Community structure of spiders in coastal habitats of a Mediterranean delta region (Nestos Delta, NE Greece)

S. Buchholz

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Abstract

Community structure of spiders in coastal habitats of a Mediterranean delta region (Nestos Delta, NE Greece).— Habitat zonation and ecology of spider assemblages have been poorly studied in Mediterranean ecosystems. A first analysis of spider assemblages in coastal habitats in the east Mediterranean area is presented. The study area is the 250 km² Nestos Delta, located in East Macedonia in the North–East of Greece. Spiders were caught in pitfall traps at 17 sites from the beginning of April to the end of June 2004. Nonparametric estimators were used to determine species richness and alpha diversity. Ordination analysis (redundancy analysis) indicated four clearly separable spider species groups (salt meadows, dunes, meadows and floodplain forests),along a soil salinity and moisture gradient. Based on these results we discuss the habitat preferences of these spiders and include the first ecological data on several species.

Key words: Araneae, East Macedonia, Habitat preference, Species richness, Spider assemblages.

Resumen

Estructura de comunidades de arañas en hábitats costeros de un delta mediterráneo (delta del Nestos, NE de Grecia).— Dentro de los ecosistemas mediterráneos la zonación según el hábitat y la ecología de las comunidades de arañas han sido poco estudiadas. Se presenta un primer análisis de las comunidades de arañas en hábitats costeros del Mediterráneo oriental. El área de estudio está constituida por los 250 km^2 del delta del Nestos, ubicado en Macedonia oriental, en el noreste de Grecia. Las arañas fueron capturadas mediante trampas de caída (pitfall) en 17 localidades durante el período que oscila entre principios de abril y finales de junio del 2004. Se usaron estimadores no paramétricos para determinar la riqueza de especies y la diversidad alfa. El análisis de ordenación (análisis de redundancia) señaló cuatro grupos de especies de arañas (prados salados, dunas, prados y bosques de planicies aluviales), los cuales se discriminaban claramente a lo largo de gradientes de salinidad del suelo y humedad. En base a estos resultados, se discuten las preferencias de hábitat de estas arañas, incluyendo los primeros comentarios ecológicos sobre varias especies.

Palabras clave: Araneae, Macedonia oriental, Preferencia de hábitat, Riqueza de especies, Comunidades de arañas.

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Introduction

Knowledge on the ground fauna of Mediterranean ecosystems is still limited. This especially concerns the eastern Mediterranean region and, in particular, the ecology of epigeal arthropods, such as spiders. Most available studies have pursued faunistic and systematic objectives. Thus, a lot of problems concerning spider taxonomy have yet to be solved. For instance, species composition, distribution patterns and ecology of spiders in eastern Mediterranean ecosystems have so far been poorly investigated (Paraschi, 1986; Chatzaki et al., 1998). Only a very few ecological studies concerning spider assemblages are available to date (Chatzaki et al., 1998, 2005a, 2005b). This is a drawback since such studies are imperative, for example, to assess the conservation value of habitats. In this context, general assemblage descriptions and more detailed knowledge of ecological relationships between species and environment should be taken into consideration when developing a nature conservation policy and determining habitat management objectives (*cf.* Bonte et al., 1998, 2000, 2002).

Spiders constitute one of the most abundant and species–rich arthropod orders. They range among the most numerous arthropods in all kinds of habitat types (Basset, 1991; Coddington et al., 1991; Borges & Brown, 2004). Spider species occupy a wide array of spatial and temporal niches. Their occurrence is frequently related to environmental factors such as vegetation structure and soil humidity as well as all types of human pressure, such as management regimes (Hatley & MacMahon, 1980; Schmidt et al., 2005; Entling et al., 2007; Finch et al., 2008). Spiders are known to respond sensitively to environmental and structural changes, which makes them suitable to study organism–habitat relationships (Wise, 1993; Bell et al., 2001; Oxbrough et al., 2005; Hendrickx et al., 2007). In coastal habitats in particular, the indicator potential of ground–dwelling spiders has been shown in several previous studies (Bonte et al., 2002, 2003; Finch et al., 2007). While the spider fauna of costal habitats in Northern Europe has been thoroughly studied in recent years (Finland: Perttula, 1984; Sweden: Almquist, 1973a; Denmark: Gajdos & Toft, 2002; England: Duffey, 1968; Germany: Schultz & Finch, 1996; Finch et al., 2007; Belgium: Bonte et al., 2003), there are only a few comparable works from the Bulgarian Black Sea coast (Deltshev, 1997; Popov et al., 2000).

The Nestos Delta is one of the most important and strictly protected wetlands in Greece (Dimopoulos et al., 2000, 2006). Due to increasing cultivation and land use the natural and semi–natural habitats of the Delta , among others, have been subjected to development of marsh and lake drainage, the reduction of flooded areas, and the construction of hydroelectric and irrigation dams and networks (Efthimiou et al., 2003). Thus, today most of these habitats are highly endangered and it is of significant importance that they should be taken into account in current nature conservation policies.

The present study is the first analysis of spider assemblages in coastal habitats of the eastern Mediterranean region in general and the Nestos Delta in particular. Apart from ecological descriptions of spider community structures, this work should provide effective data sets to characterise the ecological status of the investigated habitat types and biotic communities that could be used within the framework of conservation, and both ecological planning and management.

Methods

Study area

The Nestos Delta is situated in East Macedonia in the North–East of Greece, at an elevation of 1 to 18 m a.s.l. and covering about 250 km². The northern border follows the spur of the Lekani Mountains, while the eastern part of the Delta reaches the Nestos river. The western and the southern borders follow the coastline of the Thracian Sea (fig. 1). The climate of the Nestos Delta is continental Mediterranean. The annual temperature has an average of 11°C. The summer maximum of 40°C and winter minimum of –20°C show the huge fluctuations in yearly temperature (Philippson, 1947; Lienau, 1989). According to data from the Greek Meteorological Service, the average rainfall ranges from 668.7 to 801.6 mm (*cf.* Efthimiou et al., 2003). The potential natural vegetation is the Ostryo–Carpinion orientalis association (Horvat et al., 1974). The Nestos Delta is part of the East–Macedonian–Thracian belt of wetlands, and it provides a variety of different habitats. This and the influence of three biogeographical regions –central–European, Mediterranean, Pontic– entail great species diversity (Jerrentrup et al., 1989).

