánchez-Galván et al., 2018).

Tree hollows are an acknowledged key structure for diversity in European forests. Their microclimatic stability and high nutrient availability allow them to host a high taxonomic, functional and phylogenetic diversity of organisms, mostly arthropods (Micó et al., 2020; Müller et al., 2013). These animals are called saproxylic, that is, they depend on dead or decaying wood, wood-associated fungi or other saproxylic species at some point in their life cycle (Graf et al., 2022; Speight, 1989). Likewise, hollows could be

considered ideal natural laboratories to study interspecific competition given their semi-enclosed and confined nature (Micó, 2018). However, studies on the role of interspecific interactions in structuring saproxylic communities are relatively scarce. Several works have been conducted on Coleoptera communities, which host different trophic guilds (xylophagous, saproxylophagous, saprophagous, mycetophagous, predators, etc.) that interact differently not only with one another but also with the substrate. This heterogeneity of ecological roles often blurs competitive relationships (Sánchez-Galván et al., 2018). Very few studies have addressed relationships in predatory groups, which is the case of Odonata in phytotelmata hollows in tropical systems (Oliveira-Junior et al., 2021). Spiders also constitute a suitable model to test the contribution of interspecific competition factors because they are a very diverse group in tree hollows (Barrientos et al., 2020; Barrientos et al., 2022; Hernández-Corral et al., 2017; Machač et al., 2018), they are exclusively predatory (Coddington & Levi, 1991; Nyffeler, 1999; Turnbull, 1973) and they are influenced by the physical and biotic variables of tree hollow (Hernández-Corral et al., 2021).

In interspecific competition terms, spiders rarely compete for food, especially in web-spinners (Wise, 1993), but this can sometimes be significant between congeneric species or species belonging to the same family (Michalko et al., 2016; Michalko & Pekár, 2015; Nieto-Castañeda & Jiménez-Jiménez, 2009; Nyffeler et al., 1986). Some studies have shown that arachnids avoid competing by adopting strategies, such as spatial partitioning (Cumming & Wesolowska, 2004; Harwood et al., 2003; Michalko et al., 2016; Pekár et al., 2020; Villanueva-Bonilla et al., 2019), temporal partitioning (are active or breed on different days or times of the year, respectively; Herberstein, 1997; Herberstein & Elgar, 1994; Ward & Lubin, 1992) or trophic partitioning (consume prey of different types or sizes according to their own trophic guild, size and food preferences; Nieto-Castañeda & Jiménez-Jiménez, 2009; Richardson & Hanks, 2009; Tahir et al., 2012). However, the contribution of interspecific competition to the structuring of tree hollow spider communities and their mechanisms is unknown.

Within this framework, the main objective of this study was to determine the importance of interspecific competition as a structuring factor of predator communities. For this purpose, we chose tree hollows because: (1) of their confined nature; (2) of the high biodiversity of the arthropods that they harbour, and per se, they are key for forest diversity; (3) they can be sampled by absolute trapping methods, which allow us to collect all the fauna that coexists inside the hollow throughout a whole year, such as emergence traps (see Micó et al., 2015; Quinto et al., 2013). We also selected the taxonomic group of spiders because they are an abundant, taxonomically and functionally diverse predatory community in hollows, where

they play a fundamental ecological role by controlling other insect populations (Nyffeler & Birkhofer, 2017; Wise, 1993) and providing food for higher food chain links (Gunnarsson, 2007).

We particularly focus on detecting the presence of coexistence strategies, such as spatial, temporal and trophic niche partitioning. For this purpose, we analysed spatial co-occurrence patterns at the community and pairwise levels. We also discuss the distribution of traits like hunting strategy, body size, circadian cycle, hunting stratum, spider prey range and temporal period of activity (phenology) on the coexistence patterns obtained (i.e., aggregations and segregations). The study was conducted in *Quercus pyrenaica* forests in the Mediterranean region, where hollows, which act as an important refuge for invertebrate fauna, are currently threatened by climate change, the abandonment of traditional agricultural practices and land use changes (Hunter, 2015; Lindenmayer et al., 2012; Micó, 2018).

We hypothesize that competition will act as a modulating factor of spider assemblages in hollows by considering the confined and partially isolated nature of these microhabitats (Hernández-Corral et al., 2021; Micó, 2018) and the predatory nature of this community (Foelix, 2011). We also think that spiders will employ different niche differentiation strategies, such as trophic, spatial or temporal, given the diversity and abundance of spiders in hollows (Hernández-Corral et al., 2021). Finally, we believe that hunting strategy will be key in trophic niche differentiation because it is the most important feature for establishing trophic differences (Cardoso et al., 2011).

