

The importance of habitat productivity, stability and heterogeneity for spider species richness in coastal grey dunes along the North Sea and its implications for conservation

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Abstract. In this contribution, we report on patterns of spider species richness in large complexes of coastal grey dunes of northern France, Belgium and the Netherlands. Since grey dunes are considered a priority in Annex I of the EU Habitat Directive, conservation needs attention. Spider diversity is determined by the amount of nutrients available in grey dune patches. The richness of specific xerotherm species, however, is dependent only on the distance of the patches to the sea. Earlier investigation revealed that the richness of these species depends on the patch size. Since coastal dune management aims to focus on the conservation of dune-specific and xerotherm species, patch enlargement and grey dune restoration should receive priority attention and not internal grey dune management. Total spider richness and diversity is hence related to the functioning of the grey dune ecosystem. Eolic dynamics act as typical disturbance factors and are negatively related to species richness, as a result of the low but significant covariation with nutrient availability. The intermediate disturbance hypothesis is not applicable for spider diversity in grey dunes, possibly due to the narrow range of investigated environmental variation.

Introduction

Grey dune, known as 'Fixed coastal dunes with herbaceous vegetation' in the CORINE biotope classification (Natura 2000), is considered priority habitat in Annex I of the EU Habitat Directive (Hopkins and Radley 1998). This status implies that grey dunes deserve special conservation attention (Herrier and Killemaes 1998a,b).

Coastal 'grey dune' is most readily defined using plant communities. Vegetation includes Atlantic moss dominated dunes as well as dune grassland (with a distinct organic soil layer) belonging to the *Cladonio-Koelerietalia* in case of lime-rich grey dune and to the *Trifolio-Festucetalia ovinae* in case of decalcified grey dunes (Provoost et al. 2002). Ecologically it is merely the dry component of the 'stressed dune landscape', where ecological dynamics are situated in the field of tension between top down regulating stress factors and bottom up

(xerosere) organisation. The main differentiating processes are related to dune fixation, soil formation and vegetation development (Provoost and Hoffmann 1996; Aggenbach and Jalink 1999). Variation in nutrient availability and sand overblowing result in variation of dynamics and ecosystem stability, which are believed to be related to biodiversity (Pianka 1994; Schwartz et al. 2000). The relation between both is however unclear and certainly not causative in the inverse way.

Grey dune succession is initiated by fixation and driven by the complex of soil formation (humus accumulation) and vegetation development. Leaching and mobilisation of CaCO_3 complicate the picture and are important in nutrient dynamics. At present, rough grass and scrub encroachment greatly overrule these fine-scaled soil processes and cause substantial loss of regional biodiversity (Provoost et al. 2002). Along the western part of the Belgian coast, for example, the grey dune area decreased from 730 to 350 ha since the 1950s, mainly due to urbanisation and scrub encroachment. In addition, grey dunes are subject to internal degradation due to the grass encroachment mentioned above. Until now, this evolution was not accompanied by a drastic decline in the global number of grey dune plant species. However, there is an apparent qualitative shift toward a less specific flora, amongst others because of garden escapes of exotic species (Provoost and Van Landuyt 2001). Typical grey dune butterflies have become extinct or very rare (Maes and Van Dyck 2001) and 95% of the typical dune carabid beetles are included in the Flemish Red List (Desender et al. 1995).

Due to this encroachment, grey dunes are now heavily fragmented and patchily distributed within a matrix of dense dune vegetation (shrubs, dense grassland). For the Flemish coastal dunes, we already found that the total number of spider species is not dependent on patch size, but that the richness of xerotherm species declines in small grey dune patches. In contrast to other coastal dune habitats, grey dunes are characterised by a specific and endangered entomo- and arachnofauna (Bonte et al. 2002b).

This decline of at least regional biodiversity urges managers to take active nature management measures. Removal of scrub and woodland, mowing and grazing, have proven to be appropriate tools in dune grassland restoration (Rushton 1988; Kooijman and de Haan 1995). Well-documented examples of management schemes are available for the Dutch dunes (e.g., Annema and Janssens 1998) and the LIFE initiative at the Sefton coast in the UK (Houston et al. 1998). In Belgian dunes, around 15 ha of scrub have been removed and currently nearly 350 ha are grazed (Herrier and Killemaes 1998a,b).

