Regional and local variation of spider assemblages (Araneae) from coastal grey dunes along the North Sea

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Abstract

Aim This study aims to determine the underlying causes of local and regional patterns of variation in community structure of spiders in coastal grey dunes, and especially whether ecological time constrains the species composition in young and isolated grey dune habitats.

Location The study was conducted in coastal dunes from northern France (Boulonnais, Nord-Pas-de-Calais), Belgium (Flemish coastal dunes) and the Netherlands [Amsterdam Water Supply (AWD) dunes and Dunes from the Provincial Water Company North-Holland].

Methods Spiders were collected with pitfall traps in twenty-eight grey dune patches in the four areas under investigation. Species composition and environmental parameters (vegetation structure, distance to the sea and the patch-edge, eolic dynamics and lime richness) were determined. Assemblage composition was related to the regional and local environmental factors with the Primer software package to determine the assemblage-determining parameters. Differences in species presence were analysed as a function of their habitat preference and distribution range.

Results Differences in grey dune spider assemblage structure can mainly be attributed to differences in local sand dynamics and the region. Species from dynamic dunes are mainly present in grey dunes from Belgium and France, while species from non-dunal xerothermic habitats (chalk grasslands and heathland) occur in both the Boulonnais and the north Holland dune region. These species are absent from geologically young or other xerotherm habitat isolated Flemish coastal dunes.

Main conclusion The data show that regional variation in spider assemblage composition results from local landscape characteristics (dynamics in the dune area), the latitude and the connectivity to non-dunal xerothermic habitats. The strong and moderate geological isolation of dune areas from the Flemish coast and the AWD dunes, respectively, results in the absence of (at least some) species that are primarily bound to heathland and/or chalk grassland. This indicates the importance of ecological time for the assemblage structure. The limited dispersal capacity of the heathland and/or chalk grassland species is probably the main reason for their absence.

Keywords
Biogeography, xerotherm species, sand dynamics, heathland, chalk grassland.

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INTRODUCTION

Grey dunes, known as 'Fixed coastal dunes with herbaceous vegetation' in the CORINE biotope classification (Natura, 2000), are most readily defined using plant species composition. Vegetation includes Atlantic moss dominated dunes (mainly *Tortula ruralis*) as well as dune grassland (with a distinct organic soil layer) belonging to the *Cladonio-Koelerietalia* association in the case of lime-rich grey dunes and the *Trifolio-Festucetalia ovinae* association in the case of decalcified grey dunes (Provoost *et al.*, 2002). Ecologically, grey dunes can be defined simply as the dry component of the 'stressed dune landscape', where ecological dynamics are controlled by climatological stress and xerosere progression. The main differentiating processes are related to dune fixation, soil formation and vegetation development (Provoost & Hoffmann, 1996; Aggenbach & Jalink, 1999).

Grey dune succession is initiated by fixation of sand by mainly *Carex arenaria* roots and is driven by the complex of soil formation (humus accumulation) and vegetation development. Leaching and mobilization of $CaCO_3$ complicate the picture and are important in nutrient dynamics. But at present, rough grass and scrub encroachment greatly override these fine-scaled soil processes and cause substantial loss of regional biodiversity (Provoost *et al.*, 2002). As a result of this encroachment, grey dunes are now heavily fragmented and patchily distributed within a matrix of dense dune vegetation (shrubs and dense grassland). Bonte *et al.* (2002) identified typical species for this habitat and found that this habitat type is characterized by a specific and endangered arthropod fauna.

Assemblages are local snapshots of a spatiotemporally fluid system, having no status as distinct biological entities and hence are dependent on species life-history patterns, dispersal capacities and environmental constraints (Hengeveld & Hemerik, 2002). Dispersal and geographical factors together determine the ecological time necessary to enable potential species to establish (Pianka, 1994).

The structure of spider assemblages in European coastal dunes is now well documented (Bøggild, 1961; Duffey, 1968; Almquist, 1973; Noordam, 1996; Bonte *et al.*, 2001, 2002; Gajdos & Toft, 2002) and characterized by geographical and temporal variations. Locally, assemblages are structured mainly by vegetation development, soil and aerial humidity. Some authors also stressed the importance of sand dynamics as an important structuring parameter (Bonte *et al.*, 2002; Gajdos & Toft, 2002). Whether differences in species composition, or more specifically the absence of apparently well adapted species, is the result of insufficient ecological time to colonize young and isolated dune areas is at this moment unclear. This factor is certainly thought to be one of the causes of the general species paucity of the Flemish coastal dunes, compared with inland species (Maelfait *et al.*, 2000). Within this geological young and relatively isolated dune region (Declercq & De Moor, 1996), grey dune habitats are even younger (Provoost *et al.*, 2002) and more isolated because large dune regions are only interconnected by beach.

