Sand dynamics in coastal dune landscapes constrain diversity and life-history characteristics of spiders

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Summary

1. In fragmented landscapes where natural disturbance acts at the local level, community composition can be altered either by 'species-by-species matching', with community-wide character displacement, or by 'constrained species sorting', whereby disturbance favours species with distinct ecological traits. It is necessary to understand such species shifts when aiming to detect bottlenecks associated with changing disturbance dynamics at different spatial levels. Such an understanding also provides insight into the underlying ecological mechanisms in operation and allows identification of species of conservation concern.

2. This approach to understanding species' shifts was applied to a study of spider diversity and life-history variation in relation to sand dynamics in stabilized and dynamic grey dune landscapes located along the coasts of France, Belgium and the Netherlands.

3. Local (α) diversity appeared to decrease with increasing local sand dynamics in both stable and dynamic landscapes. In dynamic dune landscapes, β-diversity decreased significantly and approached regional (γ) diversity under local grey dune stabilization; in stabilized landscapes, β-diversity was not affected by local sand dynamics.

4. Comparative analyses of ecological traits revealed shifts in life-history patterns, suggesting that patterns in local diversity resulted from species sorting. Species from fragments characterized by high sand dynamics showed narrower niche breadths, larger body sizes and longer generation times, while summer-active species tended to become residential after sand stabilization. This provides evidence for constrained species sorting in which natural disturbance (through local sand dynamics) allows only species with distinct ecological traits to persist.

5. *Synthesis and applications.* Species with larger body sizes, longer generation times and a higher degree of habitat specialization (i.e. related to dispersal ability) would be expected to be more vulnerable at dynamic sites and more prone to extinction than their counterparts from stabilized fragments. In particular, species with a burrowing lifestyle would be expected to go extinct locally as a result of increasing soil development and soil hardness. Shifts in species composition were found to be more pronounced in dynamic landscapes. Hence ensuring conservation of sand dynamics at a landscape level rather than at a local level is of prime importance when aiming to conserve typical psammophilous spider species within local assemblages in grey dune habitats.

Key-words: body size, comparative analysis, conservation, diurnal activity, generation time, metacommunity, seasonal activity

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Introduction

Metacommunity theory predicts that the abundance of species and community composition in spatially structured, heterogeneous environments will be altered either by 'species sorting' or 'mass effects', depending on the

relative importance of dispersal for the species concerned (Leibold *et al*. 2004). In species sorting, i.e. matching of species with their favoured habitat, the patterns of species distribution among patches is expected to relate to each species' relative ability to exist and successfully interact with other species in the larger metacommunity. Mass effects influence local abundances of species with high dispersal rates through either net emigration (source populations) or net immigration (sink populations). If mass effects occur in patches with high local disturbance, some species may persist as fugitives despite being poor competitors (Lytle 2001; Leibold & Miller 2004). Trade-offs between both colonization and competitive abilities can therefore be expected to affect assemblage composition and structure.

If such trade-offs primarily occurred at a local scale, they may promote species coexistence predominantly within patches. Consequently α-diversity would be expected to be high (Kneitel & Chase 2004). Alternatively, if such trade-offs existed at a regional scale, α-diversity would be expected to be low, as only good competitors or good dispersers would be able to persist within each locality. Consequently, β-diversity would be expected to be high because species differing in their degree of specialization or dispersal would be expected to occupy different heterogeneous and homogeneous patches, respectively. If patch heterogeneity was related to disturbance, good dispersers may, however, fail to settle under disturbed conditions. Under such a scenario (i) α-diversity would be expected to be low if disturbance is high, (ii) β-diversity would be expected to increase if only a few species were adapted to survive under those conditions (Pianka 1994) and (iii) β-diversity would be expected to decrease if the assemblages experiencing disturbance were inhabited by species drawn at random from a regional species pool. Local disturbance is therefore expected to exert a minor effect on regional diversity (Chase 2003). Landscape history and patch connectivity are also assumed to affect local and regional patterns of species diversity (Loreau 2000; Chase 2003; Kneitel & Chase 2004).

However, whether such shifts in diversity and assemblage composition are constrained by disturbance-related factors remains open to question. In community-wide character displacement (CWCD), species sorting (or species-for-species matching; Schluter 2000b) is expected to produce groups of ecologically similar species, characterized by similar life-history patterns, in different localities. Such patterns are believed to have evolved by (i) natural selection promoting divergent phenotypes that reduce competition or (ii) ecological sorting in which competition induces local extinction (Marchinko, Nishizaki & Burns 2004). However, from a metacommunity perspective, species sorting along gradients in communities might result in reverse patterns in which locally coexisting species are more similar than random selections, as species combinations that are more similar in resource use appear to be less prone to invasion by new species (Leibold 1998; Leibold *et al*. 2004). Where

heterogeneous levels of local disturbance are imposed on spatially structured communities, such species shifts would be determined by environmental constraints that limit character displacement. Hence, community wide character shifts (CWCS), rather than character displacement, would be expected.

In coastal dunes, aeolic dynamics (e.g. severe sand displacement) is a geomorphological process that is essential in maintaining the landscape in its dynamic phase (Provoost 2004), i.e. characterized by an extreme microclimate, high summer temperatures and the absence of soil development. Many studies have documented significant effects on diversity patterns and the assemblage structure of plants and animals of reducing sand dynamics (Bach 2001; Bonte, Baert & Maelfait 2002; Kowalchuk, De Souza & Van Veen 2002; Snyder & Boss 2002; Franks & Peterson 2003; Bonte *et al*. 2004b; Jun, Clement & Roze 2004). However, whether shifts in species composition result from species-by-species matching with CWCD or from constrained species sorting, i.e. in which disturbance favours species with distinct ecological traits, is poorly documented in animals. In plants, aeolic disturbance is known to favour species adapted to sand burial that exhibit fast growth or tolerance to darkness (Maun 1998; Garcia-Mora, Gallego-Fernandez & Garcia-Novo 1999; Martinez & Maun 1999; Wilson & Sykes 1999), seasonal growth and flowering (Garcia-Mora, Gallego-Fernandez & Garcia-Novo 1999), below-ground spreading root networks (Garcia-Mora, Gallego-Fernandez & Garcia-Novo 1999), leaf morphology related to desiccation resistance (Garcia-Mora, Gallego-Fernandez & Garcia-Novo 1999) and/or enhanced mycorrhizal activity (Maun 1998). In animals, spiders from white dunes show higher levels of thermal tolerance than species preferring thick vegetation in stabilized dune habitats (Almquist 1970). The latter species also show a lower resistance to desiccation (Almquist 1971). In Namib desert spiders, psammophilious species show adaptations to desiccation resistance through larger size (hence reduced surface-to-volume ratio), being night active and active only during the humid season (Henschel 1997). They also have a burrowing life-style, a low metabolism and cryptic coloration.