MATERIALS AND METHODS

Study area

This study was conducted in two natural areas and one natural park in the western Iberia Peninsula: Sierra de las Quilamas, El Rebollar and Las Batuecas-Sierra de Francia, respectively (Hernández-Corral et al., 2021; Figure 1). With an area of 61 ha and an average altitude of 1100 m, the forests sampled in the study area consist mainly of old oak trees (*Q. pyrenaica* Willd.) with multiple hollows as a result of traditional management practices (e.g., pollarding and olive groves; García-López et al., 2016; Ramírez-Hernández et al., 2014). There are also other species, such as *Erica* spp. and *Arbutus unedo* (L.), in high shady areas, and *Castanea sativa* Mill. and *Ilex aquifolium* (L.) in low sunny zones (García-López et al., 2016). This territory has a western Mediterranean climate, which is defined by cold, rainy winters and hot dry summers (Blondel et al., 2010).

Sampling and taxonomic identification

Spiders in *Q. pyrenaica* hollows were collected using emergence traps. These traps consist of a black mesh connected to a container with propylene glycol, as a preservative liquid, which completely covers the cavity and prevents external fauna from entering (Hernández-Corral



FIGURE 1 Geographical location of the study area with sampling points (left) and the trap type used for sampling (right).

et al., 2021; Quinto et al., 2013; Figure 1). In this way, it is possible to collect only the animals that inhabit hollows when they emerge (Micó et al., 2015). In all, 48 emergence traps were placed, one per tree. Samples were collected monthly for 1 full year at each site, and the overall sampling period lasted 2 years (Sierra de las Quilamas in 2012–2013 and El Rebollar and Las Batuecas-Sierra de Francia in 2014–2015; see Hernández-Corral et al., 2021). Taxonomic identification was carried out by Jesús Hernández-Corral in Hernández-Corral et al. (2021).

Morphological, ecological and phenological traits

Body size measurement

Body size is a trait that is related to many spider biology aspects, such as feeding and intra- and interspecific relationships (Turney & Buddle, 2019). It has been calculated as the length from the anterior end of the prosoma to the posterior end of the opisthosoma in the dorsal view, excluding chelicerae and spinnerets (Macías-Hernández et al., 2020).

Twenty adults of each species (10 females and 10 males) were randomly selected, whenever available, and were measured using a binocular loupe (Leika M205 C) and LAS software (Leica Application Suite), version 4.10.0. For the species that could not properly be sized with our samples, measurements were complemented with information in the World Trait Database (Bosmans et al., 2010; Macías-Hernández et al., 2020; Nentwig et al., 2021; Pekár et al., 2021). Finally, measurements were obtained for 36 species.

Ecological and phenological characterization of spiders

For the ecological traits, we follow the results of Cardoso et al. (2011), that is, the collected spider families were classified according to their: **hunting strategy** (active or web-weavers in sheet, sheet-tube or spatial webs); **circadian cycle** (nocturnal, diurnal or both); **prey range** (euryphagous or stenophagous) and **hunting stratum** (ground, vegetation or both).

Given that information on species' ecological traits is scarce, we used the data available at the family level. However, there are some spider families in which not all species share the same ecological traits, which is the case of hunting strategy in the family Linyphiidae. Therefore, the hunting mode of Linyphiidae species was defined according to the subfamily that they belong to: Erigoninae (active) and Linyphiinae (web). Moreover, traits were reclassified at the species level when information on the studied parameters was available (Table S1).

For the phenology characterization, **species' activity period** was established on the basis of the months in which specimens were collected (Hernández-Corral, 2020). We understand that the months in which the specimens are collected reflect the time of greatest adult activity, which coincides with their greatest dispersal stage. This

allowed us to determine if species were temporally segregating or not according to whether their greatest activity periods coincided.

Data analysis

Species co-occurrence patterns

Co-occurrence analyses aim to understand how communities (at the matrix level) or species (at the pairwise level) are structured in space; that is, whether they tend to aggregate or segregate (Gotelli, 2000). For this purpose, we used different binary co-occurrence indices, which measure the degree of co-occurrence (Gotelli, 2000), and null models, which allow differences to be found between observed and randomly calculated co-occurrence values (Azeria, Fortin, Hébert, et al., 2009). However, depending on the type (presence/absence or abundance) and nature (homogeneous or heterogeneous environments) of data, some indices and null models are more appropriate than others. As we had two study levels (matrix and species pairs), two types of data (presence/absence and abundances) and a heterogeneous nature, we employed two binary indices, C-Score (Stone & Roberts, 1990) and the Bray–Curtis dissimilarity (BCD) index (Faith et al., 1987), and fixed–fixed null models (Gotelli, 2000).

The C-Score and the BCD index measure species' degree of co-occurrence between 0 (aggregation) and 1 (segregation) for presence/absence and abundances, respectively. C-Score is calculated using the following formula, $C_{ij} = (r_i - S_{ij})(r_j - S_{ij})$, where r_i and r_j are the sites where only species 1 and species 2 occur, respectively, and S_{ij} are the sites shared by both species (Stone & Roberts, 1990). In contrast, the BCD index is defined as $BCD(Sp1-Sp2) = (\sum |X_i - X_j|) / (\sum (X_i + X_j))$, where X_i is the abundance of species 1 and X_j is the abundance of species 2 (Faith et al., 1987). Both indices can be used at both the community and species pair levels (Oliveira-Junior et al., 2021; Sánchez-Galván et al., 2018).