Since 1945 the Nestos Delta has been subjected to intense pressure from human activities and today large parts of the Delta are agricultural areas and irrigated land, producing crops such as Indian corn, wheat and rice. Furthermore, former stands of Querco–Ulmetum bulgarium are now areas with planted poplar forests (Sziij, 1997; Efthimiou et al., 2003). Due to the increasing cultivation and land–use, natural habitat types have become rare. Nevertheless, along the shoreline there are still natural shifting white dunes which are characterised by the associations Cypero mucronati–Agropyretum juncei and Medicagini marinae–Ammophiletum australis. The association Ephedero distachyae–Silenetum subconicae is typical for older foredunes and grey dunes.

The therophytic vegetation of the inland dunes belongs mostly to the classes Helianthemetea guttati (incl. Thero–Brachypodietea), Ammophiletea and Molinio–Arrhenatheretea. Within the inland dunes the xeric grassland is characterised by a Trifolio cherleri–Plantaginetum bellardii and a *Bromus tectorum*–community. A community of *Scirpus holoschoenus* (Brizo–Holoschoenion) covers humid parts of inland dunes (Kirchner, 2005).

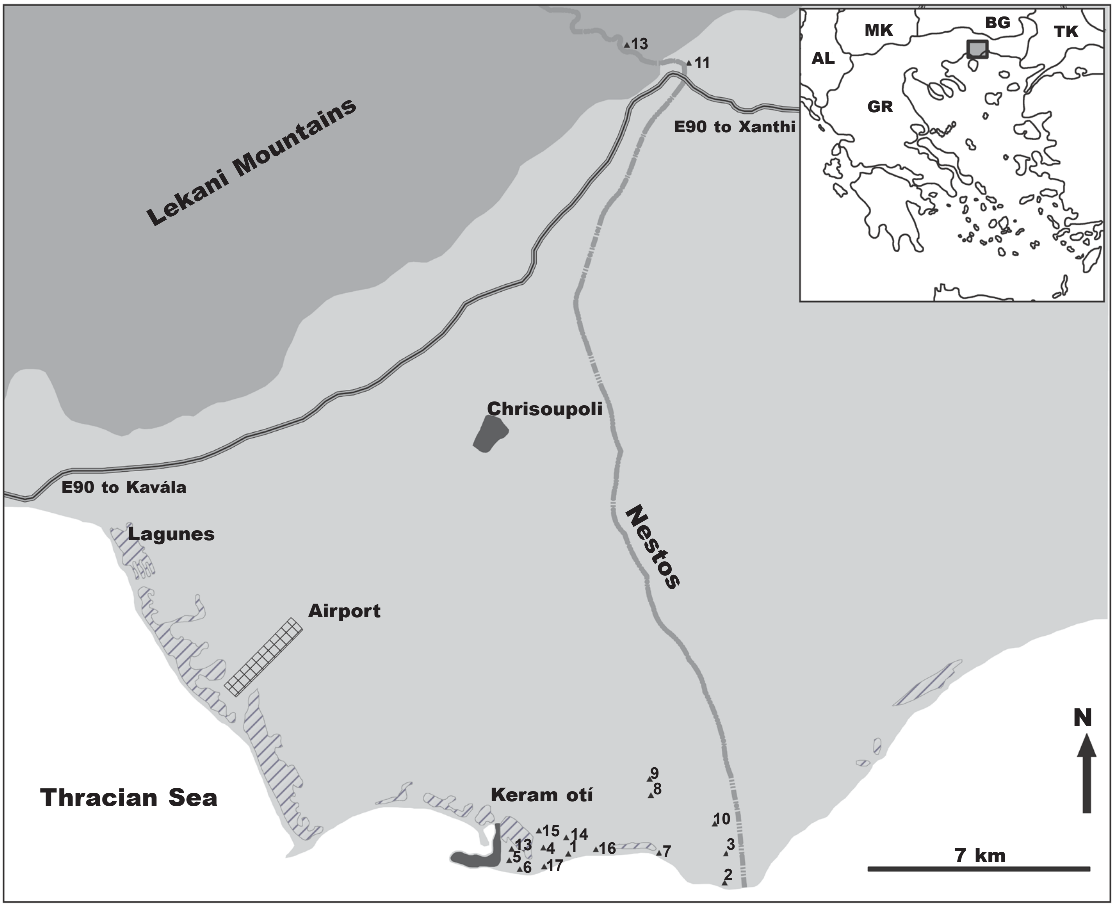

Fig. 1. Study area and location of the sampling localities (table 2).

Fig. 1. Área de estudio y ubicación de las localidades de muestreo (tabla 2).

Two types of coastal marshes can be found in the Delta area: salt marshes with a mosaic of halophilous communities (Salicornietum europaeae, Arthrocnemum glaucum–Halocnemum strobilaceum–Ass.) and brackish water meadows containing a halophilous community of Juncetum maritimo–acuti (Sziij, 1997; Kirchner, 2005). Further away from the sea, freshwater influenced sites are covered by flood meadow communities of Rorippo–Agropyretum repentis. The flood plains of the Nestos Delta are mostly dominated by the order Populetalia albae and are characterised by a large number of climbing species (e.g. *Climatis vitalba*, *Humulus lupulus*, *Solanum dulcamara*, *Vitis vinifera silvestris*). Their vegetation consists of soft wood species, such as *Salix alba*, *Salix fragilis*, *Salix amplexicaulis*, *Alnus glutinosa*, *Populus alba* and hard wood species like *Fraxinus angustifolia*, *Quercus pedunculiflora*, *Ulmus minor* etc. The banks of the Nestos are covered with Phragmitetum plants, which are replaced by halophytic species (e.g. *Limonium* spec., *Tamarix* spec.) closer to the estuary (Efthimiou, 2000; Efthimiou et al., 2003).