Earlier studies (Bonte, Maelfait & Baert 2004) revealed strong effects of dispersal ability on spider species' distributions among grey dune fragments. As dispersal is negatively related to the degree of habitat specialization (Bonte *et al*. 2003d) and hence to competitive ability in optimal habitat, patterns of species sorting under community-wide character shifts in ecologically relevant traits are particularly expected in populations subjected to stress and disturbance. Using this conceptual framework as a basis, we studied the patterns of species diversity and ecological characteristics in spiders from fragmented grey dune habitats subject to varying degrees of natural sand dynamics and anthropogenic stabilization of the dunes. To reduce confounding effects of phylogeny, analyses of ecological traits were conducted within the

most diverse spider families and hence functional groups that show similar life histories (Foelix 1996) as a result of a common evolutionary history (Blondel 2003).

Understanding shifts in arthropod assemblages is essential for the detection of bottlenecks within the process of declining sand dynamics. As time and logistics do not generally permit population studies for prioritizing conservation actions to be conducted on a species-by-species basis (Bennet & Owens 1997; Jennings *et al.* 2001; Bessa-Gomez *et al.* 2003), comparative methods may provide insight into the underlying ecological mechanisms in operation and allow prior identification of species of conservation concern (Kolar & Lodge 2002; Reed & Shine 2002). To this end, additional comparative analyses of ecological traits between congenerics were used to reduce phylogenetic effects (Gaston & Kunin 1997; Bevill & Louda 1999). As decreasing sand dynamics result in deeper soil development and higher nutrient availability, we expected an increase in eurytopic species with shorter generation times, higher local densities and better-developed aerial dispersal capacities. In addition, as sand stabilization results in a more buffered microclimate, we expected higher frequencies of summer-active, diurnal and smaller species because of their lower sensitivity to desiccation. We also considered whether species diversity and ecological patterns were affected by the interaction between local (patch related) sand dynamics and the degree of large scale sand dynamics within the entire dune landscape. Therefore patterns in α-, β- and γ-diversity and spider ecology were studied in both stabilized and dynamic dune landscapes.

Methods

STUDY AREAS AND SAMPLING STRATEGY

The study was conducted in grey dune habitats, known as fixed coastal dunes with herbaceous vegetation, varying in sand dynamics. In such habitats, the magnitude of sand dynamics is related to vegetation and soil development as sand stabilization results in soil formation, producing a stronger vegetation development ranging from moss dunes with sand blowouts towards stable, but low-productivity, dune grasslands (Provoost *et al.* 2004). The vegetation consisted of (i) dunes dominated by Atlantic moss and (ii) dunes with a distinct soil organic layer, and either *Cladonio-Koelerietalia* (on the lime-rich grey dunes) or *Trifolio-Festucetalia ovinae* (on the decalcified grey dunes) grassland (Provoost *et al.* 2004). From an ecological perspective, the grey dune habitat represents the dry component of the 'stressed dune landscape', where succession is determined by top-down regulating stress factors and bottom-up (xerosere) organization.

Field work was conducted in four dune areas along the North Sea coast of northern France, Belgium and the Netherlands: the Boulonnais dunes (BOUL), Flemish coastal dunes (FCD), coastal dunes of the Amsterdam Water Supply (AWD) and dunes of the Provincial Water

Company North-Holland (PWN). These four dune areas differ in biogeography, the level of sand dynamics and, consequently, spider fauna composition (Bonte *et al.* 2003a). BOUL and FCD are dynamic dune landscapes with large areas of mobile dunes, whereas AWD and PWN have been stabilized by human management during the last century. In each dune area, we sampled large grey dune fragments (as the richness of specific xerotherm species declines in small patches; Bonte, Baert & Maelfait 2002) covering the full range of local sand dynamics. Seven fragments were sampled in BOUL and FCD, six in AWD and eight in PWN. Within each fragment, five pitfall traps (9 cm, filled with a 6% formalin-detergent solution) were installed in a line 5 m apart. Traps were emptied every fortnight and sampling occurred between March–November 1999 to ensure the entire spider assemblage present at each site was sampled. As described in Bonte *et al.* (2003a), PCA analysis of site-specific environmental parameters revealed a single significant principal component that was strongly correlated with aspects of soil development, sand dynamics and vegetation development (vegetation dimensionality). This principal component was therefore used to indicate and quantify the degree of sand dynamics within each landscape fragment.

LOCAL DIVERSITY

α-diversity was assessed by counting the total number of species for which both five males and five females were recorded. In this way, only resident species were included and accidental vagrants were excluded (Bonte, Maelfait & Baert 2004). From a total of 190 captured species (represented by 35975 individuals), 68 species, belonging to five dominant families (Gnaphosidae, Thomisidae, Lycosidae, Erigoninae and Linyphiinae), were retained (see Appendix S1 in the supplementary material). β-diversity was estimated by dividing the regional species richness in grey dune habitats (γ-diversity) by the number of local (i.e. within patches) species (α-diversity) (Whittaker 1972).

ASSESSMENT OF LIFE-HISTORY CHARACTERISTICS

Species-specific body sizes were taken from Roberts (1985, 1998). As body size differs between sexes, mean values of the larger females were used in all subsequent analyses. In Lycosidae, two burrowing species [i.e. *Alopecosa fabrilis* (Clerck 1757) and *Arctosa perita* (Latreille 1799)] were recorded; all other species live exclusively above-ground (Roberts 1998).

Data on niche breadth were derived from Hänggi, Stöckli & Nentwig (1995), who reviewed the number of central European habitats in which species occur. Earlier analysis showed that this ranking index significantly correlated with niche breadth values based on indicator analysis in the Flemish coastal dunes (Bonte *et al.* 2003d). Average activity density was calculated

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by dividing the total number of individuals by the number of traps in which the species was captured. While we are aware that pitfall catches reflect a combined activity density pattern that shows large differences as a result of inter- and intraspecies variation (Maelfait & Baert 1975; Bonte, Maelfait & Baert 2004; Schmidt *et al.* 2005), the nature of our analysis (i.e. comparing patterns within families and, especially, between congeneric species) still allowed us to predict patterns in species density because activity patterns can be assumed to be similar among (very) related species occurring in structurally similar habitats.

