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SPIDER ASSEMBLAGE STRUCTURE AND STABILITY IN A HETEROGENEOUS COASTAL DUNE SYSTEM (BELGIUM)

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ABSTRACT. An analysis of the spider assemblage structure and the presence of indicator species in the Flemish coastal dunes are presented. The analysis is based on data from more than 170 year-round pitfall sampling campaigns from the 1970s onwards. We were able to find indicator species for all identified habitats. The assemblages are determined by variation in vegetation structure (succession), atmospheric and soil humidity and the occurrence of both natural of anthropogenic disturbance. In the fragmented habitats (grasslands and grey dunes), a clear relationship was found between the mean habitat size and the stability of the assemblage composition. In moss dominated dunes and short grasslands total species numbers do not increase with patch size. Due to microhabitat variation and the possibility of attaining viable population sizes the total number of typical species is, however, higher in larger patches. In small patches, edge effects are more important and the number of observed species is enlarged by the intrusion of species from nearby habitats.

Keywords: Araneae, indicator species, habitat size, species-area relationship

Coastal dunes in Europe have been the subject of several spider community studies which reveal that the species composition is characterized by the presence of many rare and threatened species. Especially in northern (Almquist 1973) and western Europe (Duffey 1968; Bell et al. 1998), such investigations have been carried out. Carabid beetles (Desender et al. 1992; Desender 1996) and dolichopodid flies (Pollet & Grootaert, 1996) were also studied in the Belgian coastal dunes. Such studies are necessary for the assessment of the conservation value of these habitats. General assemblage descriptions together with more detailed knowledge of landscape-level ecological relationships such as multi-habitat use (Bonte et al. 2000a), colonization abilities (Bonte et al. 1998), population genetics (Desender et al. 1998) and population dynamics (Desender 1996; Baert & Desender 1993) should be taken into account when developing a nature conservation policy.

Since the beginning of the 20th century the total area of coastal dunes that have not been built upon in Belgium diminished from approximately 6000 ha to less than 3800 ha (Vermeersch 1986). The remaining dune areas are characterized by an overall increase of competitive plant species like Sea Buckthorn *Hippophae rhamnoides*, Burnet Rose *Rosa pimpinellifolia* and Wood Small Reed *Calamagrostis epigejos*, due to the retreat of local dune farmers after World War II and a decrease in the rabbit population due to myxomatosis and other diseases. This shrub and grass encroachment is possibly triggered by atmospheric N-deposition and enhanced by positive feedbacks in the nitrogen cycle (Veer 1997) and by the increase of nitrogen-fixing Sea Buckthorn. The soil nitrogen and mineral content will influence the trophic status of the vegetation, which is strongly related to the amount of organic components in the upper soil layer (Krabbenborg et al. 1983). Current habitat management is directed to the conservation and restoration of wet, herbaceous grasslands in dune valleys and stable meso-

Table 1.—Characterization and total number of pitfall-data from the sampled dune habitats.

Type	Indicative plant species	Number of pitfall-traps
Dune woodland	Trees: *Alnus glutinosa, Acer pseudoplatanus*	3
High, woody shrubs	Shrubs: *Crataegus monogyna, Hippophae rhamnoides*	13
Thick humid *Calamagrostis* grassland	Grass: *Calamagrostis epigejos*	20
Vital humid Sea-buckthorn-Liguster shrubs	Shrubs: *Hippophae rhamnoides, Salix repens, Ligustrum vulgare*	10
Wet eutrophic open dune valleys	Sedges and grasses: *Juncus subnodulosus, Carex riparia, Iris pseudacorus*	6
Thick dry *Arrhenaterium* grassland	Grasses: *Arrhenatherium elatius, Avenula pubescens*	13
Dry Sea buckthorn shrub (in grassland mosaics)	Shrub: *Hippophae rhamnoides*	6
Dwarf shrubs	Dwarf-shrub: *Rosa pimpinellifolia*	18
Wet mesotrophic open dune valleys	Sedges and grasses: *Juncus subnodulosus, Carex trinervis, C. flacca*	12
Short grazed mesophytic grasslands	Grasses and herbs: *Luzula campestris, Galium verum, Avenula pubescens, Koeleria albescens*	15
Wet oligotrophic dune valleys	Grasses and sedges: *Juncus articulatus, Carex trinervis*	10
Marram dunes	Grass: *Ammophila arenaria*	9
Moss dominated dry oligotrophic dunes (Grey dunes)	Mosses, annual herbs and grasses: *Tortula ruralis ruraliformis, Aira praecox, Erodium circutarium, Corynephorus canescens*	29
Bare sand dunes	Grass: *Festuca rubra arenaria*	9
Anthropogenic distributed sand dunes	Herb: *Cirsium arvense*	5

phytic grasslands through large-scale removal of shrub, followed by horse and cattle grazing.

In order to develop tools for future monitoring we: 1. investigate which parameters influence the variation in species composition and 2. determine indicator spider species for all of the dune habitats occurring along our coast; and since a crucial question in habitat restoration is the effect of patch area on the presence of typical species (stenotopic species) we also 3. investigate the species-area relationships for two highly fragmented habitat types.