Sites

A total of 17 sites were selected, representing the typical natural and semi–natural habitat types in the area of the western Nestos Delta (table 1). Only homogenous plant formations excluding disturbed patches were selected. The site selection focussed mainly on highly endangered habitat types such as dunes (*cf.* Efthimiou et al., 2003; Dimopoulos et al., 2000, 2006), resulting in a higher number of dune sites in the experimental setup.

For each site, environmental data were documented in an area of 10 x 10 m (*cf.* Dierssen, 1990): the vegetation structure was recorded by measuring the average vegetation cover and the density of the herbal layer at 0 and 20 cm above the ground. Five estimation classes were defined for soil humidity and soil salinity: 1 (dry) to 5 (wet) and 1 (no salinity) to 5 (high salinity), respectively. In the latter, the amount of halophytic species (e.g. *Limonium*, *Salicornia* or *Tamarix* species) was taken as a reference for a high soil salinity. Note that neither soil humidity nor soil

Table 1. Capture statistics and environmental characteristics of investigated habitat types (SD in parentheses). Classes of ground humidity: 1. Dry; 2. Slightly humid; 3. Humid; 4. Very humid; 5. Wet. Degrees of salinity: 1. No salinity; 5. High salinity.

Tabla 1. Estadísticas de las colectas y características ambientales de los tipos de hábitat estudiados (DE entre paréntesis). Clases de humedad del suelo: 1. Seco; 2. Ligeramente húmedo; 3. Húmedo; 4. Muy húmedo; 5. Empapado. Grados de salinidad: 1. Sin salinidad; 5. Salinidad alta.

	Salt meadows	Dunes	Dune meadows	Meadows	Forests
Number of sampling sites	4	6	3	2	2
Number of pitfall traps	14	24	12	7	8
Sampling days	53	57	61	70	63
Mean					
coverage of herbal layer [%]	90 (10)	40 (25)	85 (5)	90 (7.5)	60 (30)
density of herbal layer [% 0–20 cm]	85 (5)	30 (20)	85 (30)	70 (25)	60 (20)
coverage of bare soil [%]	5 (5)	40 (30)	5 (2)	0	0
soil humidity	4 (0.5)	1	2 (0.5)	3 (0.5)	4 (1)
soil salinity	5 (1)	1 (0.5)	1	1	1
shading [%]	0	0	0	10 (7.5)	40 (2.5)

salinity were an actual measurement but a personal classification. Shading was estimated as a percentage of canopy density.

Sampling

At 17 sites spiders were caught by using pitfall traps from the beginning of April to the end of June 2004 (table 1). At each site a group of four pitfall traps (diameter 9 cm, filled with a 4% formalin–detergent solution) were installed haphazardly. Catches from three traps that were permanently damaged during the study were excluded (salt meadow sites 14 and 15: one trap each due to water, meadow site 3: one trap due to grazing). Thus, the total number of traps was 65. To avoid edge and depletion effects, traps were laid with a minimum distance of 10 m between each one and 20 m to the edge. Emptying was carried out every two weeks. The survey was limited to spring and early summer, since May and June present the optimal time for collecting spiders in Mediterranean areas (Chatzaki et al., 1998, 2005; Cardoso et al., 2007).

Analyses

For all analyses only adult specimens were considered, since the identification of immature spiders of most families is impossible or at least extremely difficult because of insufficient taxonomic knowledge (*cf.* Jiménez–Valverde & Lobo, 2006). While the entire faunistic dataset and biogeographical analyses were published by Buchholz (2007), the following analyses focused on spider community structures.

Measurements of alpha–diversity (Shannon index) and predicted species richness were calculated using SPADE (Chao & Shen, 2003a). Here, species richness was defined as the number of species in a given sample while predicted species richness means the total richness that can be assumed for a complete species inventory (Chao & Shen, 2003a; McCune & Grace, 2002). In this context, a sample was defined as total number of species per site, collected by a set of four pitfall traps during the sampling period (for number of sampling days see table 1). As opposed to this, the alpha diversity was the diversity in an individual sample unit expressed as Shannon's Index (McCune & Grace, 2002). The Jackknife estimator was used to estimate Shannon's index of diversity (*cf.* Sokal & Rohlf, 1995; Magurran, 2004; Jiménez–Valverde & Lobo, 2006). Species richness was predicted using the nonparametric estimators Chao 1, Chao 1bc, ACE, and ACE–1. Basic background and a detailed review of all estimators are given in Magurran (1988, 2004), Chao & Shen (2003b) and Chao (2005). In addition, species accumulation curves were created using the software package PAST (Hammer et al., 2001).

Spider communities were compared by Redundancy Analysis (RDA) using Canoco 4.5 (Ter Braak & Smilauer, 2002). To compare the sites, the data were standardised (individual sums/number of sampling days/number of pitfall traps). For RDA the abundance of each species was log–transformed to obtain approximately normal distributions and homogenous variances. According to Engelmann (1978) species

Table 2. Capture statistics. Abbreviations: Obs. ind. Number of observed individuals (in bold, mean number of observed individuals per biotope); Obs. spec. Number of observed species (in bold, mean number of observed species per biotope); Est. spec. Estimated number of species (mean of four estimations using Chao 1, Chao 1bc, ACE, ACE–1 estimators; range in parentheses); Compl. Percentage completeness of species inventory; H. Shannon Index of alpha–diversity using Jackknife estimator.

Tabla 2. Estadísticas de captura. Abreviaturas: Obs. ind. Número de individuos observados (en negrita, número promedio de individuos observados en cada biotopo); Obs. spec. Número de especies observadas (en negrita, número promedio de especies observadas en cada biotopo); Est. spec. Número estimado de especies (promedio de cuatro estimaciones usando los estimadores Chao 1, Chao 1bc, ACE, y ACE–1; rango entre paréntesis); Compl. Porcentaje de compleción del inventario de las especies; H. Índice de Shannon de diversidad alfa usando el estimador Jackknife.