As species-specific data on ballooning propensity (a precursor for aerial dispersal in spiders; Bell *et al.* 2005) was lacking, we assigned species to the category of 'ballooners' if aeronautic dispersal was observed either in the field or in the laboratory, irrespective of its magnitude (Bonte, Maelfait & Hoffmann 1998; Bonte *et al.* 2003d; Bell *et al.* 2005; D. Bonte, unpublished data).

Seasonal activity patterns were derived from Roberts (1985), catalogues of Belgian spiders (Alderweireldt & Maelfait 1990; Ransy & Baert 1991; Janssens 1993; Baert 1996) and personal data. Following Schaefer (1976), we assigned spiders to one of four classes: eurychrone species, in which adults are active throughout the year (type I); stenochrone species, with their main activity during March–June (type IIa); stenochrone species, with an activity peak during June–September (type IIb); and stenochrone or diplochrone species, with their main activity during October–March (type IV–V). In combination with data on temporal distribution of immatures from different size classes, this allowed us to assess species-specific generation times expressed as generation time 6 months^{-1}. Species with a biennial life cycle were assumed to require on average 1·5 years for complete development. Diurnal activity patterns were assessed by separate pitfall trapping during day and night. These data were mainly derived from coastal dunes (R. Bosmans, L. Baert, J.-P. Maelfait & J. Hublé, unpublished data; D. Bonte, unpublished data; Bonte, Hoffmann & Maelfait 2000) and from the southern part of Belgium (J.-P. Maelfait, L. Baert, D. Bonte, unpublished data). Species were classified as day active, night active or indifferent, where the species showed similar activities during day and night. An overview of all life-history traits is given in Appendix S1 in the supplementary material.

STATISTICAL ANALYSIS

Life-history variations along assemblages

Life-history characteristics were considered for the species occurring in the different fragments along the gradient of sand dynamics. No weight was given to local abundance levels. Mixed models were used to investigate differences in life-history traits in relation to sand dynamics, with 'trait' or 'diversity measure' as the dependent variable and sand dynamics as a continuous factor. Because earlier analysis revealed differences in

species composition between dynamic and stabilized dunes, landscape type was included as a fixed factor, while dune area was included as random factor nested within landscape (i.e. BOUL and FCD within dynamic landscape, AWD and PWN within stabilized landscapes). Because fragments were distant from each other, they were treated as independent units and no additional correction for spatial dependence was applied. Because several species, captured within and between landscape fragments, cannot be used as independent replicates with respect to the influence of sand dynamics on related life-history characteristics, mean values of these traits within each fragment are the appropriate unit of replication ($n = 28$). We therefore determined a weighted average of continuous life-history characteristics (niche breadth, body size, local activity-density, generation time) and analysed these traits by means of general linear models, assuming a normal distribution. Both two-factor interactions, body size × seasonal activity and body size × diurnal activity, were modelled. Categorical data (seasonal activity, aeronautic dispersal and diurnal activity) were analysed at fragment level with logistic mixed models. Analyses were conducted with Proc mixed (continuous data) or Proc glimmix (logistic models) using SAS 9·1 (SAS 2003). Backward stepwise elimination of landscape × aeolics and landscape was used where these factors did not contribute significantly to the full model. Residuals (standardized residuals in case of logistic regression) were checked for normal distribution. Random factors, even in case of low levels of explained variation, were retained in the final model in order to optimize the level of generality of the distribution models (Vaughan & Ormerod 2005). Effective degrees of freedom were approximated by the Satterthwaite procedure (Verbeke & Molenberghs 2000).

Because all the traits under study are dependent on phylogenetic effects, family effects were also taken into account. Third-order interactions with family were significant for body size ($F_{4,118} = 5·25$, $P < 0·001$), niche breadth ($F_{4,117} = 3·02$, $P = 0·002$), generation time ($F_{4,120} = 4·11$, $P = 0·003$), local abundance ($F_{4,120} = 4·34$, $P = 0·003$), aerial dispersal ($F_{4,118} = 2·711$, $P = 0·034$) and/or did not meet convergence criteria for seasonal activity and day–night activity. Analyses were therefore performed separately for five species-rich (sub)families showing substantial trait variation (Gnaphosidae, Lycosidae, Thomisidae, Erigoninae and Linyphiinae). Bonferroni correction was not applied because the chances of type I errors as a result of multiple comparisons were considered to be negligible in comparison with the level of residual variance resulting from the presence of non-typical species invading from neighbouring habitats (Bonte, Baert & Maelfait 2002; Moran 2003).

Comparative analysis

InVal-indicator analysis (Dûfrene & Legendre 1997) was applied to identify species for dynamic (PCA < −1) and stabilized (PCA > 1) fragments across all study

Table 1. Species-couples from five spider (sub) families used in the comparative analysis of life-history traits

(Sub) family	Species pairs (dynamic-stabilised)
Liocranidae	*Agroeca lusatica – proxima*
Lycosidae	*Alopecosa barbipes – cuneata*
Lycosidae	*Alopecosa fabrilis – pulverulenta*
Erigoninae	*Erigone promiscua – dentipalpis*
Erigoninae	*Oedothorax apicatus – retusus*
Erigoninae	*Parapelecopsis nemoralis – Pelecopsis parallela*
Erigoninae	*Walckenaeria stylifrons – antica*
Thomisidae	*Xysticus kochi – cristatus*
Thomisidae	*Xysticus sabulosus – ninnii*
Gnaphosidae	*Zelotes longipes – electus*

areas. Within this set, we selected 10 pairs of congeneric species from five different families (Table 1) in which paired species from each couple were indicative of stabilized vs. dynamic grey dune fragments, respectively. Comparative analysis within each of the species pairs allowed us to omit phylogenetic effects. Pairwise one-tailed tests for dependent continuous and count data (respectively *t*-tests, rank sign tests) and categorical data (McNemar χ^2-tests) were applied.