In an earlier contribution (Bonte et al. 2003), we investigated the local and regional variation of the spider fauna from grey dunes along the North Sea coasts. It appeared that regional diversity was influenced by the connectivity to other xerotherm habitats like heathland and chalk grasslands. Local factors influencing species diversity were sand dynamics and the distance to the sea (Bonte et al. 2003). In this contribution we search for general patterns in spider richness and document how they vary in function of the environmental factors, directly

influenced by nature management and how this relates to the hypothetical and scarcely documented relation between ecosystem function and variability (in which high nutrient availability is seen as an important ecosystem function – Schwartz et al. 2000). Pianka (1994) gives an overview of 10 hypothetical mechanisms, determining species diversity and richness. Most important are ecological time, evolutionary time, habitat and climatic stability, productivity, spatial heterogeneity, competition, predation and disturbance. One hypothesis suggests that intermediate disturbance supports higher species diversity than higher or lower levels of disturbance (Huston 1979, 1994; Aronson and Precht 1995). Hereafter we assess if this holds true for the important habitat disturbance factor in grey dunes, namely eolian dynamics (sand overblowing).

In our study, species richness is certainly not investigated as an indicator of the ecosystem health, but more as an indicator of the degree of stress in the ecosystem and of the natural value in function of conservation investment. Besides total species richness, the richness of in central-Europe rare xerotherm species is important from a conservationist point of view.

Material and methods

Study area

The investigations were conducted in four dune regions along the coasts from northern France, Belgium and the Netherlands (Figure 1). The dune area in the Boulonnais region (northern France, Departement Nord-Pas de Calais; approximately 4000 ha) is surrounded by and connected to a basin of lime formations from the cuesta from the Haut-Boulonnais. The cuesta originates from the Cretaceous period; the basin was filled with Pleistocene marine sediments (De Meuter et al. 1982; Colbeaux 1985). The oldest parts of the coastal dunes (Pré Communal d'Ambleteuse) were formed during the Flandrian regression (5000 BC) on a fossil lime formation. The more recent coastal dunes (from 2000 BC onwards) are situated at the seaside of the lime cuesta and consist of lime-rich sands (Antrop and Verhoeve 1980; Bellenfant et al. 1998).

The Flemish coastal dunes (approximately 3000 ha) in the most northern part of France and the west coast of Belgium originated between 2000–3000 BC and after the Roman period (300–800 AC). They are situated on marine clay sediments and isolated from older (inland) sand or lime depositions (Declercq and De Moor 1996). The coastal dunes of the Amsterdam Water Supply (AWD; 3400 ha) are situated in the provinces of South- and North-Holland, in the Netherlands and belong to the dunes of the Renodunaal district. The old dunes were formed on old sandy beaches, which originated 3000 BC. From the Roman period onwards, dune formation continued and young dunes were formed in front of the old dunes. The lime content of the sands is high (Baeyens and Duyve 1992; Ehrenburg 1994). The dunes of the Provincial Water Company North-Holland (PWN; >5000 ha) originated in

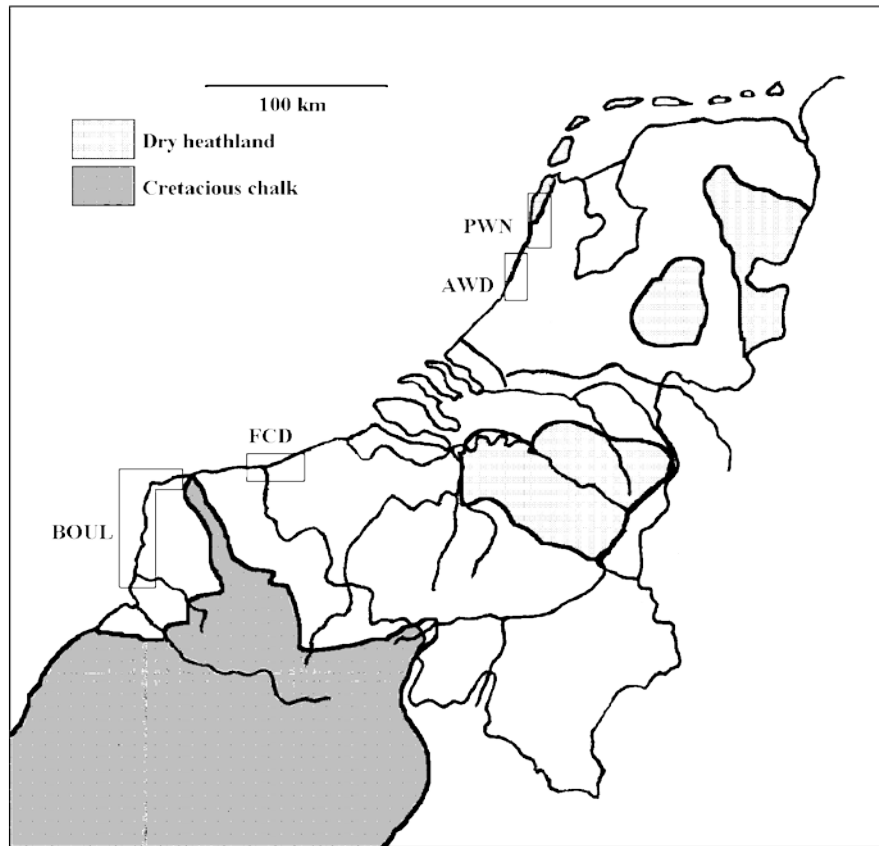


Figure 1. Location of the four sampled dune regions and the presence of suitable geological conditions for the presence of dry heathland and Cretaceous chalk grasslands in Northern France, Belgium and the Netherlands.