Biotope Site–number	Obs. ind.	Total obs. spec	Est. spec.	Compl. (%)	H
Salt meadow	**4,467**	**64**	**95 (98–106)**	**67**	**1.44**
1	2,180	19	37 (31–41)	51	0.82
2	522	38	60 (56–65)	63	2.05
14	1,169	29	35 (34–36)	83	1.42
15	596	5	6 (5–7)	83	0.48
Dune	**400**	**62**	**98 (94–106)**	**63**	**3.08**
4	201	29	36 (35–39)	81	2.57
5	85	17	51 (39–62)	33	1.72
6	38	19	31 (28–34)	61	3.04
7	10	6	14 (9–18)	43	2.03
9	42	16	28 (23–34)	57	2.49
17	24	10	18 (15–19)	56	2.11
Dune meadow	**1,040**	**66**	**92 (89–98)**	**72**	**3.06**
8	115	32	54 (47–63)	59	3.01
10	183	30	36 (34–39)	83	2.93
16	742	41	70 (64–75)	59	2.75
Meadow	**690**	**49**	**70 (63–81)**	**70**	**2.28**
3	581	37	52 (46–60)	71	2.14
12	109	17	27 (24–30)	63	2.01
Forest	**1,803**	**54**	**85 (75–95)**	**64**	**2.32**
11	694	33	42 (40–44)	79	2.24
13	1,109	36	51 (47–56)	71	2.11

that occurred with a relative abundance of < 3.2% per site were regarded as rare species and were not taken into consideration for ordination analysis. Finally, 52 spider species were subjected to the RDA. The statistical validity of the ordination was tested using a Monte Carlo permutation test (null model: 9,999 unrestricted permutations). This was carried out for every canonical axis and every environmental variable.

Results

Faunal composition and species richness

During the investigation period 8,400 mature spiders from 202 species and morphospecies and 25 families were captured. Of these, 52 species with a total of 7,849 individuals were considered in the statistical analyses (appendix 1). As shown in table

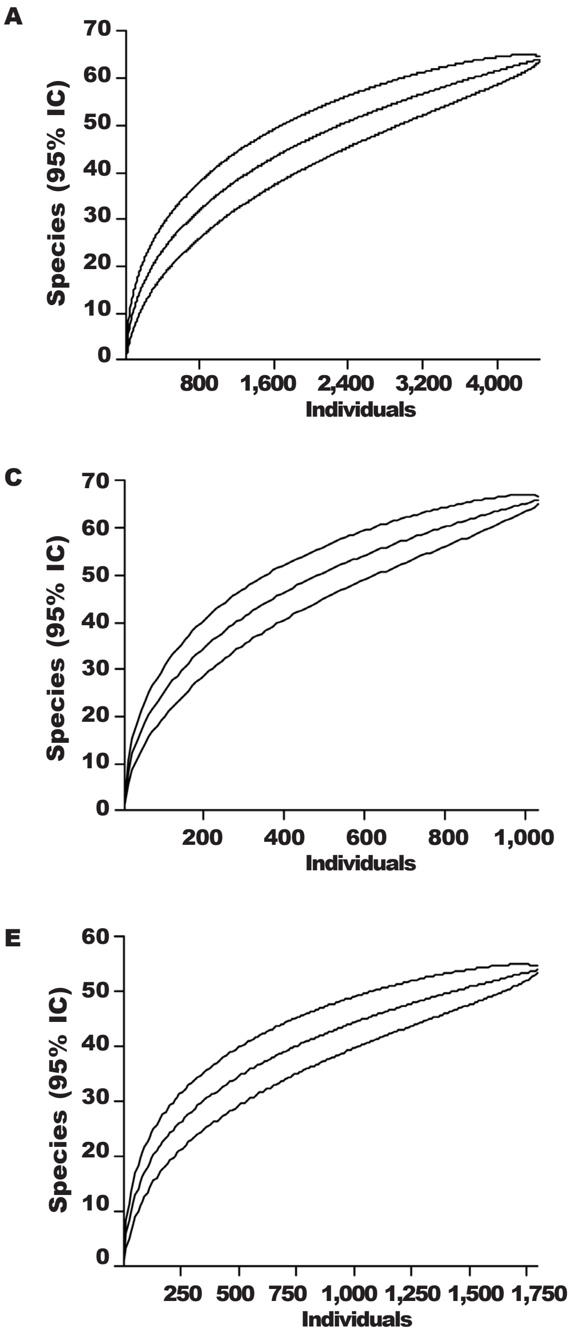

Fig. 2. Species accumulation curves for investigated habitat types: A. Salt meadows; B. Dunes; C. Dune meadows; D. Meadows; E. Forests.

Fig. 2. Curvas acumuladas de especies para los hábitats investigados: A. Praderas salinas; B. Dunas; C. Praderas en dunas; D. Praderas; E. Bosques.

2 most individuals were captured in salt meadows (4,467 individuals) and forests (1,803) while very low numbers of specimens were found at dune sites (400). The highest diversity values (Shannon–Index H) were present in dune meadows and dunes (3.06 and 3.08, respectively), while comparatively low values were calculated for salt meadows (1.44). At all sites the species inventory was incomplete, since the observed total species richness was lower than the estimates obtained by Chao 1, Chao 1bc, ACE, and ACE–1. Furthermore, the species accumulation curves indicated an asymptotic tendency (fig. 2).

Table 3. Family composition in coastal habitats of the Nestos Delta: N. Total number of species; %. Percentage of species.

Tabla 3. Composición de familias en hábitats costeros del delta del Nestos: N. Número total de especies; %. Porcentaje de especies.