The fixed–fixed null model is a type of null model that maintains species occurrence between sites (total sum of columns) and occurrence between species (total sum of rows) during the process (Gotelli, 2000). In other words, they are used when data come from environments that are not equiprobable with one another, such as tree hollows (Micó et al., 2015; Sánchez-Galván et al., 2018).

Matrix-level analysis

In order to know whether the spider community in Q. *pyrenaica* hollows was aggregated, segregated or did not follow any pattern, two matrices were previously constructed: one of presence/absence and one of abundance. Only adults were taken into account in these matrices because juveniles are very difficult to identify for not having developed sexual organs and because they may have a different biology to adults. Singletons and doubletons were also excluded because of the sensitivity of the matrix-level analysis to the inclusion of rare species (probably tourist species; Azeria, Fortin, Lemaître, et al., 2009;

TABLE 1 List of spiders included in the co-occurrence analysis with their respective abundances.

Family	Species	No. of individuals
Agelenidae	<i>Eratigena atrica</i> (C. L. Koch, 1843)	98
	<i>Eratigena bucculenta</i> (L. Koch, 1868)	27
	<i>Textrix caudata</i> L. Koch, 1872	30
	<i>Textrix denticulata</i> (Olivier, 1789)	8
	<i>Textrix pinicola</i> Simon, 1875	9
Amaurobiidae	<i>Amaurobius scopolii</i> Thorell, 1871	131
Dictynidae	<i>Lathys humilis</i> (Blackwall, 1855)	3
Dysderidae	<i>Dysdera fuscipes</i> Simon, 1882	6
	<i>Harpactea fageli</i> Brignoli, 1980	3
	<i>Harpactocrates gredensis</i> Ferrández, 1986	97
	<i>Rhode scutiventris</i> Simon, 1882	98
Gnaphosidae	<i>Drassodes fugax</i> (Simon, 1878)	9
	<i>Scotophaeus blackwalli</i> (Thorell, 1871)	12
	<i>Scotophaeus scutulatus</i> (L. Koch, 1866)	22
	<i>Sernakorba tescorum</i> (Simon, 1914)	3
Hahniidae	<i>Mastigusa arietina</i> (Thorell, 1871)	4
Linyphiidae	<i>Centromerus succinus</i> (Simon, 1884)	9
	<i>Lepthyphantes minutus</i> (Blackwall, 1833)	30
	<i>Micrargus herbigradus</i> (Blackwall, 1854)	3
	<i>Midia midas</i> (Simon, 1884)	4
	<i>Pelecopsis monsantensis</i> Bosmans y Crespo, 2010	98
	<i>Pelecopsis susannae</i> (Simon, 1915)	11
	<i>Pocadicnemis pumila</i> (Blackwall, 1841)	4
	<i>Scotinotylus vettonicus</i> Barrientos y Hernández-Corral, 2020	14
	<i>Tenuiphantes tenuis</i> (Blackwall, 1852)	5
	<i>Trichoncus trifidus</i> Denis, 1965	4
	<i>Typhochrestus bogarti</i> Bosmans, 1990	3
	<i>Walckenaeria dalmasi</i> (Simon, 1915)	6
	Liocranidae	<i>Liocranum majus</i> Simon, 1878
<i>Scotina celans</i> (Blackwall, 1841)		5
Miturgidae	<i>Zora spinimana</i> (Sundewall, 1833)	13
Theridiidae	<i>Enoplognatha testacea</i> Simon, 1884	4
	<i>Phycosoma inornatum</i> (O. Pickard-Cambridge, 1861)	5
Trachelidae	<i>Paratrachelas validus</i> (Simon, 1884)	3
Zodariidae	<i>Zodarion gregua</i> Bosmans, 1994	6
Zoropsidae	<i>Zoropsis media</i> Simon, 1878	7

Azeria et al., 2012; Stone & Roberts, 1990). Consequently, the analyses finally included 804 individuals, 36 species and 13 families of spiders (Table 1) of the 1008 individuals, 87 species and 24 families collected and identified in Hernández-Corral et al. (2021).

Then 1000 fixed-fixed random matrices with C-Score were generated for the presence/absence data using the 'oecosimu' function and the 'quasiswap' method. In contrast, the BCD index, the 'permatswap' function and the 'quasiswap' method were used for the abundance matrix. All randomizations were performed with the R statistical package vegan (Oksanen et al., 2015).

From the results of these analyses, the P and standardized effect sizes (SES) were observed. If the p was >0.05 , the null hypothesis ($BCD_{\text{observed}} = BCD_{\text{expected}}$) was fulfilled and, hence, there was a spatial or temporal random pattern of community with no apparent influence of competition. Conversely, if p was <0.05 , the null hypothesis was rejected and there was aggregation ($BCD_{\text{observed}} < BCD_{\text{expected}}$) or segregation ($BCD_{\text{observed}} > BCD_{\text{expected}}$), which is proof that competition was present. SES is a parameter used to assess the magnitude of the difference in the observed values of the index versus those generated by the null model (Camarota et al., 2016). It is calculated by dividing the difference between the observed index value and the mean of the simulated index values by the standard deviation of the simulated index values. SES can be positive or negative, but 2 and -2 are set as cut-offs of statistical significance (Azeria et al., 2012; Sánchez-Galván et al., 2018). Thus species do not co-occur (segregation) when SES is >2 ($p < 0.05$), coexist (aggregation) when SES is < -2 ($p < 0.05$) and follow a random distribution when SES is between -2 and 2 ($p > 0.05$).