the same period as the AWD and are situated at the borderline between the Renodunaal district with lime-rich sands and the Waddendistrict, which are completely decalcified (Klijn 1981). This differentiation is the result from two different sea currents, which meet each other near Bergen aan Zee (Klijn 1981). In the north (north European dunes, including the Wadden district), sand depositions are initially low in lime and nutrients, compared to those in the south (south European dunes, including the Renodunaal district).

Sampling methodology and the determination of the environmental parameters

In each region, we selected relatively large grey dune remnants (Bonte et al. (2002a) reported that the richness of specific xerotherm species declines in small

patches) in order to sample the maximal amount of regional variation. Seven sites were sampled in the Boulonnais and the Flemish coastal dunes, six in AWD and eight in PWN. In each station, five pitfall traps (diameter of 9 cm, filled with a 6% formaline–detergent solution) were linearly installed, with an inter-trap distance of 5 m (due to vandalism, only data from three traps could be used from two stations in the Boulonnais and the AWD). The sampling took place in the period March–November 1999 and traps were fortnightly emptied. Although pitfall traps register species activities from mainly ground active epigeic spiders (Topping and Sunderland 1992), and not absolute densities (Maelfait and Baert 1975), we preferred using this methodology since it is most efficient for sampling the entire spider fauna in habitats with a sparse and low vegetation (Bonte et al., unpublished data). In our experience, only (two) myrmecophilic species can be missed (*Acarthauchenius scurillus* and *Mastigusa arietina*), because of their subterranean life style.

Around each pitfall, we determined the vegetation composition by applying the Londo-scale (Londo 1975) for the cover of the dominant plant species and the cover of non-overgrown mosses, herbs and bare sand. Additionally, we measured the soil development (depth of the humus-rich A-horizon) and the height of the vegetation to the nearest cm. Thirty measurements were taken from the vegetation height with a polystyrene plate (diameter 20 cm), placed on a measuring rule. The standard deviation was determined as a measure for the variation in vegetation height. Since it is correlated with the vegetation height ($r_{132} = 0.867$; $P < 0.001$), the ratio SD/mean height was used as an independent parameter. The distance to the nearest dense vegetation was measured in the field; the distance to the sea was derived from terrain maps.

Additional environmental data were inferred from Aggenbach and Jalink (1999), who linked the presence and cover of indicator plant species to the following soil parameters in a ranked quantitative way: nutrient availability, lime content, eolian value (ranked severeness of sand overblowing) and humus development. The estimate for humus development was almost perfectly correlated to our measurements on soil development and replaced by the latter ($r_{132} = 0.834$; $P < 0.001$). It also stresses the reliability of the inferred parameters. All the determined environmental parameters are listed in Table 1.

Because of the possibility of covariation, these environmental parameters were analysed for principal components by PCA-analysis. In case of significant correlation along the principal axes, component scores were used as a new environmental parameter. All environmental parameters were averaged for each site.

Diversity estimates

The number of observed species (S_{obs}) was used as the primary indicator of species richness. The number of observed species is, however, only an approximation of the total number of expected species (which increase with an

Table 1. Pearson correlations of the determined environmental parameters with the first and only significant principal component and results of the Kruskal–Wallis ANOVA of the selected environmental parameters with region as factor. –: Not relevant.

Parameters	PCA _{nutrient}		KW-Area	
	$r_{132, \text{PCA1}}$	P	$H(3,28)$	P
Distance to the sea (m)	-0.033	NS	0.139	NS
Mean vegetation height (cm)	0.375	<0.001	–	–
Variation in vegetation height (SD/mean height)	-0.164	NS	4.827	NS
Coverage herbs and grasses (%)	0.400	<0.001	–	–
Coverage non-overgrown mosses (%)	-0.365	<0.001	–	–
Coverage bare sand (%)	-0.246	<0.01	5.964	NS
Distance to the edge-dense vegetation (m)	0.054	NS	0.593	NS
Depth of A-horizont (cm)	0.409	<0.001	–	–
Eolian value	-0.278	<0.01	0.670	NS
Lime content value	0.006	NS	2.598	NS
Nutrient availability value	0.371	<0.001	–	–
PCA _{nutrient}	–	–	4.757	NS