	Salt meadow		Dune		Dunes meadow		Meadow		Forest		All	
Family	N	%	N	%	N	%	N	%	N	%.	N	%
Linyphiidae	16	22	19	26	22	29	9	15	35	51	64	32
Gnaphosidae	14	19	12	16	13	17	13	22	3	4	29	14
Salticidae	6	8	11	15	7	9	1	2	2	3	22	11
Lycosidae	12	17	10	14	14	19	8	13	7	10	19	9
Thomisidae	5	7	10	14	5	7	6	10	4	6	18	9
Theridiidae	2	3	1	1	2	3	5	8	3	4	7	3

The Linyphiidae and Gnaphosidae were the dominant families (over 30 and 15% of species, respectively), followed by the Salticidae, Lycosidae and Thomisidae (about 10% each) (table 3). Findings were similar in nearly all site inventories, with a clear domination of linyphiid species. Mainly forested sites comprised a high proportion of the linyphiid species (> 50% of the species inventory). However, gnaphosid species made up the largest part of the meadow inventory.

Community structure

Four environmental variables were included in the RDA ordination model. The first axis (eigenvalue = 0.51) was strongly correlated with soil salinity (table 4). The second axis (eigenvalue = 0.11) correlated with the two factors shade and soil humidity. Both variables were weakly inter–correlated (Spearman's rank correlation analyses: R = 0.35).

The ordination plot showed a clear separation into four species groups (fig. 3). The variation in the spider assemblage structure was determined by two gradients. The first axis represents a soil salinity that increased from left to right. The second axis reflects a humidity gradient, or vegetation coverage gradient, respectively, with dry, bare habitats in the lower part and more humid and vegetated sites on the upper part. A further environmental factor, shade, determined the community structure along the second axis. Together both axes explain 61.7% of the variability of the spider species data.

The first group, A, comprising four species (*Arctosa leopardus*, *Devade* spec., *Oedothorax apicatus*, *Pardosa luctinosa*), was clearly separated from all other groups and correlated with high soil and surface salinity (inter–set correlation IC: 0.87). Apart from *O. apicatus* all species were exclusive for this group (appendix I). Group B, C and D were arranged along the second gradient. In general, the species of group B occurred at dry sites with a sparse herbal layer. Within this assemblage, it was possible to characterise three sub–groups. Three exclusive species *Berlandina plumalis*, *Styloctetor romanus* and *Thanatus vulgaris* as well as the typical component *Zodarion cyprium* at the left bottom of the graph seemed to be more or less restricted to dry sites with a large proportion of bare soil or sand. The second sub–group, comprising 14 species (*Aelurillus guecki*, *Arctosa perita*, *Arctosa cinerea*, *Asianellus festivus*, *Chalcoscirtus helverseni*, *Haplodrassus umbratilis*, *Malthonica nemorosa*, *Nomisia ripariensis*, *Palliduphantes byzantinus*, *Pellenes nigrociliatus*, *Philodromus fallax*, *Pisaura mirabilis*, *Scytodes thoracica*, *Steatoda albomaculata*), showed some intergrading with the third sub–group (*Alopecosa accentuata*, *Alopecosa albofasciata*, *Micaria albovittata*, *Ozyptila sanctuaria*, *Pardosa hortensis*, *Pardosa proxima*, *Phlegra fasciata*, *Trichoncus hackmanni*, *Xysticus kochi*), which occurred on dry but more vegetated sites. The assemblage of B3 had hardly any exclusive species, apart from *P. fasciata* and *T. hackmanni* (appendix 1):

Group C was formed of six species, including three exclusive components (*Arctosa tbilisiensis*, *Brachythele denieri*, *Pelecopsis krausi*) which were positioned in the middle section of the gradient, indicating a preference for more vegetated, semi–humid habitats. All species in group D correlated with high soil humidity (IC: 0.72) and shading (IC: 0.81). *Diplocephalus picinus*, *Diplostyla concolor*, *Pirata latitans* and *Silometopus reussi* were exclusive components.

Discussion

Salt meadows show ecological conditions (high salinity in soil and water) that cause environmental stress for many species (Schaefer, 1970). As a consequence, only a few habitat specialists occur in these habitats in high numbers (*cf.* Thienemann, 1918). This generally leads to low diversity

Table 4. Summary of RDA for 52 spider species (7,849 specimens) and four environmental variables (*F*–values of Monte Carlo test, ***P < 0.001, *P < 0.05). Correlation of soil humidity and shade = 0.35 (Spearman's rank correlation).

Tabla 4. Resumen del análisis de redundancia para 52 especies de arañas (7.849 especímenes) y cuatro variables ambientales (valores F *del test de Monte Carlo: ***P < 0,001; *P < 0,05). Correlación entre la humedad del suelo y el grado de sombra = 0,35 (correlación de rangos de Spearman).*

Environmental axis	1	2	3	4	*F*
Eigenvalue	0.51	0.11	0.04	0.01	
Species–environment correlations	0.88	0.95	0.83	0.91	
Variance explained (%)					
species data	50.50	61.70	65.90	67.00	
species–environment relation	74.90	91.60	97.80	99.40	
Linear correlation with					
soil salinity	**0.99**	0.03	0.03	0.03	15.24***
soil humidity	0.60	**0.76**	0.19	0.14	4.97*
shade	–0.26	**0.85**	–0.38	–0.22	2.11
coverage bare ground	–0.20	–0.47	–0.50	0.24	0.91

values in these habitats (Schultz & Finch, 1996; Irmler et al., 2002; Finch et al., 2007). In contrast, dunes are dynamic habitats. They are regularly subjected to the modifying forces of wind and water. Topographically, dunes are very diverse and they always carry mosaics of vegetation types in different stages of succession (Gajdos & Toft, 2002). Typical coastal dune profiles as described by Duffey (1968) and Ranwell (1972) are usually modified by local conditions. In the Nestos Delta, white dunes are small and often fragmented by grey dune vegetation, dune meadows, and dune slacks that form a diverse mosaic of different, small sized habitats (Kirchner, 2005). Due to migrating spiders at these sites, edge effects may cause higher diversity values (Desender, 1996). As opposed to this, the comparatively lower diversity values in the forested sites are remarkable. The structural complexity in forests offers a great variety of microclimates and plant architecture, larger variety of resources and a wider range of shelters from predators and unfavourable environmental changes. Thus, floodplain forests provide greater habitat diversity that normally yields high species diversity (Hart & Horwitz, 1991). Maybe in this case the pitfall method is not the most appropriate since spiders dwelling in trees or high vegetation strata cannot be caught by such traps. In general, pitfall trapping favours ground–dwelling spiders (Merrett & Snazell, 1983). A further explanation for the unexpected, relatively small species diversity in forests might be the flooding to which the floodplain forests of the study sites are subjected (Hildebrandt, 1995; Beyer & Grube, 1997).