Grey dune vegetation has high affinities with heathland and chalk grassland vegetation (Weeda *et al.*, 1996) and possesses a lot of common species. Therefore, we tested the hypothesis that ecological time can constrain species composition in the young and isolated grey dunes in the Flemish coastal dunes by comparing its spider species composition (from which habitat characteristics are well documented in Western and Central Europe (Hänggi *et al.*, 1995)) and assemblage structure to those from the Boulonnais area in northern France, which is directly connected to chalk grasslands, and to the Netherlands which are directly or historically connected to heathland. Evidently, ecological time had to be discriminated from local and regional environmental variation.

MATERIAL AND METHODS

Study area

The investigations were conducted in four dune regions along the coast from northern France, Belgium and the Netherlands (Fig. 1). The dune area in the Boulonnais region (northern France, Department Nord-Pas de Calais; *c.* 4000 ha) is situated in and connected to a basin of lime formations of the cuesta from the Haut-Boulonnais (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 & Verhoeve, 1980; Bellenfant *et al.*, 1998).
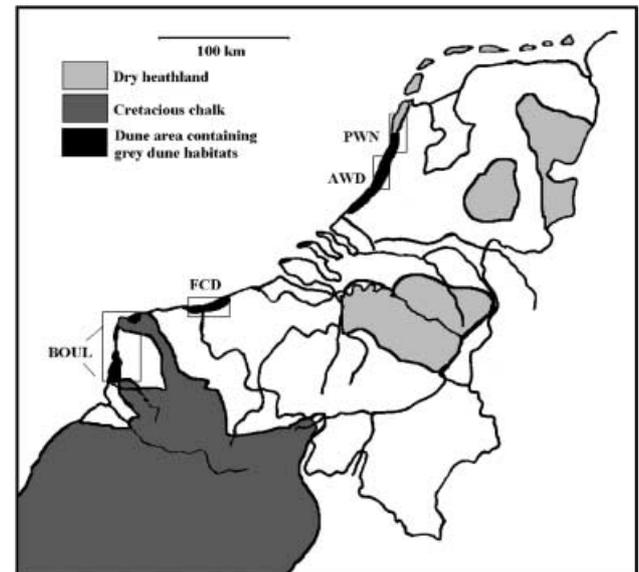

Figure 1 Location of the four sampled dune regions and the presence of suitable geological conditions for the presence of dry heathland and Cretaceous chalk grasslands in northern France, Belgium and the Netherlands.

The Flemish coastal dunes (c. 3000 ha) in the most northern part of France and the west coast of Belgium originated partly before (3000–2000 BC) and after (300–800 AD) the Romanian period. They are situated on marine clay sediments and isolated from older (inland) sand or lime depositions (Declercq & 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 c. 3000 BC. From the Romanian period onwards, dune formation continued and the young dunes were formed in front of the old dunes. The lime content of the sands is high (Baeyens & Duyve, 1992; Ehrenburg, 1994). The dunes of the Provincial Water Company (PWN) North Holland (5800 ha) originated at the same period as the AWS and are situated at the borderline between the lime-rich Renodunaal district sands and the completely decalcified Wadden district (Klijn, 1981). This differentiation is the result of two different sea currents, which meet each other near Bergen aan Zee (Klijn, 1981). The northern dunes (Wadden district) have low lime and nutrient contents in comparison with their southern counterparts (Renodunaal district).

As a result of their geological history, grey dunes from the Boulonnais region make contact with chalk grassland on the Cretacious questa, while those in the PWN are connected with well-developed dune heathlands from the Wadden district. The dune area of the AWD is historically connected to the Wadden district, but nowadays it is isolated as a result of urbanization; the Flemish coastal dunes are completely isolated from other xerothermic habitats.

Sampling methodology and determination of environmental parameters

In each region, relatively large grey dune remnants were selected in order to sample the maximum amount of regional variation in an equal way, as the richness of specific species declined in small patches (Bonte et al., 2002). Seven sites were sampled in the Boulonnais and the Flemish coastal dunes, six in AWD and eight in PWN. Additionally, well-developed heathland (two sites in PWN) and chalk grassland (two sites in the Boulonnais) were sampled in order to determine the presence and abundance of possible dune-invading species. In each station, five pitfall traps (diameter 9 cm, filled with a 6% formaline–detergent solution) were linearly installed, with an inter-trap distance of 5 m (data from only three traps could be used from two stations in the Boulonnais and the AWS). The sampling took place in March–November 1999 and the traps were emptied fortnightly.