METHODS

Data collection.—The total assemblage analysis is based on data from 178 pitfalls, which were operative during an entire year-cycle in all kinds of dune habitats of the Belgian coastal dunes from the 1970s onwards (Hublé 1975; Hublé 1976; Van Biervliet 1978; Hublé & Maelfait 1981; Baert & Desender 1993; Maelfait 1993; Bonte & Hendrickx 1997; Bonte et al. 1999; Baert et al. unpub. data). In each sampling station three to five traps were placed with a distance of 5–10 meter between each pitfall (the traps are glass jam jars with a diameter of 9.5 cm, filled with a 10% formaline solution). In total more than 65,000 adult spiders were identified, resulting in data on the occurrence of 214 species. Voucher specimens are deposited at the Royal Belgian Institute of Natural Sciences in Brussels. Of these, 159 species were represented by more than five individuals caught and can thus be considered resident species and not rare vagrants (cf. Maelfait & Baert 1988). The sampled vegetation types, the dominant plant species and the number of pitfall traps used are listed in Table 1.

Community structure and Indicator species.—The community-structure is indirectly determined via Detrended Correspondence Analysis (Hill 1979a) with the data from the separate pitfalls. Only the more abundant species were taken into account for the ordination analysis. This methodology reveals a multidimensional ordering of the samples (here traps) based on their species composition sim-

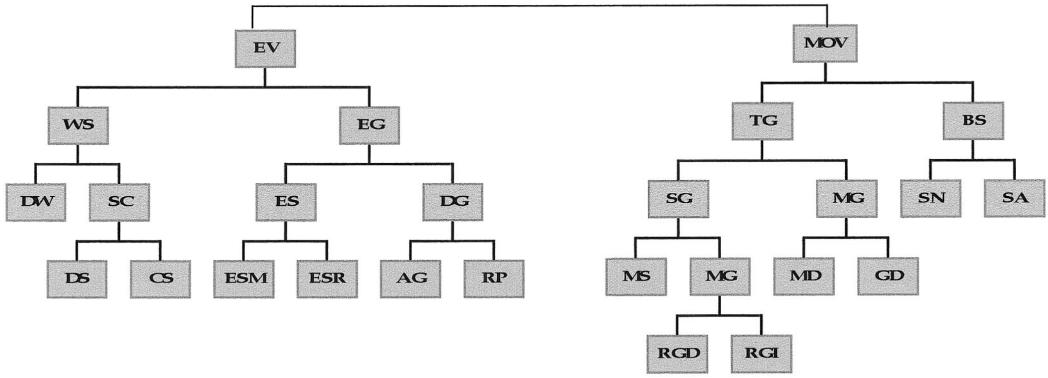

Figure 1.—Dichotomous TWINSPAN clustering of the spider composition based on the species presence/absence data. (For abbreviations of the assemblages see Table 2).

ilarity in which traps with a similar assemblage are ordered closely together, while those with a completely different species composition are positioned far apart. Since habitat characteristics were never studied in a standardized way during the several sampling campaigns, only the habitat type and the linked biotic and abiotic variables were indirectly used for the analysis of the parameters structuring the spider assemblage. Data on the stage of vegetation succession, depth of the groundwater level and different kinds of disturbance were taken from Provoost & Hoffmann (1996). Different kinds of disturbance result from natural eolic dynamics (sand overflowing) and anthropogenic factors due to different intensive nature management techniques like mowing of the vegetation (once or twice a year) and grazing (year-round) for the conservation of oligo- and mesotrophic pastures.

We used a TWINSPAN-clustering (Hill 1979b) for the determination of the different levels of assemblage similarity, based on the species composition from each pitfall trap. In this way a hierarchical ordering is obtained in which samples are dichotomously separated at different levels. The separation at the first level splits the samples in two different and large groups with common species. The samples from both groups are then again separated based on differences in their species composition. The total dataset is in this way dichotomously clustered at five levels in which the highest levels represent the most detailed sample separation.

Indicator species for all groups at the different levels from the TWINSPAN-classification were determined with the IndVal-method (Dufrêne & Legendre 1997). With this methodology, an indicator value is calculated for a species in each cluster group. The indicator value is calculated as: $\text{IndVal}_{ij} = A_{ij} * B_{ij} * 100$, where A_{ij} = N individuals_{ij} / N individuals_i and B_{ij} = N traps_{ij} / N sites_j. In this formula A_{ij} is a measure of group specificity, where N individuals_{ij} is the mean number of individuals of species *i* across traps of group *j* and N individuals_i is the sum of the mean numbers of individuals of species *i* over all groups at that level. B_{ij} is a measure of fidelity, where N traps_{ij} is the number of traps in group *j* where species *i* is present, while N sites_j is the total number of traps in that group. A_{ij} is maximum when species *i* is only present in group *j*, while B_{ij} is maximum when species *i* is present in all traps of the group *j*. A random reallocation procedure of traps among groups is used to test the significance of IndVal (500 permutations). This index (IndVal) is thus maximal when all individuals of a species are found in a single group of traps and when the species occurs in all traps of the group. As a consequence the maximal indicator value can be interpreted as a measure for habitat specificity.

Because pitfall data record (species specific) activities instead of absolute densities, we only analyzed our data by presence/absence in the ordination, clustering and IndVal calculation. In this way, bias to different climatic conditions between years are eliminated.

Assemblage stability and species-area relationships.—The mean Euclidean distance between the different axes-scores for pitfalls from the same assemblage, as derived from the multi-dimensional DCA-ordination, was used as a measure for the assemblage instability. Low Euclidean distances characterize traps that sampled analogue species composition, while traps with a completely different species composition have a high Euclidean distance (are ordered distantly). This distance measure is thus an indication for the species composition similarity between traps from the same assemblage. High similarities result thus in low distances and indicate stable species assemblages.

