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Colonisation and source-sink dynamics in spiders and ground beetles after dry dune habitat restoration along the Belgian coast

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Abstract

We monitored the spider and ground beetle assemblages of old dune and newly created dune-like habitats in the Ijzer estuary by means of four years of continuous pitfall sampling (2001-2004). The new sites built with dune sand were rapidly colonised by good dispersing species. These populations thrived so well during the first years after colonisation that they acted as sources, for which the old dune habitats were the sinks. That temporal collateral effect of nature restoration did not seem to cause persisting damage in the old dune habitats once the source populations had disappeared.

Because general stochastic environmental fluctuations, like cold winters, seem to cause important year-to-year variation in population size of a number of species, it is advisable to sample developing and restoring habitats at the same time as their targets.

The newly created habitats appeared to offer opportunities to enlarge the population size of several species of dune living ground beetles and, to a lesser degree, spiders. A multitude of more specialised dune species could not (as yet?) install viable new populations. A continuing sampling effort will be required to monitor the development, so that additional nature restoration or management measures can be taken when bio-indicated to be needed.

1 Introduction

1.1 Recent nature restoration project in the river Ijzer estuary

At the turn of the century, a major restoration project was realised on the right bank of the estuarine part of the river Ijzer, Flanders, Belgium (Deboeuf & Herrier 2002, Hoffmann 2004, Herrier et al. 2005). The first two phases consisted of the demolition of the buildings and roads of the former naval basis and the removal of the jetties and quays of the former military harbour and slipway. The excavated sandy soil from the quays was used to build dune-like hills above the pits left by the removal of the buildings as well as a dune-like dike along the tidal mud flat created after the removal of the harbour and the slipway. These works ended mid-way though March 2001 and immediately afterwards a multidisciplinary monitoring scheme was started (Hoffmann et al. 2005).

1.2 Studies on dry dune spiders and ground beetles in the Ijzer estuary

In this paper we report the results of the first four years of monitoring of two newly created dune-like habitats. We assess the spider and carabid fauna assemblages having colonised these newly created habitats in comparison with the assemblages occurring in the adjoining old dune habitats, which were already sampled from 1990 (Desender 1996, 2005). Desender et al. (this volume) give details on the former history of the IJzer estuary. We compare the spider and carabid assemblages of five sampling sites (Fig. 1). Two are situated on the fore-dune, one on the seaward side (site A), and one on the landward side (site C). These sites belong to the association Ammophiletum arenarii with a ground cover of marram grass tussocks of about 50 %. At the more protected site C, some 5 to 10 % more is covered with low growing grasses, herbs, and *Euphorbia paralias*. The third site (site E) is a grey dune belonging to the phytosociological order Cladonio-Koelerietalia (Provoost et al. 2004). During the sampling period 2001-2004 it had the characteristics of the alliance Polygalo-Koelerion, closed grassland with a well-developed sod layer. It was short-grazed by sheep. During the 1990's the site had much more open grey dune vegetation dominated by lichens and mosses and with a poorly developed organic soil layer, in other words it was rather a Tortulo-Koelerion. The change in carabid and spider assemblages due to this vegetation change will be treated elsewhere (Baert et al., in prep). The three before mentioned old dune sites are designated as priority habitats in the EU Habitats Directive. Therefore, we use them here as targets to assess the quality of the newly created sites with dune sands: sites F and G. These new sites are situated 50 m apart on a newly built dike about 500 m inland from the fore-dunes (Fig. 1). The dike was built with excavated sand with a content of finer soil particles (clay, organic matter) of about 10 %. At site G, on top of that, about 0.5 m of mineral sand with a 5 to 10 % content of shell fragments was added and planted with marram grass tussocks. By 2004, G showed a ground cover of about 50 % of marram tussocks with in between some 5 % grasses and herbs. From only about 10 % ground cover during the growing season in 2001, site F evolved in 2004 to a cover of about 95 % of sod forming grasses, mosses and herbs, kept short by sheep grazing.