Results

SPECIES DIVERSITY

α-diversity increased with decreasing sand dynamics ($r = 0.36 \pm 0.12$ SE, $F_{1,26} = 30.84$, $P < 0.0001$; Fig. 1). Neither landscape type ($F_{1,24} = 0.01$, $P > 0.05$) nor the two-factor interaction with local sand dynamics ($F_{1,23.4} = 2.04$, $P > 0.05$) was statistically significant, while no variation was attributed to the dune area ($s^2 < 0.001$). In contrast, β-diversity ($F_{sand\_dynamics} = 14.34$, d.f. = 1,23·1, $P = 0.0009$; $F_{landscape} = 0.37$, d.f. = 1,2·53, $P = 0.591$; $F_{sand\_dynamics \times landscape} = 5.15$, d.f. = 1,23·1, $P = 0.034$) decreased with decreasing sand dynamics (Fig. 1) more strongly in dynamic (estimated slope -0.23 ± 0.11 SE) than in stabilized dune landscapes (estimated slope -0.07 ± 0.10 SE). As with α-diversity, random effects did not significantly explain additional variation ($s^2 < 0.005$).

NICHE BREADTH

Erigoninae ($r = 0.67 \pm 0.34$) showed a significant increase in generalist species with decreasing local sand dynamics, independent of landscape effect (Table 2). However, shifts in community-wide niche breadth indicated significant interactions with landscape type for the families Gnaphosidae and Lycosidae: in dynamic landscapes, decreasing local sand dynamics resulted in a steeper increase of eurytopic species than in stabilized landscapes (Fig. 2a; Gnaphosidae $r_{dyn} = 2.00 \pm 0.47$ SE, $r_{stab} = -0.11 \pm 0.47$ SE; Fig. 2b; Lycosidae $r_{dyn} = 3.44 \pm 0.82$ SE, $r_{stab} = 0.92 \pm 0.84$ SE). A similar trend was observed for Thomisidae (Table 2; $r_{dyn} = 1.70 \pm 0.71$ SE, $r_{stab} = -0.68 \pm 0.72$ SE).
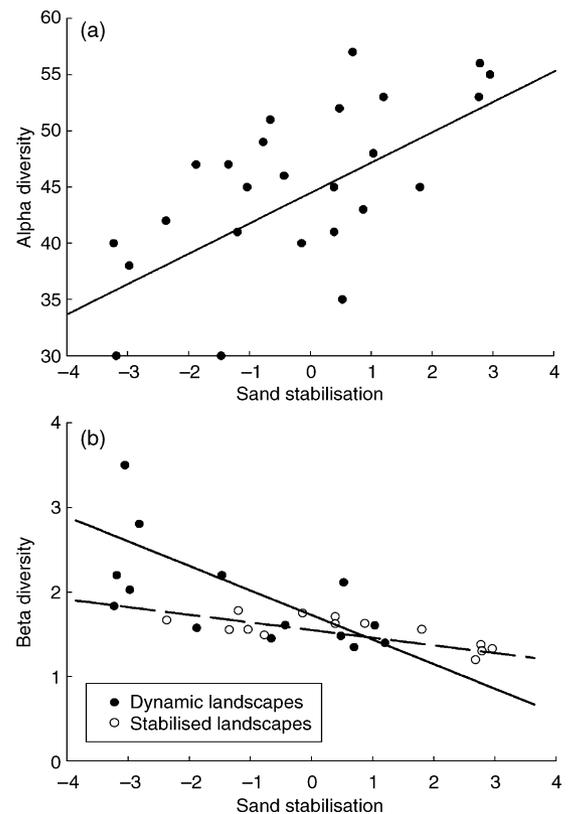
Fig. 1. Relationship between spider species diversity and the degree of sand dune stabilisation in coastal grey dune fragments. (a) α-diversity; (b) β-diversity. Points: observed data; Full line: modelled relationship for dynamic landscapes; Dashed line: modelled relationship for stabilised landscapes. The principal component scores arising from a PCA-analysis of site-specific environmental parameters is used to indicate an increasing degree of sand stabilisation along the *x* axis.
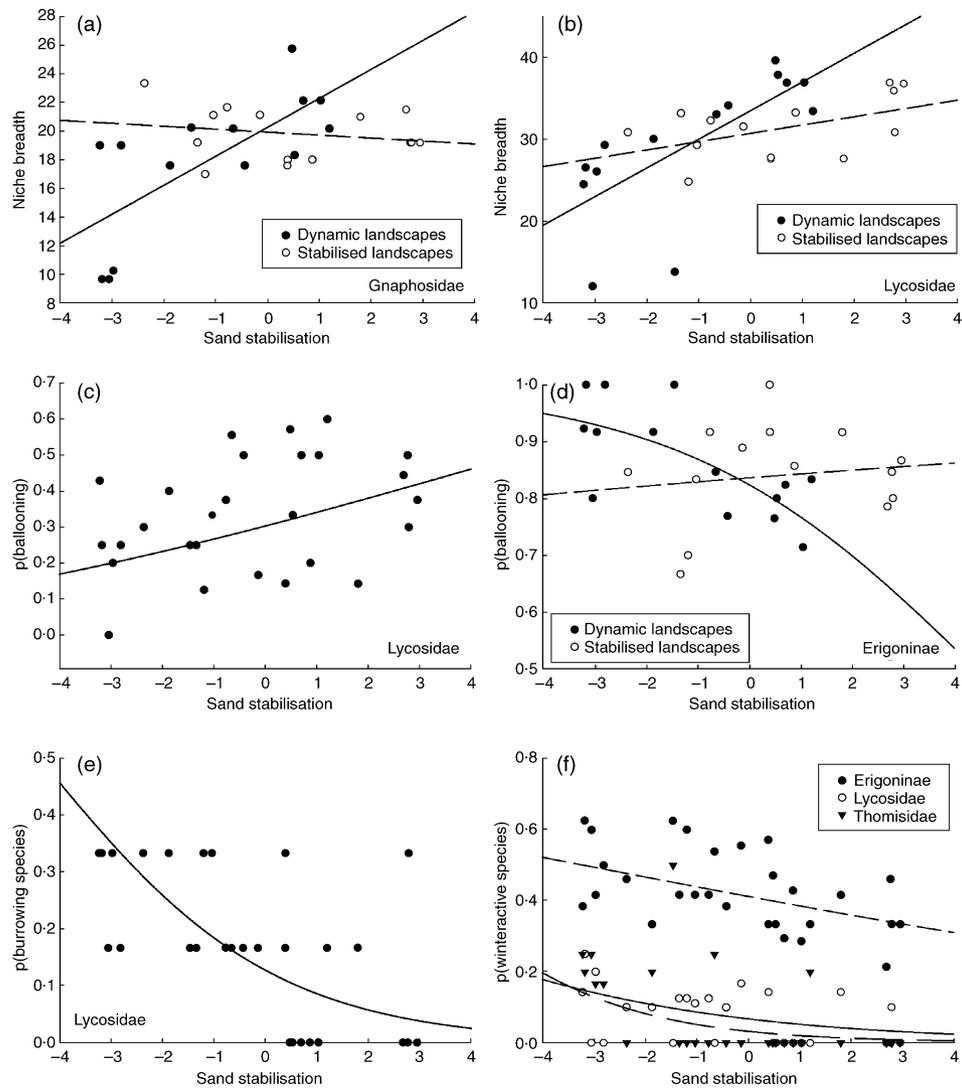
LIFE-HISTORY CHARACTERISTICS ALONG ASSEMBLAGES