Due to shrub and grass encroachment, mesophytic short grasslands and humid valley habitats became fragmented and diminished in area. A decrease in the area can influence the assemblage structure: especially for small habitat patches, the assemblage stability is expected to decrease because of the extinction of species and the presence of species from adjacent habitats. Therefore, we related the habitat (in)stability to the average area of the different fragmented habitat types as derived from digitized vegetation maps (Provoost & Bonte, unpub. data). Differences in stability between assemblage groups were assessed with Analysis of Variance and related to habitat areas with Spearman rank correlations.

For moss dominated dunes and short mesophytic grasslands (for which we have exact data on the area of the sampled patch), we also determined the relation between the total number of species and the number of indicator species, trapped in three pitfalls, and the area of the sampled grassland patch. The species number-area relationship was analyzed by Pearson correlations between the total number of species and between the number of indicator species and the area of the sampled habitat patch, separately for moss dominated dunes and short dune grasslands.

RESULTS

Assemblage structure.—A total of 15 spider species assemblages were characterized by the TWINSPAN clustering. The first division clearly separates the eutrophic vegetations from the meso- and oligotrophic, short grazed habitats. The eutrophic assemblages are separated at the lowest level in dune woodlands, shrubs, marshland and dense grasslands. The mesotrophic and oligotrophic habitats are separated within the second group (Fig. 1) in short, rabbit-grazed grasslands, mown mesotrophic dune valleys, moss dominated dunes, dynamic Marram-grass (*Ammophila arenaria*) dominated dunes and bare dunes. Significant indicator species per cluster group (Monte Carlo permutations; 500 runs) and their indicator value are listed in Table 2.

The ordination-analysis clearly shows the assemblage structure along three relevant axes. The first axis (eigenvalue 0.689) separates the different samples along a vegetation structure-gradient, where dune woodlands are plotted on the left, bare sandy habitats on the right. The second axis (eigenvalue 0.587) separates the humid from the dry habitats: dune valley vegetations (dune slacks) and Marram dunes above and moss dominated dunes (grey dunes) below (Fig. 2). Interesting is the higher position along the second axis of Marram dunes near the seaside in comparison with those along the inner dune front. This stresses the importance of atmospheric humidity in addition to soil humidity as the second important assemblage structuring parameter. The third relevant axis (eigenvalue 0.383; Fig. 2) is associated with natural (wind in Marram dunes, inundations in dune slacks) and anthropogenic dynamics (especially habitat management: mowing & grazing in short grazed pastures and dune slack meadows); all these disturbed habitats which are indeed ordered at the lower part of the ordination axis.

Stability of assemblages from oligo- and mesotrophic habitats and species-area relationships.—The assemblage stability differs between the different distinguished spider assemblages from oligo- and mesotrophic habitats (Bare sand (BS), mown eutrophic valleys (ESM), Moss dominated dunes (GD), Marram dunes (MD), Mesophytic dune slacks (MS), Dry mestrophic grasslands (RGD) and inundating mesotrophic grasslands (RGI) (one way-ANOVA, $F_{1,6} = 11.403$, $P < 0.001$). The stability is significantly different between the assemblage groups BS, ESM, GD, MD and the assemblages of MS, RGI, RGD, but does not differ within the two groups. Correlation with average patch size is nearly significant (Spearman $R = -0.750$, $P = 0.052$) and indicates that assemblages from small habitats tend to be more diverse in species composition.

The species-area relationship of the total

Table 2.—Indicator species (Monte Carlo permutations, $P < 0.01$) and indicator value (IndVal) at the different cluster levels (See Fig. 1), with description of the assemblage habitat characteristics.

Habitat (abbreviation) and habitat characteristics	Indicator species	IndVal
Eutrophic vegetation (EV) Higher, litter rich, dense	*Alopecosa pulverulenta* (Clerck, 1757) (Lycosidae)	74.97
Dry or humid	*Bathyphantes parvulus* (Westring, 1851) (Linyphiidae)	51.04
	Centromerus prudens (O.P.-Cambridge, 1873) (Linyphiidae)	60.06
	Centromerus sylvaticus (Blackwall, 1841) Linyphiidae)	87.08
	Clubiona comta C.L. Koch, 1839 (Clubionidae)	23.60
	Clubiona lutescens Westring, 1851 (Clubionidae)	25.71
	Episinus angulatus (Blackwall, 1836) (Theridiidae)	16.85
	Ero furcata (Villers, 1789) (Mimetidae)	47.03
	Euryopus flavomaculata (C.L. Koch, 1836) (Theridiidae)	49.49
	Floronia bucculenta (Clerck, 1757) (Linyphiidae)	27.77
	Gonatium rubens (Blackwall, 1833) (Linyphiidae)	69.57
	Linyphia triangularis (Clerck, 1757) (Linyphiidae)	12.94
	Maso sundevalli (Westring, 1851) (Linyphiidae)	43.76
	Meioneta saxatilis (Blackwall, 1844) (Linyphiidae)	46.09
	Neriene clathrata (Sundevall, 1830) (Linyphiidae)	25.97
	Ozyptila simplex (O.P.-Cambridge, 1862) (Thomisidae)	71.09
	Palliduphantes ericaeus (Blackwall, 1853) (Linyphiidae)	19.97
	Palliduphantes pallidus (O.P.-Cambridge, 1871 (Linyphiidae)	69.56
	Pirata hygrophillus Thorell, 1872 (Lycosidae)	49.16
	Pocadicnemis juncea Locket & Millidge, 1953 (Linyphiidae)	59.63
	Robertus lividus (Blackwall, 1836) (Theridiidae)	74.39
	Theridion bimaculatum (Linnaeus, 1758) (Theridiidae)	33.35
	Trochosa terricola Thorell, 1856 (Lycosidae)	88.01
	Walckenaeria acuminata Blackwall, 1833 (Linyphiidae)	47.11
	Walckenaeria atrotibialis (O.P.-Cambridge, 1878) (Linyphiidae)	93.17
	Zora spinimana (Sundevall, 1833) (Zoridae)	66.94
Meso-oligotrophic vegetation (MOV)	*Arctosa perita* (Latreille, 1799) (Lycosidae)	63.24
Short, sparse vegetation Rabbit grazed	*Haplodrassus dalmatensis* (L. Koch, 1866) (Gnaphosidae)	73.01
Dry or humid Sandy patches	*Meioneta rurestris* (C.L. Koch, 1836) (Linyphiidae)	34.49