Figure 1: Localisation of old (A, C, E) and newly created (F, G) dune sand sites along the river Ijzer.

1.3 Year-cycle pitfall trapping as a sampling method for studies on spiders and carabids

All sampling was done with pitfall traps, i.e. glass jars with a content of half a litre, a depth of 10 centimetres and a diameter of 9.5 centimetres. These traps are dug in the soil with their upper rim just beneath the mineral soil surface and half-filled with 4% formaline solution as a fixative and a few added drops of detergent to lower surface tension. At each sampling site, three pitfall traps are installed about five metres apart. They are emptied and refilled at fortnightly intervals. For each trap, once per fortnight, all adult male and female spiders and ground beetles were identified and counted. Each site was sampled in this manner for at least a complete year-cycle, starting from the beginning of April and ending at the end of March the next year. The total number of males and females caught during such a complete year-cycle is the figure used to assess the relative abundance of a species in a series of sites to be compared. In other words, these year-cycle numbers are used to determine the habitat preference of a species and to ascertain the year-to-year changes in abundance of a species at a particular site, sampled for several year-cycles.

Capture rates of pitfall traps not only depend on population densities (abundance) of the species caught, but also on intra- and interspecific differences in soil surface activity levels and in trappability as influenced by habitat structure (Greenslade 1964, Maelfait & Baert 1975, Baars 1979, Halsall & Wratten 1988, Topping & Sunderland 1992, Sunderland et al. 1995, Maelfait 1996, Antvogel & Bonn 2001). Therefore, they are not suited for comparisons between species in terms of their abundance. However, resulting from a long enough sampling period (a year-cycle) in not too structurally different sampling sites, pitfall capture rates give reliable estimates of the relative abundance of each particular species over the sampling sites (Maelfait & Baert 1975, Baars 1979, Desender & Maelfait 1986, Maelfait 1996, Retana & Cerdá 2000). When used for ordinations or classifications, capture rates have therefore to be relativised per species, as we did hereafter in the program PC-ORD used for Detrended Correspondence Analysis, DCA (Jongman et al. 1995, McCune & Mefford 1999).

1.4 Climate

The Belgian coast has a mild Atlantic sea climate. The mean winter and summer temperatures measured in nearby climatologic stations during the year of sampling were 4.9 and 17.3 °C. The number of frost days per month between July 2000 and July 2004 are shown in figure 2.

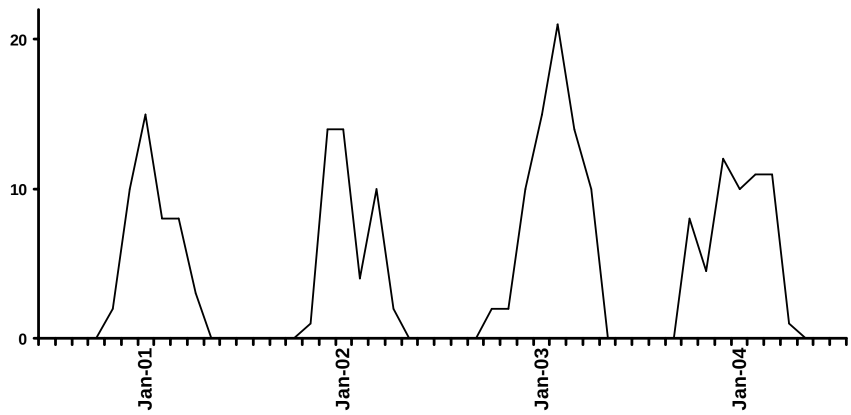

Figure 2: Number of frost days per month from July 2000 to July 2004.

2 Results

The scores of sites and species obtained after a DCA of the spatio-temporal distribution of the most abundantly caught species are plotted along the first and second axis in Fig. 3 for spiders and Fig. 4 for carabid beetles. The eigenvalues of the first, second and third axes are for spiders: 0.55, 0.26, and 0.07; for carabids: 0.53, 0.22, and 0.08.