Body size was negatively related with sand stabilization for Lycosidae, with a stronger decrease in dynamic landscapes ($r = -0.55 \pm 0.11$ SE) than in stabilized landscapes ($r = -0.20 \pm 0.11$ SE). For Thomisidae, Erigoninae and Linyphiinae, body size remained constant irrespective of aeolic dynamics (Table 3). For Gnaphosidae, an increase in body size was observed in dynamic landscapes ($r = 0.45 \pm 0.12$ SE) but not in stabilized landscapes ($r = -0.03 \pm 0.12$ SE). No community-wide interactions occurred between body size patterns and seasonal activity or diurnal activity.

With increasing sand dynamics, average Lycosidae generation time decreased ($r = -0.03 \pm 0.01$ SE; Table 3). For Gnaphosidae and Thomisidae, decreasing generation times were only observed in dynamics landscapes (Gnaphosidae, $r_{dyn} = -0.07 \pm 0.02$ SE, $r_{stab} = -0.02 \pm 0.02$ SE; Thomisidae, $r_{dyn} = -0.06 \pm 0.01$ SE, $r_{stab} = -0.01 \pm 0.02$ SE).

Local activity density patterns (Table 3) decreased for Linyphiinae ($r = -0.34 \pm 0.16$ SE) and Erigoninae ($r = -0.16 \pm 0.08$ SE) in both stabilized and dynamic

Table 2. Influence of local sand dynamics (aeolic dynamics) and landscape type (stabilised versus dynamic) on niche breadth in grey sand dune spider communities. GLM results for each of the five spider (sub) families studied. Num. d.f.: numerator degrees of freedom; Den. d.f.: denominator degrees of freedom

(Sub) family	Factor	Num. d.f.	Den. d.f.	*F*	*P*
Gnaphosidae	Aeolic dynamics	1	24	8·26	0·008
	Landscape	1	24	0·08	0·776
	Aeolic dynamics * Landscape	1	24	12·46	0·002
Lycosidae	Aeolic dynamics	1	24	16·69	0·004
	Landscape	1	24	1·69	0·206
	Aeolic dynamics * Landscape	1	24	5·06	0·034
Thomisidae	Aeolic dynamics	1	25·6	2·28	0·143
	Landscape	1	2·19	0·30	0·656
	Aeolic dynamics * Landscape	1	22·4	3·19	0·088
Erigoninae	Aeolic dynamics	1	25·8	3·73	0·064
	Landscape	1	2·16	0·06	0·822
	Aeolic dynamics * Landscape	1	22·5	0·10	0·753
Linyphiinae	Aeolic dynamics	1	23·7	0·17	0·682
	Landscape	1	2·2	3·39	1·195
	Aeolic dynamics * Landscape	1	22·7	1·11	0·303

Fig. 2. Relationship between spider life-history characteristics and the degree of sand stabilisation in coastal grey dune fragments. (a) Gnaphosidae niche breadth; (b) Lycosidae niche breadth; (c) Lycosidae ballooning ability; (d) Erigoninae ballooning ability; (e) incidence of burrowing lycosid species; (f) winter activity in Erigoninae, Lycosidae, Thomisidae. Points: observed data; in (b) and (d) full line: regression model dynamic landscape, dashed line: regression model stabilised landscape; in (f) full line: regression model for Lycosidae, medium dashed line: regression model for Erigoninae, large dashed line: regression model for Thomisidae.

Table 3. Influence of local sand dynamics (aeolic dynamics) and landscape type (stabilised versus dynamic) on body size, local activity and generation time in grey sand dune spider communities. GLM results for each of the five spider (sub) families studied. Num. d.f.: numerator degrees of freedom; Den. d.f.: denominator degrees of freedom

Trait	(Sub) family	Factor	Num. d.f.	Den. d.f.	F	P
Body size	Gnaphosidae	Aeolic dynamics	1	22·8	6·91	0·015
		Landscape	1	2·23	1·73	0·307
		Aeolic dynamics * Landscape	1	22·8	6·81	0·016
	Lycosidae	Aeolic dynamics	1	24	27·29	< 0·001
		Landscape	1	24	7·82	0·010
		Aeolic dynamics * Landscape	1	24	4·36	0·047
	Thomisidae	Aeolic dynamics	1	24	2·67	0·115
		Landscape	1	1·98	5·40	0·148
		Aeolic dynamics * Landscape	1	22·8	2·28	0·145
	Erigoninae	Aeolic dynamics	1	25	0·14	0·713
		Landscape	1	26	3·96	0·057
		Aeolic dynamics * Landscape	1	24	0·43	0·519
	Linyphiinae	Aeolic dynamics	1	25	0·29	0·595
		Landscape	1	26	20·88	< 0·001
		Aeolic dynamics * Landscape	1	24	0·86	0·363
Local activity-density	Gnaphosidae	Aeolic dynamics	1	24	14·19	0·001
		Landscape	1	24	2·21	0·499
		Aeolic dynamics * Landscape	1	24	9·59	0·005
	Lycosidae	Aeolic dynamics	1	24	6·00	0·022
		Landscape	1	24	0·00	0·996
		Aeolic dynamics * Landscape	1	24	4·33	0·048
	Thomisidae	Aeolic dynamics	1	26	0·53	0·482
		Landscape	1	25	0·00	0·964
		Aeolic dynamics * Landscape	1	24	2·97	0·698
	Erigoninae	Aeolic dynamics	1	26	3·93	0·058
		Landscape	1	25	0·01	0·923
		Aeolic dynamics * Landscape	1	24	0·13	0·720
	Linyphiinae	Aeolic dynamics	1	26	4·47	0·044
		Landscape	1	2·29	0·38	0·592
		Aeolic dynamics * Landscape	1	22·9	1·17	0·290
Generation time	Gnaphosidae	Aeolic dynamics	1	23·6	19·14	< 0·001
		Landscape	1	25	2·33	0·242
		Aeolic dynamics * Landscape	1	23·6	6·77	0·016
	Lycosiclae	Aeolic dynamics	1	26	9·89	0·004
		Landscape	1	25	0·50	0·488
		Aeolic dynamics * Landscape	1	24	0·46	0·505
	Thomisidae	Aeolic dynamics	1	24	10·71	0·003
		Landscape	1	24	23·36	< 0·001
		Aeolic dynamics * Landscape	1	24	4·88	0·037
	Erigoninae	Aeolic dynamics	1	26	0·53	0·471
		Landscape	1	25	2·23	0·148
		Aeolic dynamics * Landscape	1	24	0·31	0·583
	Linyphiinae	Aeolic dynamics	1	24·7	0·74	0·399
		Landscape	1	2·56	13·38	0·046
		Aeolic dynamics * Landscape	1	24	0·73	0·401