Table 2.—Continued.

Habitat (abbreviation) and habitat characteristics	Indicator species	IndVal
	Parapelecopsis nemoralis (O.P.-Cambridge, 1884) (Linyphiidae)	53.85
	Styloctetor romanus (O.P.-Cambridge, 1872) (Linyphiidae)	37.22
	Tegenaria agrestis (Walckenaer, 1802) (Agelenidae)	24.72
	Xysticus sabulosus (Hahn, 1832) (Thomisidae)	40.28
Woodland and woody shrubs (WS) High vegetation and litter rich	*Tapinopa longidens* (Wider, 1834) (Linyphiidae)	19.35
Presence of trees (*Crataegus monogyna*)	*Walckenaeria nudipalpis* (Westring, 1851) (Linyphiidae)	44.13
Dense grasslands (EG) Dense and tall grass layer	*Clubiona diversa* O.P.-Cambridge, 1862 (Clubionidae)	8.09
Litter-rich Dry or humid	*Cnephalocotes obscurus* (Blackwall, 1834) (Linyphiidae)	35.07
	Enoplognatha thoracica (Hahn, 1833) (Theridiidae)	30.89
	Ero cambridgei Kulczynski, 1911 (Minetidae)	11.53
	Pachygnatha degeeri Sundevall, 1830 (Tetragnathidae)	71.92
	Pisaura mirabilis (Clerck, 1757) (Pisauridae)	18.92
	Walckenanaeria antica (Wider, 1834) (Linyphiidae)	41.61
Thermophilious grasslands (TG) Short, no or scarce litter	*Agroeca lusatica* (L. Koch, 1875) (Liocranidae)	37.57
Dry or humid Dynamics: wind, grazing or mowing	*Alopecosa barbipes* (Sundevall, 1833) (Lycosidae)	34.59
	Bolyphantes luteolus (Blackwall, 1833) (Linyphiidae)	16.00
	Centromerita concinna (Thorell, 1875) (Linyphiidae)	62.25
	Walckenaeria monoceros (Wider, 1834) (Linyphiidae)	32.82
	Xysticus kochi Thorell 1872 (Thomisidae)	64.91
Bare sand (BS) No vegetation	*Erigone longipalpis* (Sundevall, 1830) (Linyphiidae)	57.14
Dune woodland (DW) Dominance of trees (*Alnus glutinosa*)	*Ceratinella scabrosa* (O.P.-Cambridge, 1863) (Linyphiidae)	43.48
Litter-rich Humid	*Diplocephalus picinus* (Blackwall, 1841) (Linyphiidae)	82.86
	Enoplognatha ovata (Clerck, 1757) (Theridiidae)	14.29
	Macrargus rufus (Wider, 1830) (Linyphiidae)	19.05
	Pardosa saltans Töpfer-Hofmann, 2000 (Lycosidae)	66.67
	Tapinocyba insecta (L. Koch, 1869) (Linyphiidae)	56.60
	Tenuiphantes zimmermanni (Betkau, 1890) (Linyphiidae)	85.19
Woody shrubs (SC) Dominance of Sea Buckthorn (*Hippophae rhamnoides*)	*Monocephalus fuscipes* (Blackwall, 1836) (Linyphiidae)	88.92
and *Calamagrostis epigejos* Presence of trees (*Crataegus monogyna*)	*Saaristoa abnormis* (Blackwall, 1841) (Linyphiidae)	44.44

Table 2.—Continued.