Around each pitfall, the vegetation composition was determined 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, soil development (depth of the humus-rich A-horizon) and the height of the vegetation to the nearest centimetre was measured. Thirty measurements of the vegetation height were taken with a polystyrene plate (diameter 20 cm) placed on a measuring rule. The standard deviation was determined as a measure of the variation in vegetation height. As it is correlated with 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 & 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 with measurements made on soil development, and was replaced by the latter in this study ($r_{132} = 0.834$; $P < 0.001$). 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

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 remaining environmental parameters with region as factor. – not relevant

Parameters	PCA$_{nutrient}$ $r_{132,PCA1}$	P	KW-region $H(3,28)$	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
Cover herbs and grasses (%)	0.400	<0.001	–	–
Cover non-overgrown mosses (%)	−0.365	<0.001	–	–
Cover bare sand (%)	−0.246	<0.01	5.946	NS
Distance to the edge – dense vegetation (m)	0.054	NS	0.593	NS
Depth of A-horizon (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

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.

Main habitat of the species

The main habitat of the species was derived from Hänggi *et al.* (1995), Roberts (1995), Maelfait *et al.* (1998), Bonte *et al.* (2002) and Nentwig *et al.* (2002). Additional sampling occurred in dune heathland and chalk grassland in the PWN and Boulonnais area, respectively (Bonte, 1999; Bonte *et al.*, 2001). In this way, species could be categorized as eurytopic or stenotopic for dynamic coastal dunes, for xerothermic habitats (coastal and inland dunes and a variety of oligotrophic dry grasslands), heathland, chalk grassland or for both heathland and chalk grassland. Finally, southern- and northern-limited species were identified.

Data analysis

Pitfall traps register arthropod activity patterns, and are affected by both the population density and the species-specific movement rates (Maelfait & Baert, 1975). As a result, they are biased by inter- and intra-specific activity variation due to different climate and population characteristics. Therefore, presence–absence data are used instead of the relative or absolute numbers.

As a consequence, data are binomially distributed, and classical (canonical) correlation-based multivariate ordination techniques cannot be used for analysis. The use of PRIMER (Clarke & Ainsworth, 1993) is, however, an elegant and extremely suitable alternative. By applying this algorithm, a dissimilarity Bray–Curtis matrix of the species data (most common species, at least five caught individuals at one site) is compared by rank correlation with a Euclidian similarity matrix of all possible combination (subsets) of environmental data ($n!$ combinations; n = number of environmental parameters). The best subset of environmental variables that provides the best match between the two configurations reveals the 'best explanation' of the biotic structure, analogous to a forward multiple regression. All the determined environmental parameters and the region, ranked by latitude, were included in the environmental data set.

The dissimilarity between the sites were visualized by nonmetric multidimensional scaling (NMDS, with indication of the stress value as an indication of the stability of the ordination) and the Bray–Curtis dissimilarity tree.

An earlier analysis (Bonte *et al.*, 2003a) revealed that the total number of species caught increases with the number of sampled sites (and traps), but that >95% of all specific xerothermic species from one region are caught with twenty-five pitfall traps, distributed over a variety of grey dunes. Locally, all specific species are caught with three to five traps. As a consequence, absolute counts were used to compare diversity of specific species between regions.

The proportions of all species of the sampled habitats were compared between the four dune areas with multiple χ^2-comparisons and *post hoc* Tukey tests (Zar, 1996). Basic statistical tests (Kruskal–Wallis ANOVA; correlations) were conducted with Statistica 5.5 (Statsoft, Inc., 2000); PCA with PCORD 4.17 (McCune & Mefford, 1999).

RESULTS

Local and regional environmental variation of the sampled grey dune habitats

The PCA 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 composition and diversity cannot be attributed to differences in environmental conditions of the sampled sites between the four regions.

Local and regional variation in spider assemblage structure

The variation in spider assemblage structure is primarily determined by differences in the aeolian value and the region. The cover of bare sand is an important assemblage-structuring factor. The variation in aeolics explains 23.81% of the assemblage variation. The amount of explained variation is increased with 6.44% when region is included. The combination of the three parameters results in the best subset, explaining 41.34% of the assemblage variation. If more parameters are included, the explaining power decreases significantly (Table 2). The NMDS ordination of the sites, based on the species presence–absence records, indicates the same pattern of assemblage composition: although no differences between the environmental parameters were recorded (Table 2), the regions are differentiated along the first NMDS axis [Kruskal–Wallis ANOVA; $H(3,28) = 15.312$, $P = 0.002$] but not along the second axis [Kruskal–Wallis ANOVA; $H(3,28) = 7.461$, $P = 0.059$] (Fig. 2). Spearman correlation of the first NMDS axis indicates that this differentiation is only the result of differentiation in the eolian value ($R_{28} = -0.525$; $P = 0.004$) and the PCA$_{nutrient}$