Pairwise analysis

The co-occurrence analysis at the pairwise level, unlike the community level, indicates which species of the community aggregate or segregate. As in the previous case, the species with three individuals or more were analysed (Table 1), and the same methodology for the presence/absence matrices was followed. However, abundance matrices were transformed into dissimilarity matrices prior to the null models with the 'vegdist' function and the vegan 'bray' method. In addition, the 'oecosimu' function and the 'quasiswap' method of this package were used for these matrices because their values were then between 0 and 1. Afterwards, both the P and SES obtained in the analysis were observed, which allowed us to know whether the interactions between each pair of species were significant or not.

All analyses were performed using the statistical software R 4.1.1 (R Core Team, 2021).

Distribution of phenology, body size and ecological traits in significant species-pair interactions

Pairs of species that co-occur spatially and significantly must also coincide temporally to be considered 'true aggregations'. Therefore, we established that there would be temporal co-occurrence between two species, and thus 'true aggregation', when coincidence was $\geq 50\%$ of months (presence/absence data) or $\geq 50\%$ of individuals (abundance data).

We then analysed whether there were significant differences between the body size of the aggregated or segregated species. To do so,

TABLE 2 Co-occurrence patterns between pairs of species with abundance data.

	Species 1	Species 2	BCD obs.	BCD esp.	SES	p-value	Interaction
a	<i>Amaurobius scopolii</i>	<i>Scotophaeus scutulatus</i>	0.385	0.554	-2.168	0.049	Aggregation
b	<i>Liocranum majus</i>	<i>Textrix caudata</i>	0.455	0.725	-2.387	0.039	Aggregation ^a
c	<i>Amaurobius scopolii</i>	<i>Textrix caudata</i>	0.368	0.573	-2.541	0.027	Aggregation ^a
d	<i>Eratigena atrica</i>	<i>Liocranum majus</i>	0.500	0.699	-2.582	0.017	Aggregation
e	<i>Dysdera fuscipes</i>	<i>Zoropsis media</i>	0.400	0.834	-2.836	0.053	Aggregation ^a
f	<i>Eratigena bucculenta</i>	<i>Zora spinimana</i>	0.400	0.734	-2.854	0.019	Aggregation ^a
g	<i>Eratigena bucculenta</i>	<i>Walckenaeria dalmasi</i>	0.500	0.822	-2.909	0.025	Aggregation ^a
h	<i>Harpactocrates gredensis</i>	<i>Liocranum majus</i>	0.407	0.705	-3.100	0.003	Aggregation ^a
i	<i>Harpactea fageli</i>	<i>Rhode scutiventris</i>	0.333	0.889	-3.210	0.049	Aggregation ^a
j	<i>Harpactocrates gredensis</i>	<i>Textrix caudata</i>	0.151	0.597	-4.913	0.001	Aggregation ^a
k	<i>Harpactocrates gredensis</i>	<i>Textrix denticulata</i>	1.000	0.756	2.733	0.009	Segregation
l	<i>Eratigena atrica</i>	<i>Textrix denticulata</i>	1.000	0.759	3.297	0.001	Segregation

Note: Pairs of species are lettered from 'a' to 'l' as in Figure 2.

Abbreviations: BCD, Bray-Curtis dissimilarity; SES, standardized effect sizes.

^aAggregations between species whose activity periods do not coincide.

we performed Student's *t*-test (with equal variances) and Welch's *t*-test (with different variances) on each co-occurrence pattern. The analysis was carried out with the R statistical software 4.1.1 (R Core Team, 2021).

Finally, we studied whether there were differences in the hunting strategy, circadian cycle, prey range and hunting stratum of the species pairs with significant co-occurrence patterns.

RESULTS

Matrix-level analysis

The presence/absence data indicated a random distribution of spider species (SES = 0.896, *P* = 0.348). In contrast, the analysis performed with the abundance data showed a predomination of species segregation (SES = 3.033, *p* < 0.01).

Pairwise analysis

Eleven different co-occurrence patterns (9 aggregations and 2 segregations), in which 13 of the 36 analysed species were involved, were obtained with presence/absence data. In contrast, the analyses with abundance data added further aggregation (*Amaurobius scopolii*-*Scotophaeus scutulatus*) to the previously obtained co-occurrence patterns. Consequently, 10 aggregations and 2 segregations were identified in the analysis with the abundance data (Table 2).

Traits distribution in significant species-pair interactions

Spatial aggregations involved the species that differed in one trait or more, except for the ecologically similar pair formed by *Harpactea*

fageli and *Rhode scutiventris* (see Figure 2i and Table S2 for body size and Table 3 for ecological traits).