Habitat (abbreviation) and habitat characteristics	Indicator species	IndVal
Eutrophic wet dune valleys (ES) Humid, Winter inundations High, dense vegetation Dominance of *Carex riparia*	*Centromerita bicolor* (Blackwall, 1833) (Linyphiidae)	42.17
	Ceratinella brevipes (Westring, 1851) (Linyphiidae)	29.78
	Clubiona reclusa O.P.-Cambridge, 1863 (Clubionidae)	34.38
	Dicymbium nigrum (Blackwall, 1834) (Linyphiidae)	63.62
	Gnathonarium dentatum (Wider, 1834) (Linyphiidae)	15.63
	Pachygnatha clercki Sundevall, 1823 (Tetragnathidae)	50.86
	Pardosa palustris (Linnaeus, 1758) (Lycosidae)	83.92
	Pardosa pullata (Clerck, 1757) (Lycosidae)	71.79
	Pirata latitans (Blackwall, 1849) (Lycosidae)	85.49
	Pirata piraticus (Clerck, 1757) (Lycosidae)	42.19
	Tiso vagans (Blackwall, 1834) (Linyphiidae)	71.12
	Troxochrus cirrifrons (O.P.-Cambridge, 1871) (Linyphiidae)	30.95
	Troxochrus scabrosa (Westring, 1851) (Linyphiidae)	34.57
Mesotrophic grasslands (SG) Dry or humid (winter indundations)	*Pardosa monticola* (Clerck, 1757) (Lycosidae)	53.43
Marram and moss dominated dunes (MG) Sandy, scarce vegetation	*Agroeca cuprea* Menge, 1873 (Liocranidae)	66.98
Mainly mosses and lichens *Ammophila arenaria*-tussocks	*Drassodes cupreus* (Blackwall, 1834) (Gnaphosidae)	50.05
	Dysdera crocata C.L. Koch, 1838 (Dysderidae)	17.81
	Metopobactrus prominulus (O.P.-Cambridge, 1872) (Linyphiidae)	37.83
	Poeciloneta variegata (Blackwall, 1841) (Linyphiidae)	15.79
	Sitticus saltator (O.P.-Cambridge, 1868) (Salticidae)	32.50
	Thanatus striatus C.L. Koch, 1845 (Thomisidae)	39.97
Antropogenic disturbed sandy soils (SA) Bare sand, human activities	*Pardosa proxima* (C.L. Koch, 1847) (Lycosidae)	57.14
Dense shrubs (DS) Dominance of *Hippophae rhamnoides* and *Ligustrum vulgare*	*Agyneta subtilis* (O.P.-Cambridge, 1847) (Linyphiidae)	29.70
	Gongylidium rufipes (Linnaeus, 1758) (Linyphiidae)	61.78
	Microneta varia (Blackwall, 1841) (Linyphiidae)	24.48
	Ozyptila praticola (C.L. Koch, 1837) (Thomisidae)	31.43
	Pholcomma gibbum (Westring, 1851) (Theridiidae)	11.54
	Walckenaeria cucculata (C.L. Koch, 1836) (Linyphiidae)	43.50
Degradating Shrub (CS) Shrub with open patches, colonized by *Calamagrostis epigejos*	*Agyneta decora* (O.P.-Cambridge, 1871) (Linyphiidae)	10.77

Table 2.—Continued.

Habitat (abbreviation) and habitat characteristics	Indicator species	IndVal
Humid	*Ceratinella brevis* (Wider, 1834) (Linyphiidae)	22.00
	Kaestneria pullata (O.P.-Cambridge, 1863) (Linyphiidae)	41.95
Wet rough litter rich vegetation (ESR) Rough, eutrophic vegetation	*Clubiona phragmites* C.L. Koch, 1843 (Clubionidae)	35.71
Inundations, no management	*Xysticus ulmi* (Hahn, 1831) (Thomisidae)	16.67
Dry dense grasslands-shrub mosaics (AG) Mosaics of low shrubs and *Avenula*-grassland	*Agyneta conigera* (O.P.-Cambridge, 1863) (Linyphiidae)	11.48
Dry, no management	*Hahnia nava* (Blackwall, 1841) (Hahniidae)	31.79
	Metellina mengei (Blackwall, 1870) (Tetragnathidae	14.29
	Maso gallicus Simon, 1894 (Linyphiidae)	20.21
	Philodromus cespitum (Walckenaer, 1802)	17.54
High dwarf shrubs (RP) Dominance of *Rosa pimpinellifolia* and *Arrhenaterium elatius*	*Alopecosa cuneata* (Clerck, 1757) (Lycosidae)	28.18
High grass layer	*Heliophanus flavipes* (Hahn, 1832) (Salticidae)	26.67
Presence of litter	*Xysticus erraticus* (Blackwall, 1834) (Thomisidae)	36.42
	Trachyzelotes pedestris (C.L. Koch, 1837) (Gnaphosidae)	27.78
Mesotrophic dune valleys (MS) Dominance of *Juncus subnodulosus*	*Arctosa leopardus* (Sundevall, 1833) (Lycosidae)	33.79
Yearly mowed Winter inundations	*Clubiona trivialis* C.L. Koch, 1843 (Clubionidae)	36.11
	Collinsia innerans (O.P.-Cambridge, 1855) (Linyphiidae)	20.00
	Erigone arctica (White, 1852) (Linyphiidae)	65.51
	Erigone promiscua (O.P.-Cambridge, 1873) (Linyphiidae)	74.74
	Prinerigone vagans (Audouin, 1826) (Linyphiidae)	56.45
	Gongylidiellum vivum (O.P.-Cambridge, 1975) (Linyphiidae)	39.46
	Oedothorax apicatus (Blackwall, 1850) (Linyphiidae)	41.59
	Oedothorax fuscus (Blackwall, 1834) (Linyphiidae)	74.22
	Oedothorax retusus (Westring, 1851) (Linyphiidae)	58.23
Short Mesoptrophic grasslands (RG) Wet (inundating) or dry, rabbit grazed	*Thyphochrestus digitatus* (O.P.-Cambridge, 1872) (Linyphiidae)	42.21
Marram dunes (MD) Dominance of Marram grass (*Ammophila arenaria*)	*Clubiona frisia* Wunderlich & Schuett, 1995 (Clubionidae)	75.41
Strong wind dynamics, close to the sea Scarce vegetation	*Clubiona subtilis* L. Koch 1867 (Clubionidae)	31.07
	Micaria pulicaria (Sundevall, 1831) (Gnaphosidae)	55.56
	Porrhomma microphthalmum (O.P.-Cambridge, 1871) (Linyphiidae)	14.81
	Tibellus maritimus (Menge, 1875) (Thomisidae)	18.52
	Trochosa ruricola (De Geer, 1778) (Lycosidae)	28.70

Table 2.—Continued.