Table 2 Combination of variables, k at time, giving the largest rank correlation between biotic (spider presence/absence) and environmental similarity matrices

k	Best variable combination (R)
1	Eolics (0.488)
2	Eolics × region,7 (0.550)
3	**Eolics × region × bare sand (0.643)**
4	Eolics × region × bare sand × PCA$_{nutrients}$ (0.584)
5	Eolics × region × bare sand × PCA$_{nutrients}$ × distance to the sea (0.560)
6	Eolics × region × bare sand × PCA$_{nutrients}$ × distance to the sea × variation vegetation height (0.510)
7	Eolics × region × bare sand × PCA$_{nutrients}$ × distance to the sea × variation vegetation height × lime value (0.438)
8	All parameters (0.388)

In bold: final subset of parameters, explaining the largest amount of assemblage variation.

scores ($R_{28} = 0.603$; $P < 0.001$). No linear relationships were found along the second axis.

The Bray–Curtis dissimilarity tree also reveals the existence of five distinct groups: all the sites of the Netherlands (I) and one partial group of the Boulonnais (IIa) and the Flemish coastal dunes (IIIa) are separated from two other groups (sites with aeolic dynamics) from the latter regions (IIb and IIIb) (Fig. 2).

Regional variation in species richness

The number of eurytopic species is significantly different between the four regions ($\chi^2 = 17.901$; $n_{tot} = 130$; $P < 0.001$) and is highest in PWN ($n = 88$), moderate in FCD ($n = 70$) and BOUL ($n = 71$) and lowest in AWD ($n = 53$). The number of widespread xerothermic species is however not significantly different in the four regions ($n_{tot} = 31$; $n_{Boul} = 27$; $n_{FCD} = 30$; $n_{AWD} = 27$; $n_{PWN} = 28$; $\chi^2 = 2.298$; $P > 0.05$).

The number of species from dynamic coastal dunes is higher in the Boulonnais and the Flemish coastal dunes than in the dunes from the Netherlands ($\chi^2 = 11.917$; $n_{tot} = 7$; $P < 0.001$; Fig. 3a) and occur in high abundance (Appendix 1). Southern species are mainly present in the Boulonnais

dune area ($\chi^2 = 25.567$; $n_{tot} = 11$; $P < 0.001$; Fig. 3b). Only one northern continental species was recorded in the coastal dunes of the Netherlands.

Typical species for chalk grasslands are only present in the Boulonnais dunes (Fig. 4a). Heathland species are only present in the coastal dunes of the Netherlands and more numerous in the dune area of PWN (Yates corrected $\chi^2 = 8.423$; $P < 0.01$) than in AWD (Fig. 4b). Species, which have their optimum in both habitat types are equally present in the dunes of the Boulonnais, AWD and PWN. Only the Flemish coastal dunes are characterized by an almost complete absence of these species ($\chi^2 = 22.209$; $n_{tot} = 17$; $P < 0.001$; Fig. 4c). For all the xerothermic species taken together, the deficit in the Flemish coastal dunes is even more pronounced ($\chi^2 = 45.998$; $n_{tot} = 34$; $P < 0.001$). The number of species, belonging to this lumped category, is higher in the AWS than in the Flemish coastal dunes, but significantly lower than in the dune area of the PWN and the Boulonnais.

Of these, the heathland species *Cercidia prominens*, *Textrix denticulata* and *Zelotes subterraneus*, the chalk grassland species *Hypsosinga pygmaea*, *Walckenaeria furcillata*, *Dysdera erythrina*, *Euophrys herbigrada* and *Steatoda albomaculata*, and four species typical for both habitats (*Cheiracanthium erraticum*, *Haplodrassus umbratillis*, *Micrargus subaequalis* and *Araeoncus humilis*) are only encountered in very low numbers in the coastal grey dunes (Appendix 1). The other non-typical dune species were abundant and some of them also occurred in the more isolated, although historically connected, dune area of AWD.