increasing sampling effort (Bonte et al. in press)). Therefore, we additionally calculated two estimates, which are less biased (but still non-asymptotic) at a low sampling intensity and suitable for extrapolation of activity-based pitfall data (Bonte et al. in press): the Chao2 and the ICE estimator (Colwell and Coddington 1994). These estimates were calculated with EstimateS (Colwell 2000). Specific species are xerotherm species, typical for grey dune habitats in our region, but also occurring in other habitats like heathland and chalk grassland (Bonte et al. 2003; see Appendix 1 for an overview). In an earlier study, we found that almost all xerotherm species in grey dune patches are already captured with five traps (Bonte et al. in press). The observed richness of specific xerotherm species (from now on abbreviated as S_{spec}) can hence be used as an unbiased and important richness measurement. Although ICE and Chao2 estimates include local density (traps in which the species was caught only once or twice), we use the term species richness (S_{obs} , S_{spec}) (Pianka 1994) for all estimators in this paper. Diversity estimators, which include species number (or at least single- and doubletons) were not calculated because of the earlier mentioned biased nature of pitfall traps (captured numbers are a measure of the species' activity and not of the general density or rareness).

Data analysis

Patterns in species diversity were investigated for S_{obs} , ICE and Chao2. We also focus on the diversity of the specific xerotherm species, since nature management should primarily aim to conserve the typical fauna. General relationships between these diversity estimates and the environmental parameters

were firstly described with a forward multiple regression. Additionally, we test diversity patterns in a univariate way for the determined environmental parameters. The slope, shape (are points concentrated in a defined left or right triangle, pyramid or inverted pyramid of the bivariate plot – cf. methodology of Enquist et al. 1995) and the possible presence of an ecological (evolutionary) boundary (is one of the corners in the bivariate plot unusually empty) in relation to the diversity parameters were tested against the null hypothesis that the observed pattern is part of a random ordering of the measurements. The observed pattern was compared to the null model by generating 1000 randomisations by reshuffling the observed x and y variables.

The following specific hypotheses were tested, based on hypothetical relationships defined by Pianka (1994) and Huston (1979):

1. Spider diversity increases with *productivity* (nutrient availability) and/or is never high at low values of productivity,
2. Spider diversity increases with *spatial heterogeneity* (distance to the dense vegetation at the patch edge) and/or is never high at high distances,
3. Spider diversity increases with (micro) *climatic stability* (sites close to the sea are climatologically more buffered than those far from the seashore (Ampe and Langohr 1996), and
4. Spider diversity is influenced by *disturbance* resulting from eolian dynamics or the presence of bare sand due to eolic and trampling processes. This relation can either be positive, negative or intermediately optimal.

Additionally, we investigate trends (positive and negative relationships and intermediate optima) in diversity of the dune specific xerotherm species in function of the determined environmental parameters.

Multiple regression analyses were done with Statistica 5.5 (Statsoft 2000); generation of null models with EcoSim 6.0 (Gotelli and Entsminger 2001).

Results

Variation in environmental data

The PCA-analysis revealed only one significant principal component, which explained 34.642% of the total variation (eigenvalue = 4.503 > broken stick eigenvalue = 3.180). This principal component was significantly correlated and explained more than 10% covariation with the mean vegetation height, the cover of the grass/herb layer and the moss layer, the depth of the A-horizon and the nutrient availability (Table 1). Although other significant relationships exist, we consider them as ecologically independent because of the low amount (<10%) of explained covariation. In summary, the principal component reflects variation in nutrient availability, resulting in a higher cover and height of grasses, herbs, a deeper soil development and a lower cover of non-overgrown

mosses. In further analyses, we will refer to this principal component as PCA_{nutrient} .

The values of the final seven independent environmental parameters do not differ between the four regions (Kruskal–Wallis ANOVA; $H(3,28)$; Table 1), so differences in spider species richness cannot be attributed to initial differences in environmental conditions of the sampled sites between the four regions. Total patch diversity, as indicated by S_{obs} and the two estimates, does not differ between the regions. The number of xerotherm species is also independent of the region and the grazing type (Kruskal–Wallis ANOVA: NS).