It is nearly impossible to compile complete inventories within a short sampling period (in the present study merely three months) (McArdle & Gaston, 1993; Scharff et al., 2003) and consequently there are undiscovered species in almost every species inventory (Coddington et al., 1996). Cardoso et al. (2007, 2008) stated that May and June are the most favourable months to collect spiders in Mediterranean areas. Chatzaki et al. (1998) also reported the highest spider catches in spring months when they investigated ground spider fauna in a mountain habitat in Crete. Nevertheless, it might be essential to extend the sampling season at least throughout the summer and autumn (McArdle & Gaston, 1993). As Linyphiidae play an important role in species composition in the present study, it is important to consider the winter season for sampling, too. Many species of Linyphiidae, especially males, are active only during winter (Chatzaki et al., 1998, 2005a; Bosmans, pers. comm.).

In previous studies concerning spiders in dry Mediterranean habitats, Gnaphosidae have proven to be the dominant family captured by pitfalls (Chatzaki et al., 1998; Cardoso et al., 2007), a feature stated to be common in all Mediterranean biomes. This contrasts with the family composition in habitats of the Nestos Delta. There, Linyphiidae dominated nearly all communities, especially in forested habitats, a composition usually found at higher latitudes in temperate climates. The location and the habitat type of the present study could perhaps account for this (cf. Jerrentrup et al., 1989). Northeastern Greece is located on the border zone of three climatic regions, apparently dominated by the central European temperate climate.