DISCUSSION

The results show that spider assemblage structure and species richness in the four large dune regions along the North Sea of Northern France, Belgium and the Netherlands are region-specific and locally determined by variation in sand dynamics. Species from dynamic coastal dunes are present in the Flemish coastal dunes and northern France, but are almost absent from the Netherlands, although environmental variation in the sampled patches was not different. Species with optima in chalk grassland and heathland were only present in grey dunes from the Boulonnais and the north

Figure 2 NMDS ordination (left) and Bray–Curtis dissimilarity tree (right, branches of the sites belonging to the same group are merged) of the sites, based on the absence–presence of the spider species. Filled circles: Boulonnais region (IIa,b); open circles: Flemish coastal dunes (IIIa,b); filled triangles: Amsterdam Water Supply dunes (I); open triangles: Dunes North-Holland PWN (I).
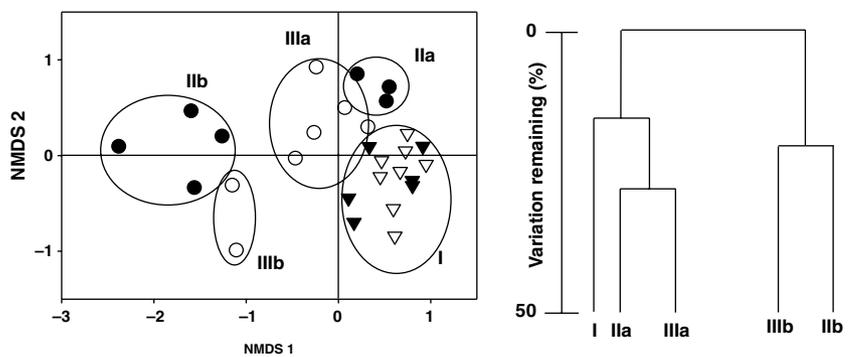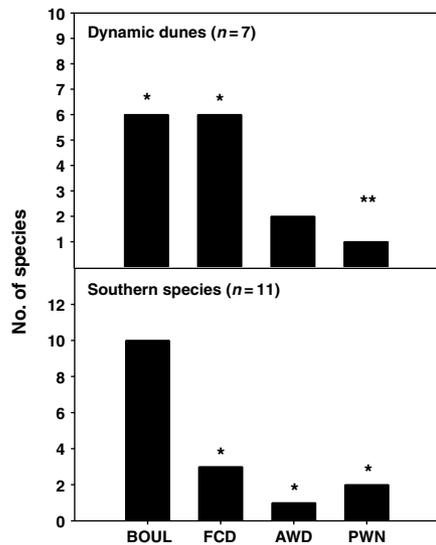
Figure 3 The number of typical dynamic dune species (a) (above) and southern species (b) (under) in the four dune regions. Bars with the same symbol indicate non-significant differences (Tukey-test; $P > 0.05$). BOUL: Boulonnais; FCD: Flemish coastal dunes; AWD: Amsterdam Water Supply dunes; PWN: Provincial Water Company dunes North-Holland.

Figure 4 The number of stenotopic xerothermic species in the four dune regions. Bars with the same symbol indicate non-significant differences (Tukey-test; $P > 0.05$). (a) (top): chalk grassland species; (b) (middle): heathland species; (c) (bottom): species typical for heathland and chalk grassland. BOUL: Boulonnais; FCD: Flemish coastal dunes; AWS: Amsterdam Water Supply dunes; PWC: Provincial Water Company dunes north Holland.

Holland dune regions, respectively, directly connected to the former xerothermic habitats. These species were absent from the isolated and geologically young Flemish coastal dunes but present to a lesser extent in the AWD dunes, which are distantly and historically connected to dune heathland. Regional variation in spider assemblage structure and species richness can hence be attributed to general landscape and ecological time constraints (the time needed for species to colonize distant and young suitable habitats).