General relationship between patch diversity and environmental conditions

The total number of observed species is significantly influenced by the amount of nutrients (PCA_{nutrient}) and the distance to the rough vegetation ($F(2,25)=9.9602$; $R^2=0.553$; $P<0.001$). The scores of PCA_{nutrient} and the distance to the edge (although not significant) again explain variation in species richness, as estimated by ICE ($F(2,25)=5.816$; $R^2=0.318$; $P<0.01$). The Chao2 diversity estimate is best explained by the eolian value, the distance to the rough vegetation and the lime value ($F(3,24)=4.096$; $R^2=0.338$; $P<0.05$).

The distance to the sea is the only significant contributor in explaining the richness in xerotherm species, although the amount of sand and variation in the vegetation are included in the final regression, which is nearly significant ($F(3,24)=2.435$; $R^2=0.226$; $P=0.059$). Residuals are normally distributed without outliers in all analyses. Variation in species richness, explained by the different environmental parameters, is visualised in Figure 2.

Null models: patch diversity in function of specific environmental conditions

Testing of the observed bivariate patterns of the different diversity measurements against the selected environmental parameters indicates that total species richness increases with an increase of the nutrient availability (Observed slope (0.044) > Expected slope (-0.0002); $P<0.001$). If sand dynamics (eolian value) increase, total species richness decreases (Observed slope (-0.287) < Expected slope (0.001); $P<0.01$), possibly due to a significant, although low explanative covariation with the PCA_{nutrient} scores. This relationship, however, explains less variation than those with PCA_{nutrient} .

The same trend was observed for S_{obs} in the function of the surface of nude sand (Observed slope (-0.315) < Expected slope (0.0029); $P<0.05$). The Chao2 and the ICE richness estimates show the same trend for PCA_{nutrient} and the eolian value (observed slopes respectively 0.032 and -0.276, significantly different ($P<0.05$) from the expected slopes of -0.0006 and 0.0004 for Chao2; slopes of 0.035 and -0.229, significantly different ($P<0.05$) from the respec-

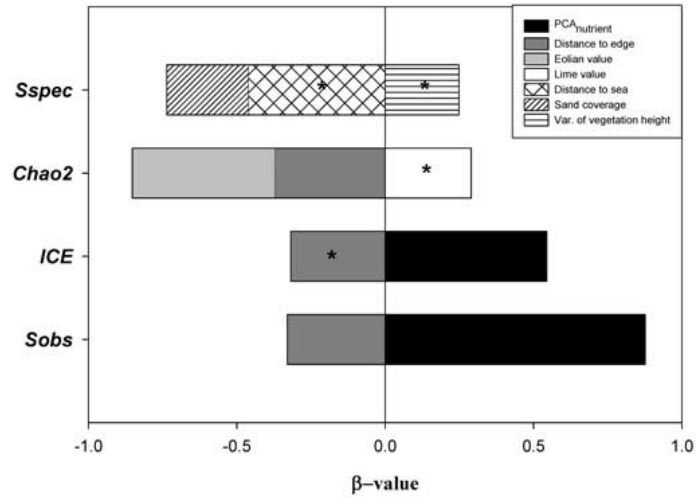


Figure 2. Environmental parameters explaining variation in the different used species richness estimators. The sign of the b-value indicates the direction of the contribution. *: non significant ($0.05 < P < 0.1$) contributing factors in the multiple regression. Only the regression of S_{spec} is not significant ($P=0.059$).

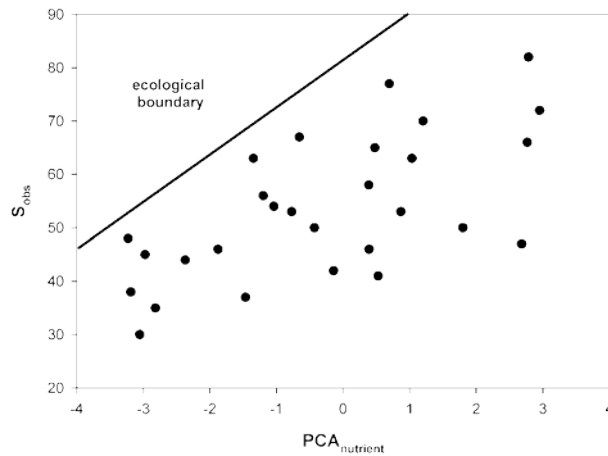


Figure 3. Ecological boundary for the observed species richness at low nutritious grey dunes (Observed number of cases above boundary $<$ expected by random resampling; $P < 0.05$).

tively expected slopes of -0.0006 and 0.0004 for the ICE estimator). Chao2 richness is additionally influenced by the distance to patch edge (Observed slope $(-0.055) <$ Expected slope (0.0029) ; $P < 0.05$).