landscapes. Gnaphosidae only showed an activity density decrease in dynamic landscapes compared with stabilized landscapes ($r_{dyn} = -0.29 \pm 0.06$ SE, $r_{stab} = -0.01 \pm 0.06$ SE). In contrast, Lycosidae showed an increasing activity density pattern in relation to increasing sand stabilization, although only in dynamic landscapes ($r_{dyn} = 2.84 \pm 0.80$ SE, $r_{stab} = 0.23 \pm 0.83$ SE).

Lycosidae species with ballooning ability increased with decreasing local sand dynamics (Table 3; $r = 0.18 \pm 0.09$ SE; Fig. 2c). In Erigoninae (Table 4), frequencies of ballooning species declined only in dynamic dune landscapes ($r_{dyn} = -0.35 \pm 0.08$ SE, $r_{stab} = 0.05 \pm 0.08$ SE; Fig. 2d). In Lycosidae, burrowing species were replaced by epigeic, wandering species under declining sand dynamics ($r = -0.439 \pm 0.13$ SE, $F_{1,23} = 11.68$, $P = 0.002$; Fig. 2e). The relative occurrence of day-active, night-active, type I and type IIa species did not vary in relation to sand dynamics (all $F < 1.00$, $P > 0.10$), independent of landscape type. Lycosidae ($r = -0.279 \pm 0.12$ SE, $F_{1,23} = 3.18$, $P = 0.087$), Thomisidae ($r = -0.511 \pm 0.19$, $F_{1,23} = 4.09$, $P = 0.055$) and Erigoninae ($r = -0.111 \pm 0.06$ SE, $F_{1,23} = 3.36$, $P = 0.080$) tended to show shifts towards winter activity (type IV–V) in dynamic localities (Table 4 and Fig. 2f). Only in the latter family was this shift accompanied by a decrease in type IIb (summer-active) species ($r = 0.143 \pm 0.08$ SE, $F_{1,23} = 4.59$, $P = 0.043$).

Table 4. Influence of local sand dynamics (aeolic dynamics) and landscape type (stabilised versus dynamic) on the proportion of species with aerial dispersal propensity and the proportion of winter-active species in grey sand dune spider communities. GLZM results for each of the five spider (sub) families studied. Num. d.f.: numerator degrees of freedom; Den. d.f.: denominator degrees of freedom

Trait	(Sub) family	Factor	Num. d.f.	Den. d.f.	*F*	*P*
Aerial dispersal propensity	Gnaphosidae	Aeolic dynamics		Model did not show convergence		
		Landscape		Model did not show convergence		
		Aeolic dynamics * Landscape		Model did not show convergence		
	Lycosidae	Aeolic dynamics	1	23	4·17	0·053
		Landscape	1	2	8·07	0·105
		Aeolic dynamics * Landscape	1	22	0·57	0·456
	Thomisidae	Aeolic dynamics	1	23	0·03	0·866
		Landscape	1	2	0·26	0·660
		Aeolic dynamics * Landscape	1	22	0·01	0·912
	Erigoninae	Aeolic dynamics	1	23	1·26	0·273
		Landscape	1	2	0·11	0·757
		Aeolic dynamics * Landscape	1	22	4·17	0·053
	Linyphiinae	Aeolic dynamics	1	23	0·25	0·619
		Landscape	1	2	8·35	0·119
		Aeolic dynamics * Landscape	1	22	0·33	0·571
Winter activity	Gnaphosidae	Aeolic dynamics		Model did not show convergence		
		Landscape		Model did not show convergence		
		Aeolic dynamics * Landscape		Model did not show convergence		
	Lycosidae	Aeolic dynamics	1	23	3·18	0·087
		Landscape	1	2	2·91	0·231
		Aeolic dynamics * Landscape	1	22	1·47	0·238
	Thomisidae	Aeolic dynamics	1	23	4·09	0·055
		Landscape	1	2	3·02	0·178
		Aeolic dynamics * Landscape	1	22	0·17	0·684
	Erigoninae	Aeolic dynamics	1	23	3·36	0·080
		Landscape	1	2	0·62	0·514
		Aeolic dynamics * Landscape	1	22	0·02	0·891
	Linyphiinae	Aeolic dynamics	1	22	0·69	0·415
		Landscape	1	2	7·61	0·110
		Aeolic dynamics * Landscape	1	21	0·26	0·615

Table 5. Comparative analysis of spider life history traits for congeneric species indicative of dynamic and stabilised coastal grey dune fragments. The species couplets used in the analysis are shown in Table 1

| Trait	Test statistic	*P*	Mean *value/freq.* dynamic fragments	Mean *value/freq.* stabilised fragments
Body size	$Z = 2·00$	0·045	5·932	4·890
Generation time	$Z = 2·84$	0·004	1·455	1·273
Winter activity	$X^2 = 8·25$	0·016	70%	0%
Night activity	$X^2 = 0·13$	0·723	60%	30%
Ballooning	$Z = 1·23$	0·221	60%	80%
Niche breadth	$Z = 2·85$	0·004	15·818	38·272
Local activity	$Z = -0·32$	0·752	5·492	5·797

COMPARATIVE ANALYSIS

Direct comparisons among congeneric spider species confirmed community-wide shifts in the above reported life-history traits (Table 5). Indicator species from dynamic grey dunes were characterized by larger body sizes, longer generation times, a higher frequency of winter activity and narrower niche breadths (Fig. 3).