Habitat (abbreviation) and habitat characteristics	Indicator species	IndVal
Moss dominated dunes & Marram dunes near the inner dune front (GD)	*Alopecosa fabrilis* (Clerck, 1757) (Lycosidae)	20.85
Dominance of lichens and mosses	*Micaria dives* (Lucas, 1846) (Gnaphosidae)	18.97
Scarce Marram grass vegetation Near inner dune front	Walckenaeria stylifrons (O.P.-Cambridge, 1875) (Linyphiidae)	30.38
	Zelotes longipes (L. Koch, 1866) (Gnaphosidae)	66.70
Dry mesotropic grasslands (RGD) Rabbit grazed, short grass layer	*Pelecopsis parallella* (Wider, 1834) (Linyphiidae)	35.81
Dominance of *Luzula campestris*	*Trichopterna cito* (O.P.-Cambridge, 1872) (Linyphiidae)	45.98
Inundating mesotrophic grasslands (RGI) Inundating, short *Carex*-vegetation	*Cheiracanthium virescens* (Sundevall, 1833) (Clubionidae)	51.43
Presence of Creeping willow (*Salix repens*)	*Lepthothrix hardyi* (Blackwall, 1850) (Linyphiidae)	26.98
	Xerolycosa miniata (C.L. Koch, 1834) (Lycosidae)	64.55

number of species and the total number of specific (indicator) species as a function of the area of moss dominated dune and short dune grassland patches is illustrated in Fig. 3. The relationship between patch size and total number of species is not significant for either the moss dominated or the short dune grasslands (Fig. 4: Pearson correlation, $r < 0.20$; $P > 0.05$). The number of resident indicator species however is higher in large patches in both vegetation types (Fig. 4: Pearson correlation for moss dunes: $r = 0.87$, $P < 0.01$ and for dry mesoptrophic dune grasslands: $r = 0.93$, $P < 0.01$).

DISCUSSION

Our results indicate that almost all dune system habitat types are characterized by the presence of indicator species, dependent on the cluster level. Desender (1996) showed that typical dune carabid species have a strong year-to-year fluctuation in population size, but were never completely lacking from the samples. This variation could be explained by variation in climatological variables. We therefore used only absence/presence data, so true indicators that are always present (independent of their yearly abundance) are unambiguously identified. Besides year-to-year fluctuations, species assemblages can vary as a function of habitat conditions and landscape structure. Our analysis is based on an extensive data set from habitats of different size and from different landscape configurations, so the determined indicator species can be used as bio-indicators for future monitoring of the management of both open (dominance of grasslands, Marram dunes) and closed (shrub dominated) dune landscapes.

That fact that the variation in species assemblages can be explained by variation in the vegetation structure or succession stage is not surprising and has been documented several times in other studies of invertebrate assemblages (spiders: Duffey 1968; Almquist 1973; carabid beetles: Desender et al. 1992; Empidid and dolichopdid flies: Pollet & Grootaert 1996). Our study indicates the importance of atmospheric and soil humidity as a second important assemblage structuring component since wet vegetation types are clearly separated from dry ones, and Marram dunes near the seaside were separated from those of drier more inland dunes. The importance of atmospheric humidity is demonstrated by the presence of species from dune valleys (*Clubiona frisi*a and *C. subtilis*) in Marram dunes near the seaside, while they are completely absent from the same habitat near the inner dune front (1–2 km from the seaside), where atmospheric humidity is significantly lower (Provoost & Hoffmann 1996). The same phenomenon (defined as a double ecological occurrence) has also been documented by Duffey (1968) in British coastal dunes. A third