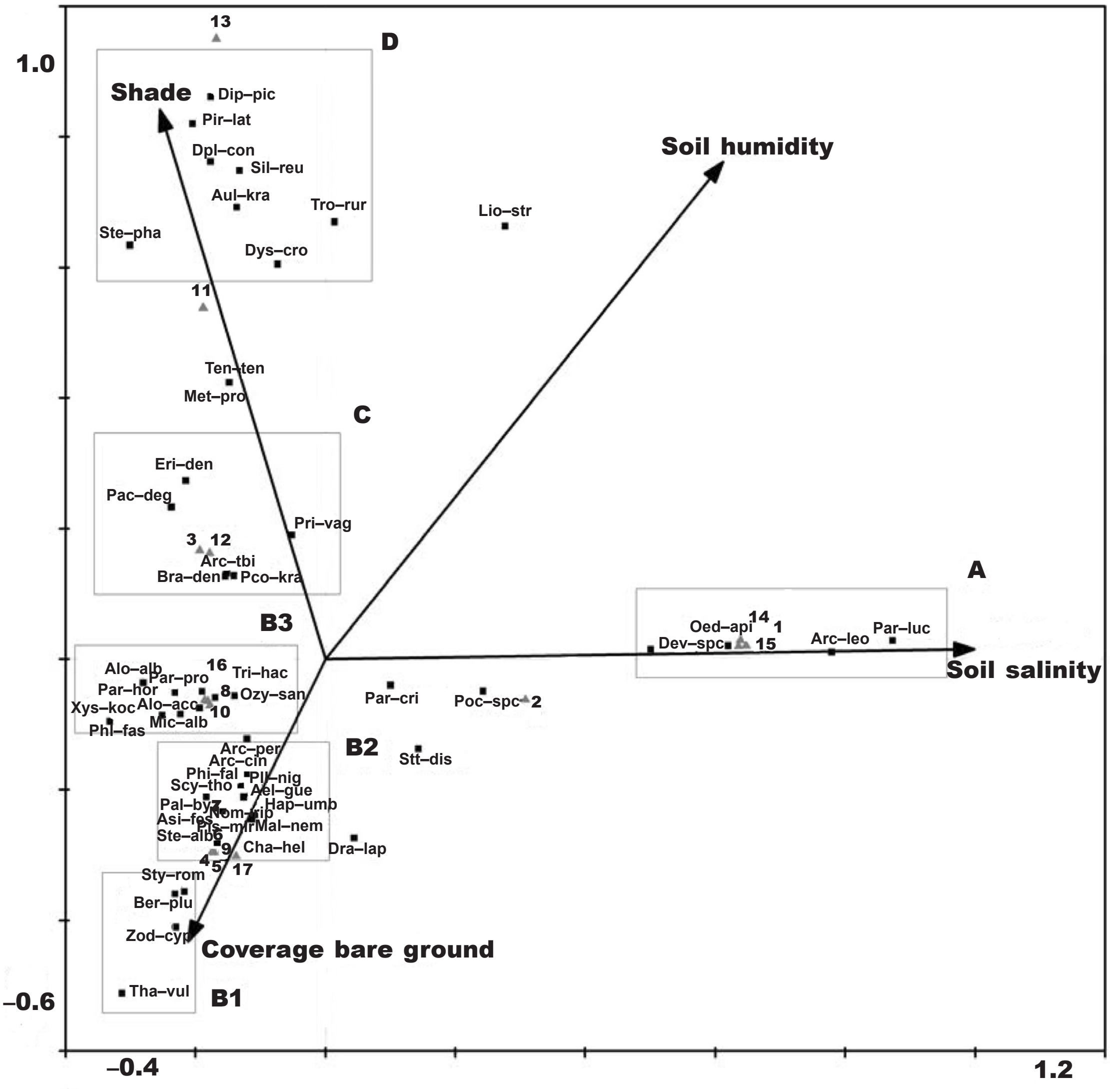

Fig. 3. Redundancy analysis of spider communities (A–D) and environmental data from coastal habitats (1–17, see table 2) of the Nestos Delta. Specific name abbreviated for each group: A (Arc–leo. *Arctosa leopardus*; Dev–spc. *Devade* spec.; Oed–api. *Oedothorax apicatus*; Par–luc. *Pardosa luctinosa*). B1 (Ber–plu. *Berlandina plumalis*; Sty–rom. *Styloctetor romanus*; Tha–vul. *Thanatus vulgaris*; Zod–cyp. *Zodarion cyprium*). B2 (Ael–gue. *Aelurillus guecki*; Arc–per. *Arctosa perita*; Arc–cin. *Arctosa cinerea*; Asi–fes. *Asianellus festivus*; Cha–hel. *Chalcoscirtus helverseni*; Hap–umb. *Haplodrassus umbratilis*; Mal–nem. *Malthonica nemorosa*; Nom–rip. *Nomisia ripariensis*; Pal–byz. *Palliduphantes byzantinus*; Pll–nig. *Pellenes nigrociliatus*; Phi–fal; *Philodromus fallax*; Pis–mir. *Pisaura mirabilis*; Scy–tho. *Scytodes thoracica*; Ste–alb. *Steatoda albomaculata*). B3 (Alo–acc. *Alopecosa accentuata*; Alo–alb. *Alopecosa albofasciata*; Mic–alb. *Micaria albovittata*; Ozy–san. *Ozyptila sanctuaria*; Par–hor. *Pardosa hortensis*; Par–pro. *Pardosa proxima*; Phl–fas. *Phlegra fasciata*; Tri–hac. *Trichoncus hackmanni*; Xys–koc. *Xysticus kochi*). C (Arc–tbi. *Arctosa tbilisiensis*; Bra–den. *Brachythele denieri*; Eri–den. *Erigone dentipalpis*; Pac–deg. *Pachygnatha degeeri*; Pco–kra. *Pelecopsis krausi*; Pri–vag. *Prinerigone vagans*). D (Aul–kra. *Aulonia kratochvili*; Dip–pic. *Diplocephalus picinus*; Dpl–con. *Diplostyla concolor*; Dys–cro. *Dysdera crocota*; Pir–lat. *Pirata latitans*; Sil–reu. *Silometopus reussi*; Ste–pha. *Steatoda phalerata*; Tro–rur. *Trochosa ruricola*). Further species: Dra–lap. *Drassodes lapidosus*; Lio–str. *Liocranoeca striata*; Met–pro. *Metopobactrus prominulus*; Par–cri. *Pardosa cribrata*; Poc–spc. *Pocadicnemis* spec.; Stt–dis. *Sitticus distinguendus*; Ten–ten. *Tenuiphantes tenuis*.

Fig. 3. Análisis de redundancia para las comunidades de arañas (A–D) y datos ambientales de los hábitats costeros (1–17, ver cuadro 2) del delta del Nestos. (Para las abreviaturas de los nombres específicos ver arriba.)

Within Mediterranean ecosystems, habitat zonation and ecology of spider assemblages have been poorly studied (Chatzaki et al., 1998). The present study is the first analysis of spider assemblages in coastal habitats in the east Mediterranean area. Comparisons concerning habitat preference and distribution of species mainly concern studies from Central European coasts. Therefore, as spiders in different regions select different habitats, further research along these lines is needed to validate present findings (Duffey, 2005).

Based on the position of the four different assemblages of species (including three sub–groups) it seems acceptable to characterise group A as typical of salt meadows, B of dunes, C of meadows and D of humid forests –in this case the floodplain forests of the Nestos river. Considering the subdivision of group B, sub–group B1 stands for white dunes and and B3 for grey dunes, while B2 comprises species of dune habitats in general.

Among other species, *Arctosa leopardus* and *Pardosa luctinosa* are exclusive for the salt meadow community. The latter is known to be an extremely halophilous species which is almost exclusive of habitats with high water and soil salinity (Tongiorgi, 1966; Buchar, 1968). Also, Deltshev (1997) and Popov et al. (2000) recorded few specimens of *Pardosa luctinosa* at dry sandy sites and floodplains of the Black Sea coast. According to Thaler et al. (2000) and Bonte et al. (2002) *Arctosa leopardus* is typical of moist meadows and seems to tolerate high salinity (Finch et al., 2007). Deltshev (1997) found this species in coastal grassy vegetation and detritus, in sandy sites with low vegetation, and in clay shores with low vegetation and stones. *Oedothorax apicatus* usually occurs in wet habitats (Heimer & Nentwig, 1991) and was found to be a typical component of dunes and salt meadows of the North Sea coast (Schultz & Finch, 1996). In Northern Europe the species is very frequent in *Ammophila arenaria*–communities (Almquist, 1973a, 1973b).

On white dunes of the Nestos Delta 11 species can be considered as unique but only three species show higher dominances: *Steatoda albomaculata* and *Styloctetor romanus* are mainly described as xerophilous spiders (Schultz & Finch, 1996; Maelfait et al., 2000; Bonte et al., 2002). According to Levy (1995) and Chatzaki et al. (2002), *Berlandina plumalis* prefers dry habitats, such as sand dunes and phrygana, but is also found in damp sites. For example, the species was found all over the island of Gavdos, in the far south of Crete. There it was the dominant ground spider species in many dry habitats but also in wetlands and salt marshes. Thus, it seems that this spider somehow favours riverbanks but may also accept high aridity (Chatzaki, pers. comm.). On the other hand, *Phlegra fasciata* and *Trichoncus hackmanni* can be regarded as typical components of dry habitat types (Roberts, 1998; Metzner, 1999), the latter apparently being restricted to coastal habitats (Almquist, 1973a; Maelfait et al., 2000).