Discussion

LOCAL AND REGIONAL EFFECTS ON SPECIES DIVERSITY

As has also been documented for agricultural landscapes (Schmidt *et al.* 2005), loss of sand dynamics in coastal grey dunes affected patterns of local spider diversity, but in a landscape-related way. Under decreasing sand
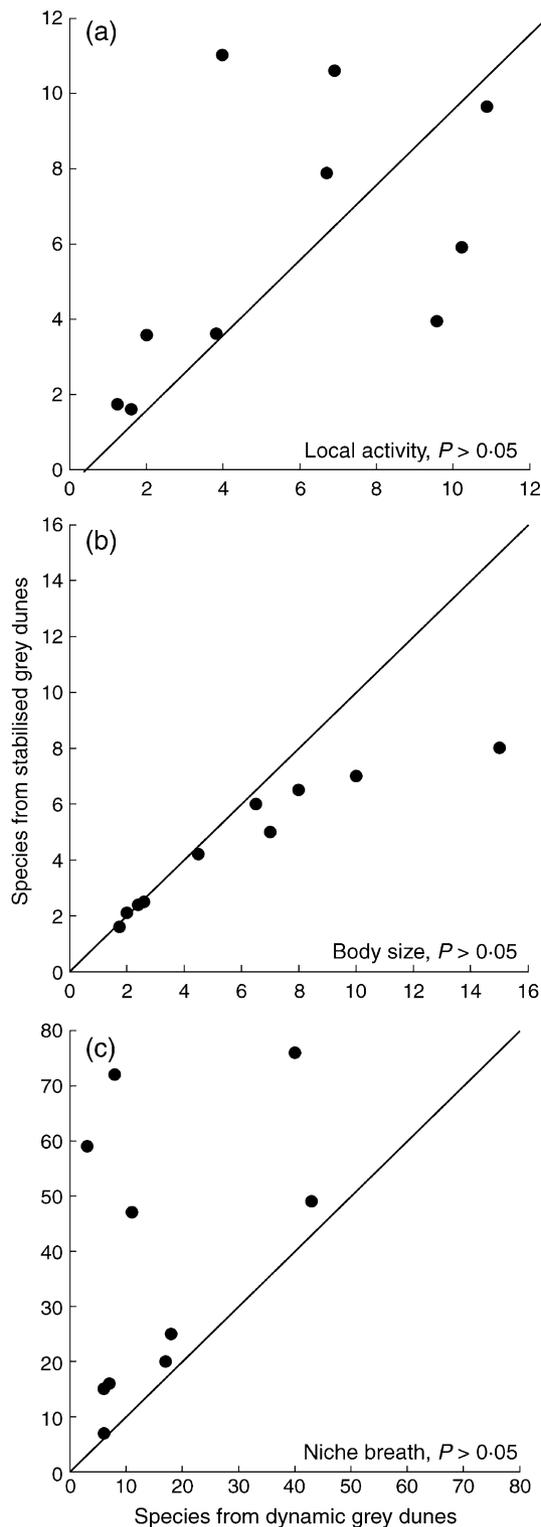
Fig. 3. Comparative analysis of spider life history traits for species indicative of dynamic (*x*-axis) and stabilised (*y*-axis) coastal grey dune fragments. (a) local activity, (b) body size, (c) niche breadth. In each graph the line indicates identical values for species from both situations.

More complex vegetation promotes coexistence of species using different structures for activities such as web building (Canard 1990; Scheidler 1990; Uetz 1990; Dennis, Young & Bentley 2001). Patterns in assemblage (dis)similarity showed different relationships, with the level of local sand dynamics depending on landscape dynamics (and hence stabilization history): in dynamic dune landscapes, β-diversity decreased significantly and approached regional (γ) diversity under local grey dune stabilization; in stabilized landscapes, β-diversity was not affected by local sand dynamics. This suggests that all species from a regional pool are able to coexist in stabilized fragments within dynamic landscapes. In both landscape types, patches were poorer in species and more dissimilar under increasing sand dynamics. As dynamic dunes consist of open landscapes (Provoost 2004), high levels of landscape connectivity for grey dune arthropods (Bonte *et al.* 2003c; Maes *et al.* in press) appear to affect diversity patterns (Chase 2003), allowing specialist species from dynamic habitats to coexist with species from stable grey dunes under decreasing sand dynamics. Hence mass effects (Leibold *et al.* 2004) appear to be responsible for the high degree of local coexistence. In contrast, dispersal limitation as a result of reduced patch connectivity is likely to cause higher dissimilarity under stabilized local conditions in stabilized landscapes. According to Leibold *et al.* (2004), such a pattern is in accordance with the patch-dynamic paradigm, where local species diversity in identical patches is limited by dispersal while spatial dynamics are determined by local extinction and colonization.

For Thomisidae and Lycosidae, species adapted to dynamic conditions disappeared from the regional species pool in stabilized landscapes, reflected by a lower β-diversity and a more homogeneous species composition under high levels of sand dynamics in stabilized coastal dune landscapes. As a result, local (α) diversity may be constrained by increased sand dynamics at a local scale, and by decreased sand dynamics at a landscape scale.

PATTERNS IN DIVERSITY AS A RESULT OF ENVIRONMENTAL CONSTRAINTS

Changes in species diversity were linked to community-wide character shifts in most of the spider families studied: species living in highly dynamic habitats showed adaptations to avoid extreme microclimatic conditions, i.e. reflected by higher frequencies of winter activity, larger body sizes, longer generation times and a burrowing life-style for wolf spiders. Only in Gnaphosidae, which are dominated by night-active species, opposite patterns were observed for body size, suggesting that body size is only constrained in day-active species that are subject to intense solar radiation. However, these contrasting patterns disappeared when phylogenetic dependence was taken into account through comparative analysis, indicating bias as a result of the

dynamics, local (α) diversity increased in both stable and dynamic landscapes, probably as a result of higher nutrient availability resulting in a higher and more complex vegetation structure (Provoost *et al.* 2004).