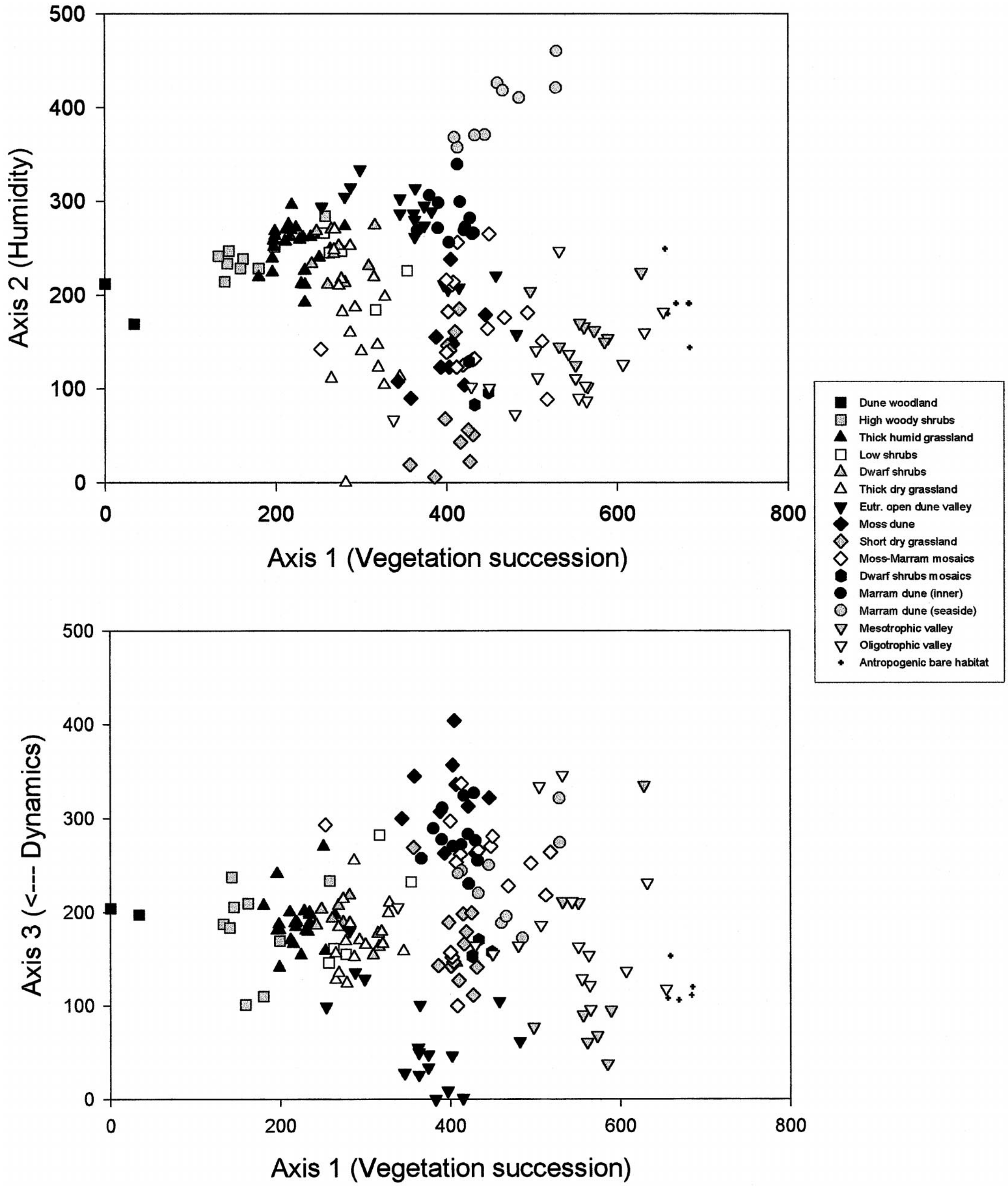

Figure 2.—DCA ordination of the pitfall data based on the species absence/presence data with indication of the habitat type. Above: ordination along the first and second axes; below: ordination along the first and third axes.

important abiotic source of variation is defined here as habitat disturbance. The third axis separates stable habitats without disturbance (woodland, shrubs, dwarf shrubs, rough permanent grasslands) from habitats with high natural (inundations: wet open dune slacks; eolic dynamics: Marram dunes, bare dunes) or anthropogenic disturbance (grazing and mowing management). These habitats are characterized by ruderal species like *Erigone atra*, *E. dentipalpis*, *E. arctica*, *Oedothorax fuscus*, *O. retusus*, *O. apicatus* and *Bathyphantes*

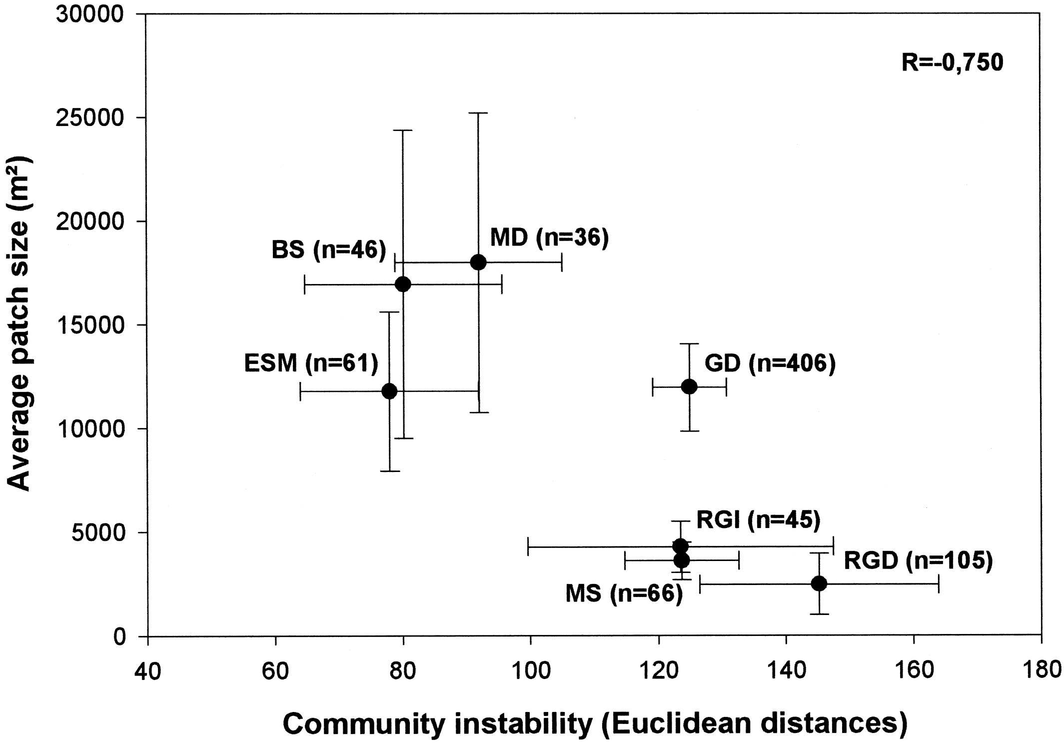

Figure 3.—Assemblage instability of fragmented grassland and dune valley habitats (mean Euclidean distances of DCA scores and 95% confidence intervals; n = number of distance measurements) in function to the average habitat patch size (means and 95% confidence intervals). For abbreviations see Table 2.

gracilis which are all short-living spiders with a rapid juvenile development and a well developed ballooning dispersal capacity.