Liocranum majus and *Textrix caudata* differed in hunting strategy, as did *Eratigena bucculenta* and *Zora spinimana* (Table 3), while *A. scopolii* and *T. caudata* were distinguished by body size (Figure 2c). In turn, co-occurring species *Dysdera fuscipes*-*Zoropsis media*, *E. bucculenta*-*Walckenaeria dalmasi*, *Harpactocrates gredensis*-*L. majus* and *H. gredensis*-*T. caudata* differed in two traits or more, mainly body size (Figure 2g,h,j) and hunting strategy (Table 3). For example, *D. fuscipes* had distinct circadian cycle, hunting strategy and prey range from *Z. media* (Table 3 and Figure 2e).

Only the spatial aggregations of *A. scopolii*-*S. scutulatus* and *Eratigena atrica*-*L. majus* also occurred over time (the same phenological trait; Tables 2 and 3). Both spatio-temporal aggregations were characterized by grouping species with different hunting strategies (Table 3).

Spatial segregations also occurred between species with one different ecological trait or more. *Harpactocrates gredensis* and *Textrix denticulata* differed in hunting strategy, body size and prey range (Table 3 and Figure 2k), while only body size distinguished *E. atrica* and *T. denticulata* (Figure 2l).

DISCUSSION

Studies on the co-occurrence patterns in forest microhabitats are scarce (Azeria et al., 2012; Doerfler et al., 2020; Müller et al., 2022; Sánchez-Galván et al., 2018; Thorn et al., 2016). Co-occurrence studies in exclusively predatory groups, such as spiders, are even scarcer (Birkhofer et al., 2010; Oliveira-Junior et al., 2021). Furthermore, the fact that interspecific competition is described as rare in the Order Araneae, especially between species belonging to different genera or families and in web-weaving spiders (Wise, 1993), may be a deterrent. However, our study detected significant co-occurrence patterns in the predatory