occurrence of species belonging to one genus under stabilized conditions (i.e. *Drassodes*). Shifts in aerial dispersal ability showed different patterns among families. Assemblages in landscape fragments experiencing high local sand dynamics were dominated by lycosid species that did not show ballooning, while contrasting patterns were observed for Erigoninae in dynamic landscapes. The latter resulted from the presence of early pioneer species typical of disturbed conditions, i.e. *Erigone* and *Oedothorax* species, which are frequent ballooners (Thomas, Brain & Jepson 2003). These species are widely distributed in dynamic habitats, such as young dune slacks (Bonte, Baert & Maelfait 2002), and invade habitat outside their fundamental niche (mass effects) (Bonte *et al.* 2004a). In stabilized dunes, source populations of the latter species are almost absent (Provoost 2004), thereby reducing their presence in (rare) fragments under aeolic dynamics. Erigoninae species occurring in dynamic fragments tended to show narrower niches. Similar patterns were observed for Gnaphosidae, Lycosidae and Thomisidae in dynamic landscapes, because stenotopic species were absent from stabilized landscapes (e.g. *Haplodrassus dalmatensis* (L. Koch 1866), *Walckenaeria stylifrons* (O.-P. Cambridge 1875), *Xerolycosa miniata* (C.L. Koch 1834) and *Xysticus sabulosus* (Hahn 1832); Bonte *et al.* 2003a). Comparative analyses of ecological traits revealed shifts in body size, generation time, seasonal activity and niche breadth, suggesting that patterns in local diversity resulted from species sorting (Leibold *et al.* 2004) and were constrained by local sand dynamics (i.e. favouring only pre-adapted species). Winter-active species were not entirely replaced by summer-active species under stabilized conditions, hence providing evidence for constrained species sorting (Leibold *et al.* 2004) in which natural disturbance (sand dynamics) allowed species with distinct ecological traits to persist only under these conditions. Hence complete community-wide character displacement appeared restricted under disturbed (non-equilibrium) conditions (Leibold 1998). Consequently, trade-offs between ecological traits at a local scale will only be expressed at low levels of disturbance, allowing coexistence between good competitors and good colonizers. This in turn may result in high levels of α-diversity, approaching regional diversity if patch connectivity is high (dynamic landscapes). Under high local sand dynamics, communities will show higher levels of dissimilarity compared with more stabilized conditions because of the strict occurrence of stenotopic (pre-) adapted species. Under these conditions, local trade-offs seem less pronounced (Kneitel & Chase 2004), restricting persistence to good competitors (large specialists) with low dispersal ability. In Erigoninae, but not in other families, good competitors (habitat specialists) may coexist with good colonizers in dynamic landscapes because of mass effects.

Analyses at the family level, however, may obscure more detailed shifts in ecological traits. However, comparison of ecological traits within couples of sister species, in which congenerics are indicative of stabilized or dynamic sites, showed comparable patterns. As expected, traits prevailing under high local sand dynamics were related to desiccation resistance (body size) or desiccation avoidance (winter activity, burrowing life style). These shifts resemble those in desert spiders, as documented by Henschel (1997), and adaptations in psammophilous spiders appear similar in subtropical desert and temperate dune ecosystems, indicating comparable environmental constraints.

ENVIRONMENTAL CONSTRAINTS AND SENSITIVITY TO HABITAT FRAGMENTATION

Species from fragments characterized by high levels of sand dynamics showed larger body sizes and longer generation times, while summer-active species tended to become residential after sand stabilization. Although a shift in average activity density was recorded at the family level in species from four families, comparative analysis did not suggest lower activity density levels in dynamic sites. Because bias as a result of species-specific activity patterns is minimized in the latter kind of analysis, we cannot conclude that population sizes decline under increasing aeolic dynamics (under the assumption that activity is related to population density; Maelfait & Baert 1975). However, assemblages experiencing high sand dynamics were characterized by species with smaller niche breadths. Consequently, connectivity levels within fragmented landscapes with matrices consisting of heterogeneous vegetation can be expected to be lower (Bonte *et al.* 2003a). Furthermore, species from grey dunes with narrow niches showed a lower propensity to undertake aerial dispersal (Bonte *et al.* 2003d). In this study, we were only able to distinguish between species with and without (reported) ballooning dispersal ability, possibly resulting in a failure to detect community-wide shifts in ballooning propensity in relation to local sand dynamics. Species from dynamic sites with larger body sizes (Boughton & Malvadkar 2002; Henle *et al.* 2004), longer generation times and a higher degree of habitat specialization (which is related to dispersal rates; Hanski 1999; Malmqvist 2000; Thomas *et al.* 2001; Bonte *et al.* 2003d) can be expected to be more vulnerable and more prone to extinction than their counterparts from stabilized fragments. In particular, species with a burrowing life style can be expected to disappear because of increasing soil development and soil hardness (Bonte *et al.* 2003b). In addition, if sand dynamics diminish at the landscape level, fragmentation of grey dune fragments may increase and local sand dynamics may further decrease (Provoost *et al.* 2004). Conserving sand dynamics at the landscape level is therefore of prime importance when aiming to conserve typical psammophilous spider species within local grey sand dune assemblages. The absence of specialized Gnaphosidae, Lycosidae and Thomisidae species in local assemblages with strong sand dynamics in stabilized landscapes (Bonte *et al.* 2003a) illustrates

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the type of adverse impact that can occur when such factors are not taken into consideration.

MANAGEMENT IMPLICATIONS

Our study provides evidence that spider species inhabiting grey dune fragments subject to high local sand dynamics undergo shifts in life-history characteristics that render them more vulnerable to extinction than their counterparts from stabilized fragments (Henle *et al.* 2004). Whereas grey dune fragments impose strong levels of isolation on specialist arthropod populations (Bonte *et al.* 2003c; Maes *et al.* in press), community-wide shifts in life-history traits appear less pronounced as a result of the absence of many specialized species in stabilized landscapes. Hence efforts to conserve highly specialized species should focus mainly on maximizing population sizes (hence minimizing chances of stochastic extinctions) by enlarging the remaining fragments and stimulating local sand dynamics. Because large-scale sand dynamics (at the landscape level) have an explicit positive effect on both grey dune connectivity and the magnitude of local sand dynamics (Provoost *et al.* 2004), the restoration of local sand dynamics should be integrated with programmes that aim to conserve or stimulate sand dynamics at a landscape level. The latter could be achieved by restoring beach–dune transitions, allowing net sand replacement into the dune area and/or by connecting large dynamic dunes through the dismantlement of urban infrastructures such as roads. In addition, if sand dynamics were restored at a local level by creating blowouts, this would most probably be accompanied by additional anthropogenic disturbance such as trampling (by humans or cattle) or removal of the top soil layer and vegetation. Although such disturbance would create similar environments comparable to those under natural sand dynamics, it is likely that specialized spider species would be negatively affected by this additional disturbance, although the empirical evidence for this is mostly lacking (but see Koehler *et al.* 1996). In conclusion, ensuring conservation of sand dynamics at a landscape level rather than at a local level is of prime importance when aiming to conserve typical psammophilous spider species within local assemblages in grey dune habitats.

Acknowledgements

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Supplementary material

The following supplementary material is available as part of the online article (full text) from http://w.w.w.blackwell-synergy.com.

Appendix S1. Species list and trait values.