Ecological constraints in the species richness pattern were only observed for the boundary in the upper left triangle for S_{obs} (Figure 3), indicating the

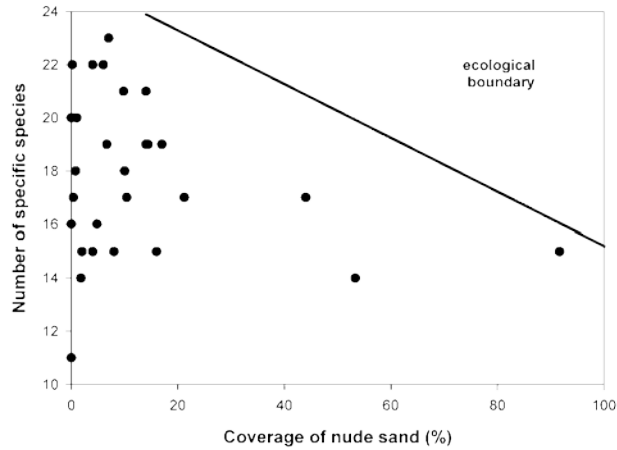


Figure 4. Ecological boundary for the observed number of xerotherm species in grey dunes with a high sand coverage (Observed number of cases in upper triangle, above boundary < expected by random resampling; $P < 0.05$).

intrinsic absence of a high observed species richness in oligotrophic grey dune patches. The richness of xerotherm species is also constrained in patches with a large amount of nude sand coverage since the bivariate points are significantly absent from the right upper triangle (Figure 4).

Discussion

In this contribution, we investigate species richness patterns of spiders in one distinct habitat type – grey dunes – in the coastal dunes of northern France, Belgium and the Netherlands. Although a lot of research on the invertebrate fauna has already been conducted, no documented analyses of faunal richness patterns in one habitat type are available. Studies, which focus on diversity and richness patterns, are related to patterns between different habitats (Coastal dunes: Desender and Baert 1995; Pollet and Grootaert 1996; Bonte et al. 2002b), between regions (Bonte et al. 2003) or in function of the applied nature management (Coastal dunes: Maelfait et al. 1997; Bonte et al. 1999; WallisDeVries and Raemakers 2001). In these studies, and in contrast to the results presented in this contribution, differences in species richness do not result from subtle differences in environmental factors, but from large structural and biotic differences between the investigated sites.

The community structure and spider diversity is neither equal nor similar in different types of grey dunes. Bonte et al. (2002a) found that the richness of xerotherm species was influenced by patch size. This relationship is probably the result of a higher variation in micro-environmental conditions, which

positively influence the presence of a more diverse species composition. Analogous results were obtained by Whitehouse et al. (2002) for spider communities in semi-arid scrubland. Here, we investigate how spider richness reacts on narrow ranges of variation in nutrient availability, eolian dynamics, variation in vegetation height, coverage of nude sand, distance to litter rich vegetation at the edge of the patches. Additionally we study richness patterns in relation to the distance to the seashore, which is related to different exposures to salt spray and aerial humidity (Provoost and Hoffmann 1996). The linkage of diversity and species richness to ecosystem functioning (disturbance and productivity, here determined by respectively eolian dynamics or the presence of nude sand and nutrient availability) and to structural environmental features related to habitat heterogeneity (variation in the vegetation height, distance to the patch's edge) enable us to understand the relation between biodiversity (although only a small proportion of the total biodiversity is investigated) and ecosystem function and its implications for proper implementable conservation strategies. According to recent literature (review by Schwartz et al. 2000), only few observational studies demonstrated improved ecosystem function (stability, biomass) at high levels of species richness. Patterns of diversity and species richness, in function of these parameters are important to understand the functioning of the ecosystem and hence of primordial importance for the conservation of grey dune vegetation and its associated fauna.

Although spider communities from grey dunes differ between and within the investigated region as a result of differences in landscape connectivity and eolic dynamics (Bonte et al. 2003), both total richness and the richness of xerotherm species within the survived patches are comparable between the four studied regions. In coastal grey dunes, nutrient availability and the distance to the high vegetation at the edges of the patch explain most of the variation in total spider richness. Only for the diversity estimate Chao2, the eolian value seems to be the best predictor (which is inversely related to PCA_{nutrient}). Although slightly different results are obtained from the different richness estimators, we can generally conclude that total spider richness increases with higher productivity (higher nutrient availability), lower disturbance (eolic value) and with spatial heterogeneity (larger distances to the edges of the patch). Variation in richness of xerotherm species cannot be unambiguously explained by the determined environmental parameters. The increased total diversity in high-trophic grey dunes, close to the rough vegetation, hence must result from the increase of non-xerotherm eurytopic species.