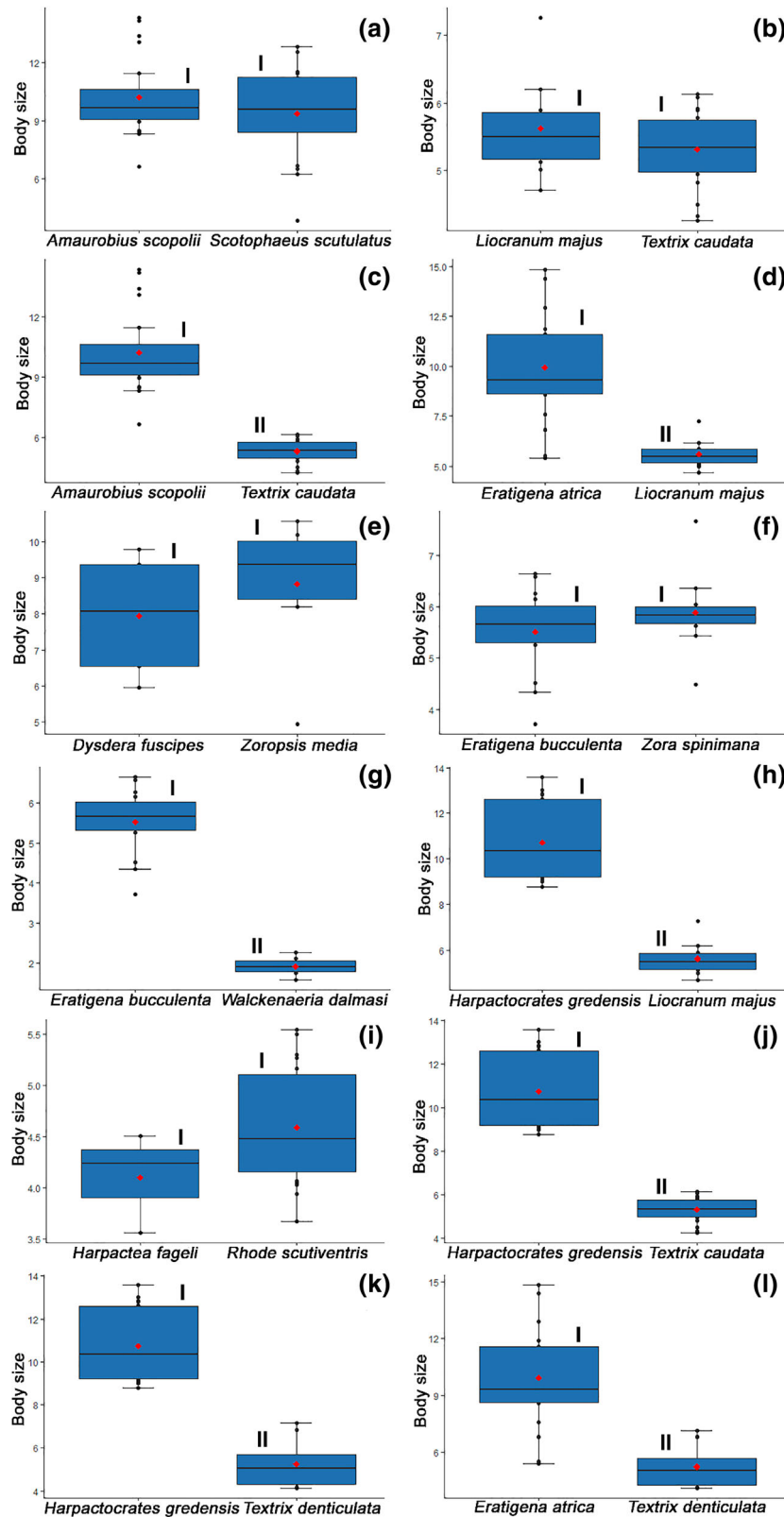


FIGURE 2 Body size differences of species that form part of significant co-occurrence patterns with abundance data. Pairs of species are lettered from ‘a’ to ‘l’ as in Table 2. Statistical differences are denoted with Roman numbers. Red dot indicates mean value.

communities of tree hollows, which suggest that competition is a possible contributing factor in the structuring of spider assemblages. Moreover, the combination of co-occurrence patterns with

species’ morphological, phenological and biological traits indicates that predators may employ different strategies that favour coexistence between them.

TABLE 3 Hunting strategy (active or web-weavers in sheet, sheet-tube or spatial webs), circadian cycle (nocturnal, diurnal or both), prey range (euryphagous or stenophagous), hunting stratum (ground, vegetation or both) and phenology (shaded) understood as months in which either male or female adults were collected (1 = January and 12 = December) of the species with significant interactions.

Species name	Hunting strategy	Circadian cycle	Prey range	Hunting stratum	Phenology (months)											
					1	2	3	4	5	6	7	8	9	10	11	12
<i>Amaurobius scopolii</i>	Web, sheet-tube	Nocturnal	Euryphagous	Ground	1	2	3	4	5	6	7	8	9	10	11	12
<i>Dysdera fuscipes</i>	Active	Nocturnal	Stenophagous	Ground	1	2	3	4	5	6	7	8	9	10	11	12
<i>Eratigena atrica</i>	Web, sheet-tube	Nocturnal/diurnal	Euryphagous	Ground/vegetation	1	2	3	4	5	6	7	8	9	10	11	12
<i>Eratigena bucculenta</i>	Web, sheet-tube	Nocturnal/diurnal	Euryphagous	Ground/vegetation	1	2	3	4	5	6	7	8	9	10	11	12
<i>Harpactea fageli</i>	Active	Nocturnal	Stenophagous	Ground	1	2	3	4	5	6	7	8	9	10	11	12
<i>Harpactocrates gredensis</i>	Active	Nocturnal	Stenophagous	Ground	1	2	3	4	5	6	7	8	9	10	11	12
<i>Liocranum majus</i>	Active	Nocturnal/diurnal	Euryphagous	Ground	1	2	3	4	5	6	7	8	9	10	11	12
<i>Rhode scutiventris</i>	Active	Nocturnal	Stenophagous	Ground	1	2	3	4	5	6	7	8	9	10	11	12
<i>Scotophaeus scutulatus</i>	Active	Nocturnal	Euryphagous	Ground	1	2	3	4	5	6	7	8	9	10	11	12
<i>Textrix caudata</i>	Web, sheet-tube	Nocturnal	Euryphagous	Ground/vegetation	1	2	3	4	5	6	7	8	9	10	11	12
<i>Textrix denticulata</i>	Web, sheet-tube	Nocturnal	Euryphagous	Ground/vegetation	1	2	3	4	5	6	7	8	9	10	11	12
<i>Walckenaeria dalmasi</i>	Active	Nocturnal/diurnal	Euryphagous	Ground	1	2	3	4	5	6	7	8	9	10	11	12
<i>Zora spinimana</i>	Active	Nocturnal	Euryphagous	Ground	1	2	3	4	5	6	7	8	9	10	11	12
<i>Zoropsis media</i>	Web, sheet	Diurnal	Euryphagous	Ground	1	2	3	4	5	6	7	8	9	10	11	12

Data type and global balance of co-occurrence patterns

The analyses of co-occurrence patterns at the community level with presence/absence data showed that spiders were randomly distributed. This result could imply that the number of aggregated species pairs was similar to the number of segregations and they could, therefore, cancel each other out in the overall score (Azeria et al., 2012). Nonetheless, although presence/absence is the most widely used data type due to a higher proportion of qualitative versus quantitative sampling methods, it should be noted that this data type simplifies biological communities because it assumes that all species are equally abundant and are, therefore, equally likely to interact (Sfenthourakis et al., 2006). Instead, abundance data better reflect reality, as our results suggest. Therefore, we found that the spiders inhabiting tree hollows follow a spatial segregation pattern based on abundance data. In general terms, this dominance of spatial segregation would indicate the existence of competition (Connor & Simberloff, 1979; Diamond, 1975). However, it is necessary to look at analyses of all the co-occurrence patterns at the pairwise level to elucidate the factors responsible for the community pattern.