For meadows, *Arctosa tbilisiensis*, *Brachythele denieri* and *Pelecopsis krausi* are characteristic components. *Arctosa tbilisiensis* has hitherto been found in moist meadows near rivers (Buchar, 1968; Thaler et al., 2000). Data concerning habitat preferences of *Pelecopsis krausi* are not available to date. However, based on this study, it is assumed that this species is to some extent related to dense vegetated sites. The same applies to *Brachythele denieri* but in this case some caution is warranted since only four specimens of this species were found on meadow sites.

The floodplain forest community is characterised by six species. Popov et al. (2000) stated *Diplocephalus picinus*, *Diplostyla concolor* and *Pirata latitans* to be typical for humid forests in landscapes of the Bulgarian Black Sea coast. As opposed to this, *Silometopus reussi* was found mainly in open and humid sites (Finch et al., 2007).

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Appendix 1. Representative values for all species that were included in the RDA. Classes for representation: ++++ R ≥ 90% (exclusive species); +++ 90% > R > 60% (typical species); ++ 60% ≥ R > 30%; + R ≤ 30%. Note that two singletons, *Malthonica nemorosa* and *Philodromus fallax*, were not considered for calculation and thus were not included in the table: A. Salt meadows; B1. Dunes; B3. Dune meadows; C. Meadows; D. Forests; N. Number of individuals.

Apéndice 1. Valores representativos para todas las especies incluidas en el análisis de redundancia. Clases para la representación: ++++ R ≥ 90% (especies exclusivas); +++ 90% > R > 60% (especies típicas); ++ 60% ≥ R > 30%; + R ≤ 30%. Nótese que dos hallazgos de un solo espécimen, Malthonica nemorosa *y* Philodromus fallax*, no fueron considerados en los cálculos ni incluidos en la tabla. (Para otras abreviaturas ver arriba.)*

	Group					
Species	A	B1	B3	C	D	N
Aelurillus guecki Metzner, 1999	.	++++	.	.	.	3
Alopecosa accentuata (Latreille, 1817)	.	+	++	+	.	11
Alopecosa albofasciata (Brullé, 1832)	.	+	+++	+	+	227
Arctosa cinerea (Fabricius, 1777)	.	++++	.	.	.	5
Arctosa leopardus (Sundevall, 1833)	++++	.	+	.	.	760
Arctosa perita (Latreille, 1799)	+	+	+++	.	.	87
Arctosa tbilisiensis Mcheidze, 1946	+	.	+	++++	.	88
Asianellus festivus (C. L. Koch, 1834)	.	++++	.	.	.	5
Aulonia kratochvili Dunin, Buchar & Absolon, 1986	+	.	+	+	++	1,091
Berlandina plumalis (O. P.–Cambridge, 1872)	.	++++	+	.	.	78
Brachythele denieri (Simon, 1916)	.	.	.	++++	.	4
Chalcoscirtus helverseni Metzner, 1999	.	++++	.	.	.	3
Devade spec.	++++	.	.	.	.	30
Diplocephalus picinus (Blackwall, 1841)	.	.	.	.	++++	303
Diplostyla concolor (Wider, 1834)	.	.	+	.	+++	49
Drassodes lapidosus (Walckenaer, 1802)	+	+++	+	.	.	11
Dysdera crocota C. L. Koch, 1838	+	+	.	+	++	13
Erigone dentipalpis (Wider, 1834)	+	+	++	.	++	11
Haplodrassus umbratilis (L. Koch, 1866)	.	++	.	++	.	2
Liocranoeca striata (Kulczyn'ski, 1882)	++	.	.	+	++	65
Metopobactrus prominulus (O. P.–Cambridge, 1872)	.	.	.	.	++++	26
Micaria albovittata (Lucas, 1846)	.	+	+++	+	.	10
Nomisia ripariensis (O. P.–Cambridge, 1872)	.	++++	.	.	.	2
Oedothorax apicatus (Blackwall, 1850)	+++	.	+	.	+	121
Ozyptila sanctuaria (O. P.–Cambridge, 1871)	.	+	+++	.	.	8
Pachygnatha degeeri Sundevall, 1830	.	.	+++	+	++	101
Palliduphantes byzantinus (Fage, 1931)	.	+	++	.	+	4
Pardosa cribrata Simon, 1876	++	.	+++	.	.	118
Pardosa hortensis (Thorell, 1872)	+	+	+++	+	+	78
Pardosa luctinosa Simon, 1876	++++	.	.	.	.	2,887
Pardosa proxima (C. L. Koch, 1847)	+	+	+++	+	.	129
Pelecopsis krausi Wunderlich, 1980	.	.	.	++++	.	34
Pellenes nigrociliatus (Simon, 1875)	.	++++	.	.	.	6

Appendix 1. (Cont.)

Species	Group A	B1	B3	C	D	N
Phlegra fasciata (Hahn, 1826)	.	.	++++	.	.	7
Pirata latitans (Blackwall, 1841)	.	.	.	.	++++	517
Pisaura mirabilis (Clerck, 1757)	+	+	++	+	.	17
Pocadicnemis spec.	++++	.	.	.	.	29
Prinerigone vagans (Audouin, 1826)	+	+	++	+	+	143
Scytodes thoracica (Latreille, 1802)	.	++++	.	.	.	2
Silometopus reussi (Thorell, 1871)	.	+	.	.	++++	66
Sitticus distinguendus (Simon, 1868)	++	+	+	.	.	9
Steatoda albomaculata (De Geer, 1778)	.	++++	.	.	.	26
Steatoda phalerata (Panzer, 1801)	.	.	+	+	++	18
Styloctetor romanus (O. P.–Cambridge, 1872)	.	++++	+	.	+	109
Tenuiphantes tenuis (Blackwall, 1852)	.	.	.	.	++++	24
Thanatus vulgaris Simon, 1870	.	++++	.	.	.	16
Trichoncus hackmanni Millidge, 1955	.	+	++++	.	.	18
Trochosa ruricola (De Geer, 1778)	++	+	+	+	++	377
Xysticus kochi Thorell, 1872	+	+	+++	+	+	91
Zodarion cyprium Kulczyn'ski, 1908	+	+++	+	.	.	8