Univariate patterns confirm the relationships between total diversity and nutrient availability, sand dynamics and distance to patch edge. Interesting is the fact that the richness of xerotherm species decreases if grey dunes are situated more distantly from the seashore. This is also the main factor determining local assemblage structure (Bonte et al. 2003). Apparently, more xerotherm species invade grey dunes close to Marram dunes (blond dunes dominated by *Ammophila arenaria*), which are proximately situated close to the seashore. Null-models revealed only few significant (but nevertheless

interesting) relationships: a high observed diversity in grey dunes with low nutrient availability seems ecologically constrained, while grey dunes with a high sand coverage are unsuitable for a high richness of xerotherm species. As hypothesised by Pianka (1994), productivity affects species richness and diversity positively, while it is negatively influenced by the amount of disturbance (eolian value). Species richness is in our case not highest at high or intermediate levels of disturbance, but at low levels. The intermediate disturbance hypothesis may, however, hold true if richness patterns are to be studied at an expanded habitat range, so within the complete dune succession gradient. Spatial heterogeneity (distance to the edge of the patch) only seems to affect the Chao2 diversity estimate, indicating its minor influence on species richness. Because our analysis reveals no differences in species richness between grey dune patches in the four investigated regions, ecological time does not restrict species richness at the patch scale. It is, however, important in determining regional patterns of diversity and species richness (Bonte et al. 2003), so different mechanisms attribute to the observed species richness at different scales (Addington et al. 1987).

The increase of species richness as a function of the nutrient availability (biomass) affirms the relationship between species richness and ecosystem functioning. Its link to conservation (Schwartz et al. 2000) must, however, be put in perspective, since grey dune habitat conservation should not focus on the maintenance of high diversity, but instead on the conservation of the specific and threatened fauna (Provoost et al. 2002). The richness of specific xerotherm species is on the counterpart not related to environmental variables, indicative for ecosystem functioning, but only to the distance of the grey dune to the seashore. Since this parameter cannot be altered by nature management, conservation efforts should focus on the maintenance of large surfaces of grey dune vegetation throughout the dune area, because an earlier study revealed that patch surface strongly affected the number of specific xerotherm species (Bonte et al. 2002a).

Besides patch surface, local spider community structure in grey dunes is primarily influenced by sand dynamics and the coverage of bare sand (certainly in the dunes along the northern French and the Belgian coast, but less in those from the Netherlands (Bonte et al. 2003)). Environmental variation should hence be maintained, especially by enhancing sand dynamics. Locally decreasing amounts of nutrients is of minor importance in comparison to the restoration and enlargement of heterogeneous patches by shrub clearance or grazing, because an increased species richness in more nutritious patches only results from the invasion of eurytopic species, occurring in widespread habitats in the dune landscape (shrub and grassland vegetation).

Striving for maximal ecosystem functioning and minimal ecosystem variability is only important if a high spider species richness is aimed. Conservation of the xerotherm fauna, which is dependent on maximal variation within and between large patches of grey dune, implies that environmental stress (sand dynamics) in the grey dune landscape has to be maintained.

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Appendix 1

List of the xerotherm species used in the richness analysis with indications of their main habitat(s) in central Europe (after Hä nggi et al. 1995).

Species	Main habitat in central Europe
<i>Acarthauenius scurrilus</i> (O.P.-Cambridge, 1872)	Coastal dunes
<i>Aelurillus v-insignatus</i> (Walckenaer, 1802)	Chalk/heathland
<i>Agroeca cuprea</i> (Menge, 1873)	Xerotherm
<i>A. lusatica</i> (L. Koch, 1875)	Heathland
<i>A. proxima</i> (O.P.-Cambridge, 1871)	Xerotherm
<i>Alopecosa barbipes</i> (Sundevall, 1833)	Xerotherm
<i>A. cuneata</i> (Clerck, 1757)	Xerotherm
<i>A. fabrilis</i> (Clerck, 1757)	Xerotherm
<i>Araeoncus humilis</i> (Blackwall, 1841)	Chalk/heathland
<i>Arctosa perita</i> (Latreille, 1799)	Xerotherm
<i>Argenna subnigra</i> (O.P.-Cambridge, 1861)	Xerotherm
<i>Atypus affinis</i> (Eichwald, 1830)	Chalk/heathland
<i>Aulonia albimana</i> (Walckenaer, 1805)	Chalk/heathland
<i>Ceratinopsis romana</i> (O.P.-Cambridge, 1872)	Xerotherm
<i>Cercidia prominens</i> (Westring, 1851)	Heathland
<i>Cheiracanthium erraticum</i> (Walckenaer, 1802)	Chalk/heathland
<i>C. virescens</i> (Sundevall, 1833)	Xerotherm
<i>Clubiona frisia</i> (Wunderlich & Schütt, 1995)	Xerotherm
<i>Crustulina guttata</i> (Wider, 1834)	Heathland
<i>Drassodes cupreus</i> (Blackwall, 1834)	Xerotherm
<i>D. lapidosus</i> (Walckenaer, 1802)	Xerotherm
<i>D. pubescens</i> (Thorell, 1856)	Xerotherm
<i>Dysdera erythrina</i> (Walckenaer, 1802)	Chalk
<i>Erigone promiscua</i> (O.P.-Cambridge, 1872)	Xerotherm
<i>Euophrus herbigrada</i> (Simin, 1871)	Chalk
<i>Euryopis flavomaculata</i> (C.L. Koch, 1836)	Chalk/heathland
<i>Evarcha falcata</i> (Clerck, 1757)	Chalk/heathland
<i>Hahnia montana</i> (Blackwall, 1841)	Chalk/heathland
<i>H. nava</i> (Blackwall, 1841)	Xerotherm
<i>Haplodrassus dalmatensis</i> (L. Koch, 1866)	Xerotherm
<i>H. signifer</i> (C.L. Koch, 1839)	Xerotherm
<i>H. umbratilis</i> (L. Koch, 1866)	Chalk/heathland
<i>Hypsosinga albovittata</i> (Westring, 1851)	Xerotherm