In general, spider and arthropod communities in coastal dunes are structured by gradients in vegetation development and both soil and aerial humidity (Duffey, 1968; Almquist, 1973; Van der Aart, 1973; Koehler *et al.*, 1995; Desender, 1996; Pollet & Grootaert, 1996; Bell *et al.*, 1998; Mattoni *et al.*, 2000). Bonte *et al.* (2002) also found that dynamics caused by sand displacement and nature management act as a determining factor for assemblage composition. The present study only investigated the variability in spider species composition of one habitat type (grey dunes) in the mainland coastal dunes along the North Sea. The most important spider assemblage-determining factors in these grey dunes are again related to sand dynamics. In grey dunes from the four regions, the two most important assemblage determinants are the aeolian value (a measure of the degree and severeness of sand overblowing) and the cover of bare sand, which should not *a priori* be related to the former parameter as trampling and digging activities, for instance, significantly affect the presence of nude sand on grey dunes, especially at places with a young soil development.
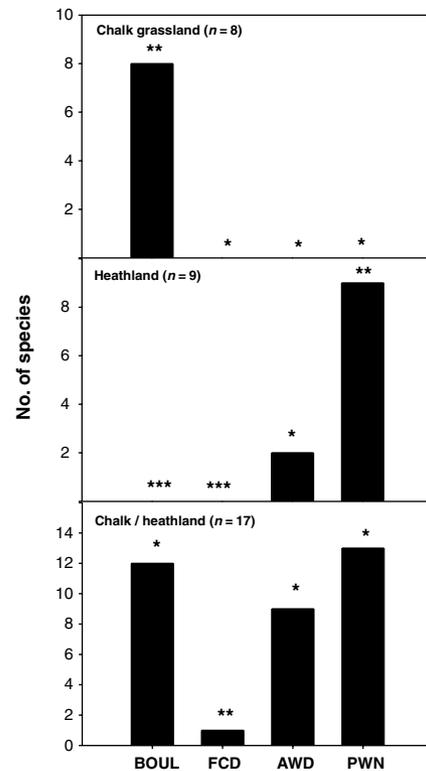
Spider assemblages are, however, not uniformly and geographically structured – a pattern also observed in inland dunes from the German lowlands (Merkens, 2002). A first interesting result from the present study is the separation of the Netherlands coastal dunes from those investigated along the Belgian and northern French coasts. Although no environmental differences were found in the sites were consideration, coastal dunes of the Netherlands were characterized by species of nutrient-rich vegetation and by the absence of species of dynamic dune systems. This indicates that although local habitats are suitable, other factors also influence the observed pattern. Mattoni *et al.* (2000) found that historical disturbance can alter the species richness of dune arthropods in a definitive way. We believe that the absence of these typical coastal dune species originates from the global dune landscape structure: in contrast to the coastal dunes from northern France and Belgium, large-scale fixation of dynamic sand dunes started in the sixteenth century and was very stringent in the nineteenth and twentieth century (Klijn, 1981), as a human response to the strong maritime inundation which affected large parts of the Netherlands. Nowadays, cattle graze in these coastal dunes

and sand dynamics are again tolerated (Anonymous, 1992; Hillen & Roelse, 1995; Janssen, 1995; van Boxel *et al.*, 1997). Although habitat restoration took place very quickly, the spider assemblage apparently reacts slowly, lacking typical coastal dune species in comparison with grey dune habitats along the Belgian and northern French coast.

An earlier analysis of the spider diversity in the Flemish coastal dunes indicated that the number of eurytopic species increases with the amount of sampled sites and the amount of used pitfall traps, but that almost all xerothermic species are caught with a limited amount of traps (Bonte *et al.*, 2003a). This means biologically that an increasing sampling effort results in a higher chance in finding non-typical species, invading from other surrounding dune habitats, but that no typical species will be caught additionally. This sampling bias explains the large amount of eurytopic species in the regions that were intensively sampled. Of more interest is the increased richness of non-dunal xerothermic species in these regions that are directly connected to heathland and chalk grassland and the paucity in the isolated Flemish coastal dunes. The increased diversity in grey dune habitats, connected to other xerothermic habitats, originates most likely from two different processes: (1) non-typical xerothermic species invade the grey dune from the adjacent optimal habitats in a source–sink system (Hanski, 1999) or (2) non-typical xerothermic species have established populations in the neighbouring coastal grey dunes but limited dispersal capacities and the lack of time have not enabled them to spread to more distant and/or geologically younger regions. For species with only marginal population sizes, grey dune habitats function as sinks, lying probably outside or at the edge of the fundamental niche, and population maintenance is only ensured by continuous colonization from the source populations in heathland or chalk grasslands. At first sight, others non-typical grey dune species have large populations, some even in the more distant AWD dunes. Grey dunes are, for these species, certainly good-quality habitats and their absence in the isolated region has to result from their inability to bridge the matrix of non-suitable habitat. A reduced ballooning performance is to be expected in these species, as this is the most important mode for distant dispersal (Bonte *et al.*, 2003b). Ecological time (Pianka, 1994) is an important process for the structuring of spider assemblages in coastal dunes along the North Sea. In spiders, analogous patterns of differentiated species presence have been observed on inland dunes in the lowland of Germany (Merkens, 2002).