The analyses at the pairwise level indicated a proportion of non-random co-occurrence patterns (1.9%), which could be

considered both low compared to other studies conducted in saproxylic environments (e.g., 28.7% in boreal forests; Azeria et al., 2012; 6%–10% in Mediterranean forests; Sánchez-Galván et al., 2018) and within the range observed in other environments (22 of the 30 matrices studied by Sfenthourakis et al., 2006 had <5% non-random co-occurrence patterns). However, there is no doubt that most of the species combinations in our study were not significant. Sánchez-Galván et al. (2018) argue that the high stochasticity of patterns may be due to the high spatial heterogeneity of the hollows (Micó et al., 2015). We also think that the exclusion of juveniles in the study, which represented 10% of the total number of individuals (Hernández-Corral et al., 2021), may have contributed to fewer significant co-occurrence patterns.

The predominance of significant aggregation patterns over segregation patterns was another notable result of the pairwise-level analyses. This is because analyses with fixed-fixed null models at this level generally detect segregations more easily than aggregations (Azeria, 2004; Azeria et al., 2012; Sfenthourakis et al., 2006). Therefore, more segregations than aggregations would be the expected outcome. Yet not all aggregations need to be 'true aggregations' because their spatial co-occurrence can be avoided by species phenology (see spatio-temporal aggregations do not rule out interspecific competition).

Explaining co-occurrence patterns

Spatio-temporal aggregations do not rule out interspecific competition

Spatial aggregations generally occur between species that share an ecological niche, as demonstrated by numerous studies (Azeria et al., 2012; Azeria, Fortin, Hébert, et al., 2009; Holt, 1984; Peres-Neto, 2004; Sánchez-Galván et al., 2018). However, studies of co-occurrence patterns often do not include the temporal dimension (Lange et al., 2021), even when ‘true’ aggregation (i.e., where an interaction between the two species is highly likely) occurs spatially and temporally. In fact, by studying species phenology together with the spatial aggregations that resulted from statistical analyses, only 20% of the non-random aggregation patterns, formed by species pairs *A. scopolii*–*S. scutulatus* and *E. atrica*–*L. majus*, occurred at the spatio-temporal level. In contrast, the remaining 80% (see * Table 2) were ‘temporal segregations’. So there were more segregations than aggregations, as explained by Azeria et al. (2012) in analyses with fixed-fixed null models.

In the spatio-temporal aggregation formed by *A. scopolii*–*S. scutulatus*, both species are very large, nocturnal and euryphagous species with a preference for hollows close to the ground and are active mainly in summer and autumn, but with completely different hunting strategies (Table 3). *Amaurobius scopolii* hunts by constructing sheet-like webs close to the ground where it waits for prey to be trapped before pouncing on them (Hernández-Corral, 2020). *Scotopaeus scutulatus*, like many species of the family Gnaphosidae, pursues prey at the ground level (Hernández-Corral, 2020). Hunting strategy is the most important characteristic for establishing trophic differences between taxa (Cardoso et al., 2011; Michalko & Pekár, 2016). Therefore, *A. scopolii* and *S. scutulatus* would have two distinct trophic niches that could allow them to avoid competition, despite them sharing the same spatial and temporal niche. However, we cannot rule out that this aggregation could also be due to a predator–prey interaction given that *S. scutulatus* is sometimes an araneophagous species (Baydizada et al., 2020) that prey on other *Amaurobius* species (Wolff et al., 2017) and spiders belonging to similar families to Amaurobiidae (Jäger, 2002). Future molecular analyses of gut contents may shed light on this question. Likewise, we also speculate that a few individuals of both species per hollow in combination with prey abundance might reduce competition to such an extent to allow species to aggregate. Thus hunting strategy, araneophagy and prey–predator abundance are the three possible explanations for the aggregation between *A. scopolii* and *S. scutulatus*.

The second spatio-temporal aggregation, formed by *E. atrica*–*L. majus*, groups together euryphagous species (both diurnal and nocturnal and living close to the ground), although *E. atrica* can also be found in vegetation (Table 3). Both species’ maximum activity periods (August–November) also coincide. However, these species differ in both their hunting strategy, similarly to the *A. scopolii*–*S. scutulatus* aggregation, and their body size. According to several studies (Michalko et al., 2016; Nieto-Castañeda & Jiménez-Jiménez, 2009;

Tahir et al., 2012; Woodward & Hildrew, 2002), spider size is related to prey size and useful for determining the trophic overlap between species. With very few exceptions (Robinson & Valerio, 1977), spiders feed on prey that are no larger than twice their size and prefer prey that are approximately 20%–50% smaller than spider size (Nentwig & Wissel, 1986). However, the range of prey sizes also depends on hunting strategy. Web-weaving spiders are able to hunt large prey by immobilizing them without touching them at all (Nentwig, 1987; Robinson et al., 1969). Although agelenids do not immobilize their prey, the web in which prey are held makes escape difficult and capture easier (Nentwig, 1987; Nentwig & Wissel, 1986). In contrast, cursorial spiders prefer smaller insects because they have to come into direct contact with them to hunt them (Nentwig, 1987). Consequently, *E. atrica* mostly preys on species with a larger body size than those that *L. majus* would hunt, which minimizes competition. In other words, these two ‘true’ aggregations may reflect how species avoid competition when they occupy the same spatial and temporal niche. This supports our hypothesis of competition as a structuring factor, which was obtained with matrix-level segregation.