Appendix 1 (continued)

Species	Main habitat in central Europe
<i>H. pygmaea</i> (Sundevall, 1832)	Chalk
<i>Lathys puta</i> (O.P.-Cambridge, 1861)	Chalk
<i>Lepthyphantes mengei</i> (Kulczynski, 1887)	Heathland
<i>Marpissa nivoyi</i> (Lucas, 1846)	Xerotherm
<i>Mastigusa arietina</i> (Thorell, 1872)	Xerotherm
<i>Metopobactrus prominulus</i> (O.P.-Cambridge, 1872)	Xerotherm
<i>Micaria dives</i> (Lucas, 1846)	Xerotherm
<i>Micrargus subaequalis</i> (Westring, 1851)	Chalk/heathland
<i>Ozyptila atomaria</i> (Panzer, 1841)	Xerotherm
<i>O. nigrita</i> (Thorell, 1875)	Chalk/heathland
<i>Pardosa monticola</i> (Clerck, 1757)	Xerotherm
<i>Pelecopsis nemoralis</i> (Blackwall, 1841)	Coastal dunes
<i>Peponocranium ludicrum</i> (O.P.-Cambridge, 1861)	Chalk/heathland
<i>Philodromus fallax</i> (Sundevall, 1833)	Coastal dunes
<i>Phlegra fasciata</i> (Hahn, 1826)	Xerotherm
<i>Scotina celans</i> (Blackwall, 1841)	Chalk
<i>S. gracilipes</i> (Blackwall, 1859)	Heathland
<i>S. palliardi</i> (L. Koch, 1881)	Chalk/heathland
<i>Sitticus distinguendus</i> (Simon, 1868)	Coastal dunes
<i>S. saltator</i> (O.P.-Cambridge, 1868)	Coastal dunes
<i>Steatoda albomaculata</i> (De Geer, 1778)	Chalk
<i>S. phalerata</i> (Panzer, 1801)	Chalk/heathland
<i>Textrix denticulata</i> (Olivier, 1789)	Heathland
<i>Thanatus striatus</i> (C.L. Koch, 1845)	Xerotherm
<i>Trichopterna cito</i> (O.P.-Cambridge, 1872)	Xerotherm
<i>Typhochrestus digitatus</i> (O.P.-Cambridge, 1872)	Xerotherm
<i>Walckenaeria capito</i> (Westring, 1861)	Heathland
<i>W. dysderoides</i> (Wider, 1834)	Heathland
<i>W. furcillata</i> (Menge, 1869)	Chalk
<i>Xerolycosa miniata</i> (C.L. Koch, 1834)	Coastal dunes
<i>Xysticus acerbus</i> (Thorell, 1872)	Chalk
<i>X. erraticus</i> (Blackwall, 1834)	Xerotherm
<i>X. sabulosus</i> (Hahn, 1832)	Coastal dunes
<i>Zelotes electus</i> (C.L. Koch, 1839)	Xerotherm
<i>Z. latreilli</i> (Simon, 1878)	Chalk/heathland
<i>Z. longipes</i> (L. Koch, 1866)	Xerotherm
<i>Z. pedestris</i> (C.L. Koch, 1837)	Chalk/heathland
<i>Z. pusillus</i> (C.L. Koch, 1833)	Chalk/heathland
<i>Z. subterraneus</i> (C.L. Koch, 1833)	Heathland

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