Species occurring in isolated regions should, as a result, possess well-developed dispersal. Unfortunately, no ballooning data are available for most of these species. For other arthropods, carabid beetles (Desender *et al.*, 1995; Turin, 2000) and butterflies (Bink, 1992), analogous distribution patterns are observed and dispersal capacities can be measured directly (wing development in carabid beetles) or observed directly (migration propensity). In these groups, xerothermic species from heathland and chalk grassland, absent in the Belgian coastal grey dunes, but present in the coastal dunes of the Netherlands and the Boulonnais, have lower dispersal abilities, compared with species present in the Flemish coastal dunes (D. Bonte, unpublished data). Butterflies absent in the Flemish coastal dunes had a significantly lower range of migration behaviour (Bink, 1992), while carabid beetles, only present in the dune region of north Holland, are significantly more brachypterous (Desender *et al.*, 1995; Turin, 2000). Geological (historical) habitat isolation and ecological time is thus, at least partially, responsible for the observed species paucity of coastal grey dunes in Belgium and AWD.

Our data consequently indicate that differences in dune dynamics, latitude and connectivity to other xerothermic habitats influence the species composition of spiders in coastal grey dunes along the coast of the North Sea. The assemblage composition of spiders in grey dunes is, as a result, determined by sand dynamics and the linked habitat instability (Bonte *et al.*, 2002) and by ecological time.

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BIOSKETCHES

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Appendix 1 Abundance (number of individuals/no. traps) of the non-eurytopic species from coastal grey dunes, with indication of their optimal habitat and abundance in the sampled coastal grey dunes, chalk grassland and heathland

Species	Habitat	Chalk	BOUL	FCD	AWS	PWC	Heath
Acarthauchenius scurrilus (O.P.-Cambridge, 1872)	Xerotherm		r	r		r	r
Aelurillus v-insignatus (Walckenaer, 1802)	Chalk/heathland				fc	c	c
Agroeca cuprea Menge, 1873	Xerotherm		fc	c	c	c	c
Agroeca lusatica (L. Koch, 1875)	Heathland				fc	c	c
Agroeca proxima (O.P.-Cambridge, 1871)	Xerotherm		c	c	fc	c	c
Alopecosa barbipes (Sundevall, 1833)	Xerotherm	c	c	c	c	c	c
Alopecosa cuneata (Clerck, 1757)	Xerotherm		c	c	c	c	c
Alopecosa fabrilis (Clerck, 1757)	Xerotherm		c	c	c	c	
Araeoncus humilis (Blackwall, 1841)	Chalk/heathland	fc			r		r
Arctosa perita (Latreille, 1799)	Xerotherm		c	c	fc	fc	
Argenna subnigra (O.P. Cambridge, 1861)	Xerotherm		c	c	c	c	fc
Atypus affinis Eichwald, 1830	Chalk/heathland	fc	fc				
Aulonia albimana (Walckenaer, 1805)	Chalk/heathland				fc	c	c
Centromerus incilium (L. Koch, 1881)	North				c	c	c
Ceratinopsis romana (O.P.-Cambridge, 1872)	Coastal dunes		c	c	fc		
Cercidia prominens (Westring, 1851)	Heathland					r	fc
Cheiracanthium erraticum (Walckenaer, 1802)	Chalk/heathland		r			r	
Cheiracanthium virescens (Sundevall, 1833)	Xerotherm		fc	c	fc	c	
Clubiona frisia Wunderlich and Schütt 1995	Xerotherm		r	r	r	fc	
Crustulina guttata (Wider, 1834)	Heathland					r	c
Diplocephalus graecus (O.P-Cambridge, 1872)	South			c			
Drassodes cupreus (Blackwall, 1834)	Xerotherm	c	c	fc	fc	c	c
Drassodes lapidosus (Walckenaer, 1802)	Xerotherm		fc	fc	fc	fc	
Drassodes pubescens (Thorell, 1856)	Xerotherm	c	r	fc	r	r	
Dysdera erythrina (Walckenaer, 1802)	Chalk	c	r				
Erigone promiscua (O.P.-Cambridge, 1872)	Xerotherm	c	c	c	r		
Euophrus herbigrada (Simin, 1871)	Chalk		r				
Euryopis flavomaculata (C.L. Koch, 1836)	Chalk/heathland	fc	r	r	r	fc	fc
Evarcha falcata (Clerck, 1757)	Chalk/heathland	fc	r				
Hahnia montana (Blackwall, 1841)	Chalk/heathland	c	c			r	
Hahnia nava (Blackwall, 1841)	Xerotherm	c	r	c	c	c	c
Haplodrassus dalmatensis (L. Koch, 1866)	Xerotherm	r	c	c	fc	fc	
Haplodrassus signifer (C.L. Koch, 1839)	Xerotherm		c	c	c	c	c
Haplodrassus umbratilis (L. Koch, 1866)	Chalk/heathland		r			r	
Hypsosinga albovittata (Westring, 1851)	Xerotherm	r	c	c	fc	c	
Hypsosinga pygmaea (Sundevall, 1832)	Chalk	fc	r				
Lathys puta (O.-P. Cambridge, 1861)	Chalk	c	c				
Lepthyphantes mengei Kulczynski, 1887	Heathland				r	r	
Marpissa nivoyi (Lucas, 1846)	Xerotherm					r	
Mastigusa aerietina (Thorell, 1872)	Xerotherm			r			
Mecopisthes peusi Wunderlich 1972	South	r	c				
Metopobactrus prominulus (O.P.-Cambridge, 1872)	Xerotherm		r	fc		fc	c
Micaria dives (Lucas, 1846)	Xerotherm			fc	r	fc	
Micrargus subaequalis (Westring, 1851)	Chalk/heathland					r	
Ozyptila atomaria (Panzer, 1841)	Xerotherm	c	fc	c	fc	c	c
Ozyptila nigrita (Thorell, 1875)	Chalk/heathland	c	c		c	c	c
Ozyptila sanctuaria (O.-P. Cambridge, 1871)	South	fc	c			r	
Pardosa hortensis (Thorell, 1872)	South	r	r				
Pardosa monticola (Clerck, 1757)	Xerotherm	c	c	c	c	c	fc
Pelecopsis nemoralis (Blackwall, 1841)	Coastal dunes		c	c		r	r
Pellenes nigrociliatus (C.L. Koch, 1839)	South		r				
Peponocranium ludicrum (O.P.-Cambridge, 1861)	Chalk/heathland	c	c		fc	c	c
Philodromus aureolus (Clerck, 1757)	South		r				
Philodromus fallax Sundevall, 1833	Coastal dunes			r			
Phlegra fasciata (Hahn, 1826)	Xerotherm	fc	c	c	fc	fc	
Scotina celans (Blackwall, 1841)	Chalk	c	r				
Scotina gracilipes (Blackwall, 1859)	Heathland	r				fc	fc
Scotina palliardi (L. Koch, 1881)	Chalk/heathland	r	r			r	r