Can differences in phenologies avoid interspecific competition?

Phenological differences between the involved species are considered by several studies to be a mechanism that reduces competition in predators like spiders (Herberstein, 1997; Herberstein & Elgar, 1994; Richards & Windsor, 2007; Tretzel, 1955; Valderrama, 2000; Ward & Lubin, 1992) and in confined microhabitats like tree hollows (Fincke, 1999). At the European and latitudinal levels, Entling et al. (2010) observe that the dominance of large-bodied spider families (e.g., Agelenidae) increases with temperature as a consequence of physiological factors, such as desiccation (Remmert, 1981) or a higher metabolic rate (Mousseau, 1997), and of biotic factors like competition. This same pattern occurs on the local scale between seasons (larger families tend to appear in summer, while smaller families appear in winter; Hernández-Corral et al., 2021). Therefore, competition may lie behind the phenological differences in spatial aggregations herein observed. However, the body size–temperature relation at the family and species levels does not always correspond (Entling et al., 2010) and, more importantly, species with a distinct phenology also have different body sizes or hunting strategies (see Tables 2 and 3). Differences in the activity period of the species involved in co-occurrence patterns, thus, seem to be the result of factors other than competition.

Spatio-temporal segregations are best explained by habitat preferences

Regarding spatio-temporal segregations, differences in the ecological or morphological traits of the involved species suggest that habitat preferences appear or habitat suitability seem to be the cause of this

pattern (Azeria et al., 2012; Azeria, Fortin, Lemaître, et al., 2009; Gotelli et al., 1997). In fact, recent studies conducted with predatory arthropods (Coleoptera and Odonata) in tree hollows show that communities segregate as a consequence of habitat preferences rather than competition (Oliveira-Junior et al., 2021; Sánchez-Galván et al., 2018). Moreover, knowing that hollows are physically and chemically heterogeneous from one another (Micó et al., 2015) and that the Order Araneae is a very sensitive group to variations in environmental conditions (Jiménez-Valverde & Lobo, 2007; Košulič et al., 2016; Malumbres-Olarte et al., 2018; Müller et al., 2020), it is understandable that spiders are distributed in these saproxylic micro-environments according to their ecological preferences (Hernández-Corral et al., 2021). For instance, in the *H. gredensis*–*T. denticulata* pair (Tables 2 and 3), the former species prefers humid environments (Bidegaray-Batista et al., 2014) and requires little space for hunting (Hernández-Corral et al., 2021), while the latter species is usually found in sunny environments (Hernández-Corral, 2020) and needs larger spaces to build its hunting webs (Hernández-Corral et al., 2021). Likewise in the *E. atrica*–*T. denticulata* segregation (Table 2 and Figure 2), the difference in their sizes may mean that they prefer larger or smaller hollows, respectively. Nonetheless, spiders are constantly hungry (Wise, 1993), which means that their presence in different environments will also be conditioned by prey availability. As hollows have high insect diversity (Micó, 2018), there is prey for all predators (Szinetár & Horváth, 2005). However, the abundance and richness of prey in hollows are also conditioned by the characteristics of this microhabitat (Micó et al., 2015; Quinto et al., 2014). Therefore, those predators with a more specialized prey range (stenophagous; hypothetically *H. gredensis*; Table 3) are likely to be found mainly in those hollows where their favourite prey abounds. Consequently, segregation between two species with different prey ranges is more likely to be due to prey habitat preference than to competition. However, we are aware that further studies on their feeding ecology would be necessary to test the hypothesis.

CONCLUSIONS

The present study of co-occurrence patterns with abundance data proposes that interspecific competition is involved, together with habitat preferences, in the spatio-temporal structuring of spider assemblages in tree hollows. It also suggests that spatial and trophic niche differentiation, through hunting strategy and body size, would be the coexistence mechanisms, which may reduce competitive interactions. However, the ecology of spider communities in tree hollows is still complex and requires further studies. Field experiments and molecular analyses of predators' gut contents, as well as improved knowledge of species autoecology, would help to further advance our understanding of the structuring of predatory communities in confined saproxylic environments.

AUTHOR CONTRIBUTIONS

Gerard Martínez-Devesa: Conceptualization; investigation; writing – original draft; writing – review and editing; visualization; validation; methodology; software; formal analysis. **Jesús Hernández-**

Corral: Conceptualization; investigation; writing – review and editing; visualization; validation; methodology; supervision; resources. **Estefanía Micó:** Conceptualization; investigation; writing – review and editing; visualization; validation; methodology; project administration; resources; supervision; data curation; funding acquisition.

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CONFLICT OF INTEREST STATEMENT

The authors state there are no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Ecological traits reclassified at the species level in this study.

Table S2. Mean body size of the species that form part of significant co-occurrence patterns with abundance data. Statistical differences were assessed by a Student's or Welch's t-test.

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