This data analysis is based only on the presence of adult spiders. Earlier studies have indicated that species typical for open habitats like short grasslands and moss dominated dry dunes (grey dunes) need proximate patches of dense and litter-rich vegetation for their juvenile development and/or retreat during unfavorable periods in their mature life-stage (Bonte et al. 2000 a & b). Thus, habitat variation can strongly alter the presence of spider species bound to these dense vegetation patches for their juvenile development. Although not documented for spider populations, a minimal patch area can determine the presence of viable population size (Hanski 1999). In both cases, an increasing patch area should affect the spider assemblage directly because patch area influences the population size or indirectly because an increasing patch size enhances internal microhabitat variation. Our results on the assemblage level show that the stability in species composition of spider assemblages in patchy habitats depends on the mean patch area, indicating that differences in the spider assemblage vary more in small habitat patches than in larger ones. Edge effects in small habitats can alter the spider assemblage dramatically, because of the intrusion of species typical for other habitat types in the patch, due to the high circumference-surface ratio. This is certainly true for moss dominated dunes and short grasslands: total species numbers do not differ as a function of the patch size while the number of indicator species significantly increases with an increasing patch size. An explanation of this species-area relationship cannot be given without further research on both internal micohabitat heterogeneity and minimal population sizes. Variation in soil conditions can explain the aggregation of soil-dwelling arthropods like springtails *Collembola* (Bonte & Mertens, unpub. data). Since these are the main prey for typical juvenile wolf spiders and adult dwarf spiders, a larger patch size can alter the total

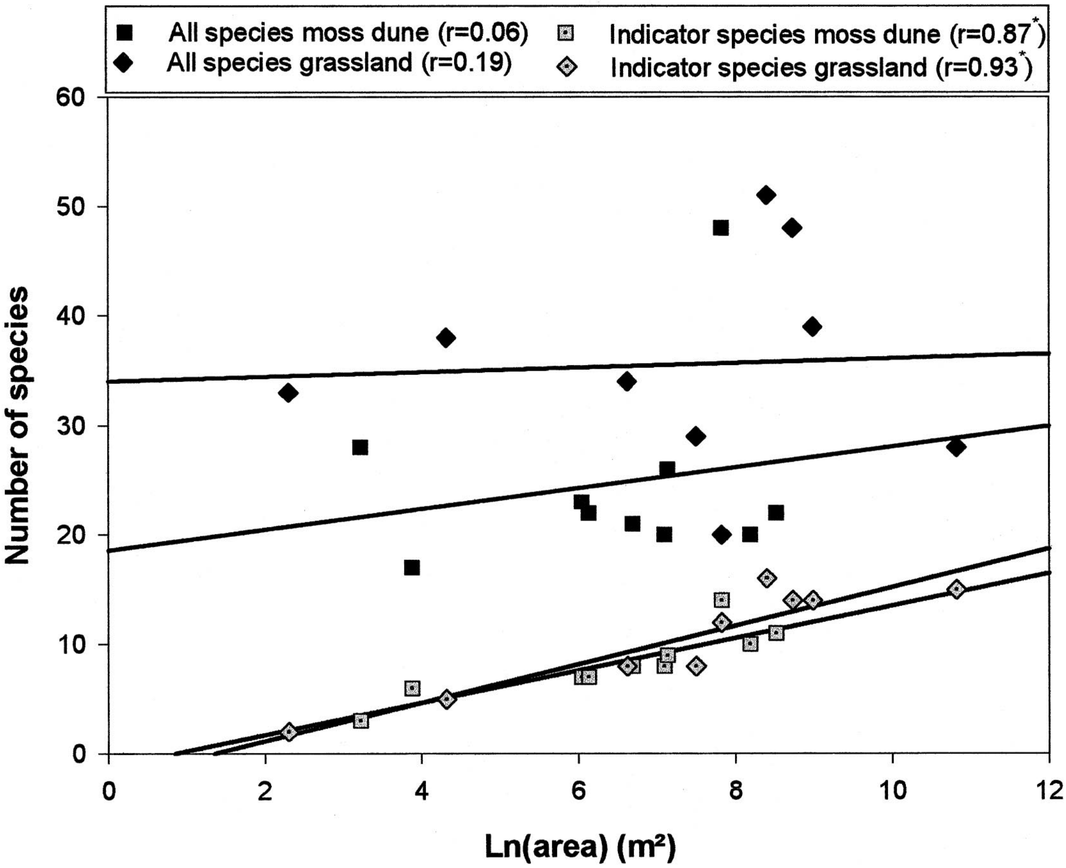

Figure 4.—Species-area relationship for all species and indicator species caught on moss dominated dry dunes and short grasslandsfrom different sizes (Spearman corelation, *: $P < 0.01$).

number of indicator species indirectly by the presence of higher internal microhabitat variation. For the study of minimal patch size and related population size, more detailed studies are needed on meta-population dynamics, based on the survey of a higher number of habitat patches.

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