Appendix 1 *continued*

Species	Habitat	Chalk	BOUL	FCD	AWS	PWC	Heath
Sitticus distinguendus (Simon, 1868)	Coastal dunes		fc				
Sitticus saltator (O.P.-Cambridge, 1868)	Coastal dunes		c	c	fc		
Steatoda albomaculata (De Geer, 1778)	Chalk		r				
Steatoda phalerata (Panzer, 1801)	Chalk/heathland	c	fc		r	r	
Syedra gracilis (Menge, 1866)	South	c	r				
Textrix denticulata (Olivier, 1789)	Heathland					r	
Thanatus arenarius Thorell, 1872	South		c				
Thanatus striatus C.L. Koch, 1845	Xerotherm			r		r	
Trichopterna cito (O.P.-Cambridge, 1872)	Xerotherm		c	c	c	c	
Typhochrestus digitatus (O.P.-Cambridge, 1872)	Xerotherm		c	c	c	c	
Walckenaeria capito (Westring, 1861)	Heathland					r	
Walckenaeria dysderoides (Wider, 1834)	Heathland				r	fc	r
Walckenaeria furcillata (Menge, 1869)	Chalk	r	r				
Walckenaeria stylifrons (O.P.-Cambridge, 1875)	South		fc	fc			
Xerolycosa miniata (C.L. Koch, 1834)	Coastal dunes		fc	c			
Xysticus acerbus Thorell, 1872	Chalk	c	c				
Xysticus erraticus (Blackwall, 1834)	Xerotherm	c	c	fc	fc	c	r
Xysticus kempelini Thorell, 1872	South		fc				
Xysticus ninnii Thorell, 1872	South	fc	c	fc	c	c	
Xysticus sabulosus (Hahn, 1832)	Coastal dunes		c	c			
Zelotes electus (C.L. Koch, 1839)	Xerotherm		c	c	c	c	c
Zelotes latreilli (Simon, 1878)	Chalk/heathland	c	c		fc	r	
Zelotes longipes (L. Koch, 1866)	Xerotherm		c	c	c	c	
Zelotes pedestris (C.L. Koch, 1837)	Chalk/heathland	c	fc			r	
Zelotes pusillus (C.L. Koch, 1833)	Chalk/heathland	fc	r		c	c	c
Zelotes subterraneus (C.L. Koch, 1833)	Heathland					r	

Abundance legend: rare (r): abundance < 0.1; fairly common (fc): abundance [0.1–0.5]; common (c): abundance > 0.5.