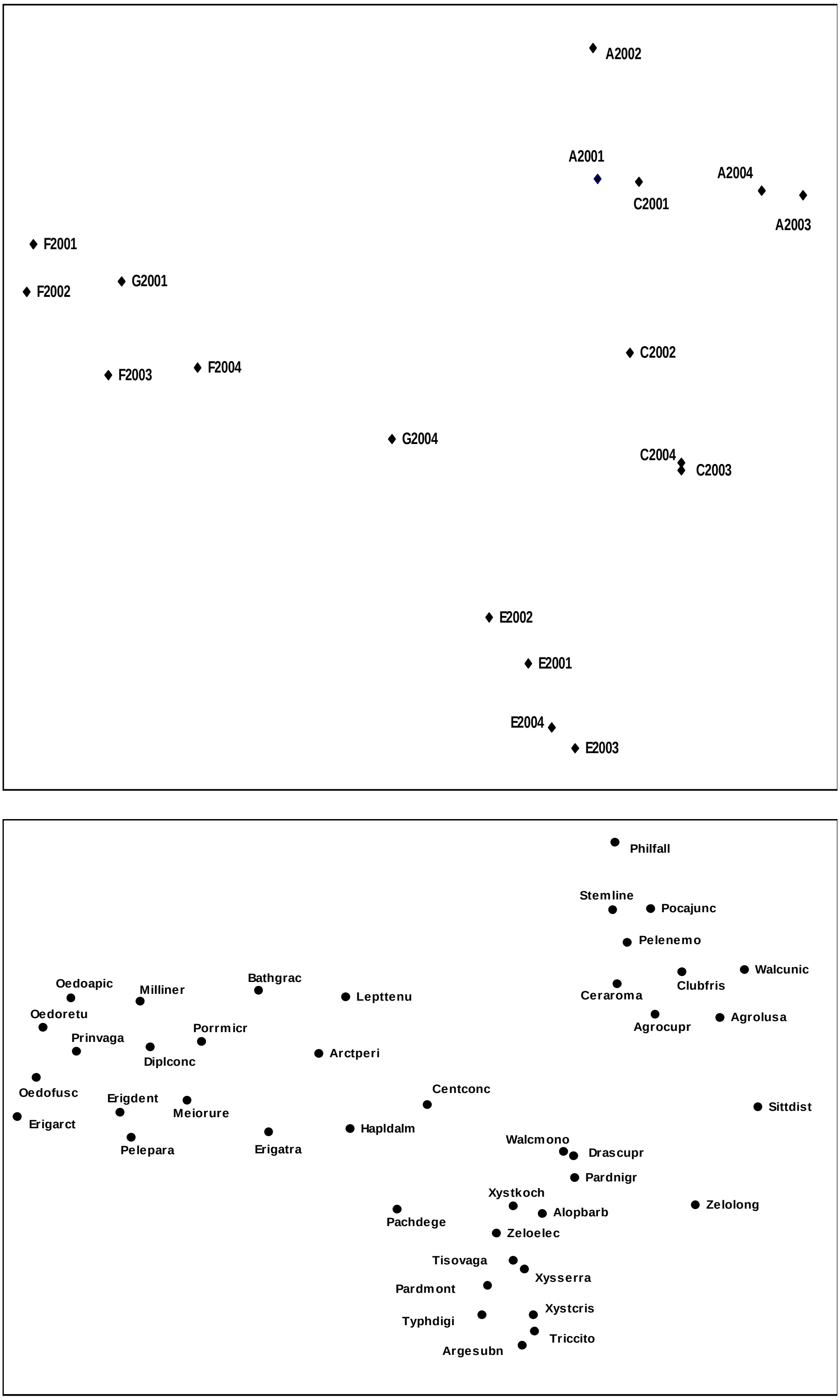

Figure 3: Scores of the year-sites (above) and the species (below) along first and second axis after DCA ordination of the spatio-temporal distribution over old and new dune sand sites of the 42 most abundant spiders. For full species names of abbreviations used here: see Table 1.

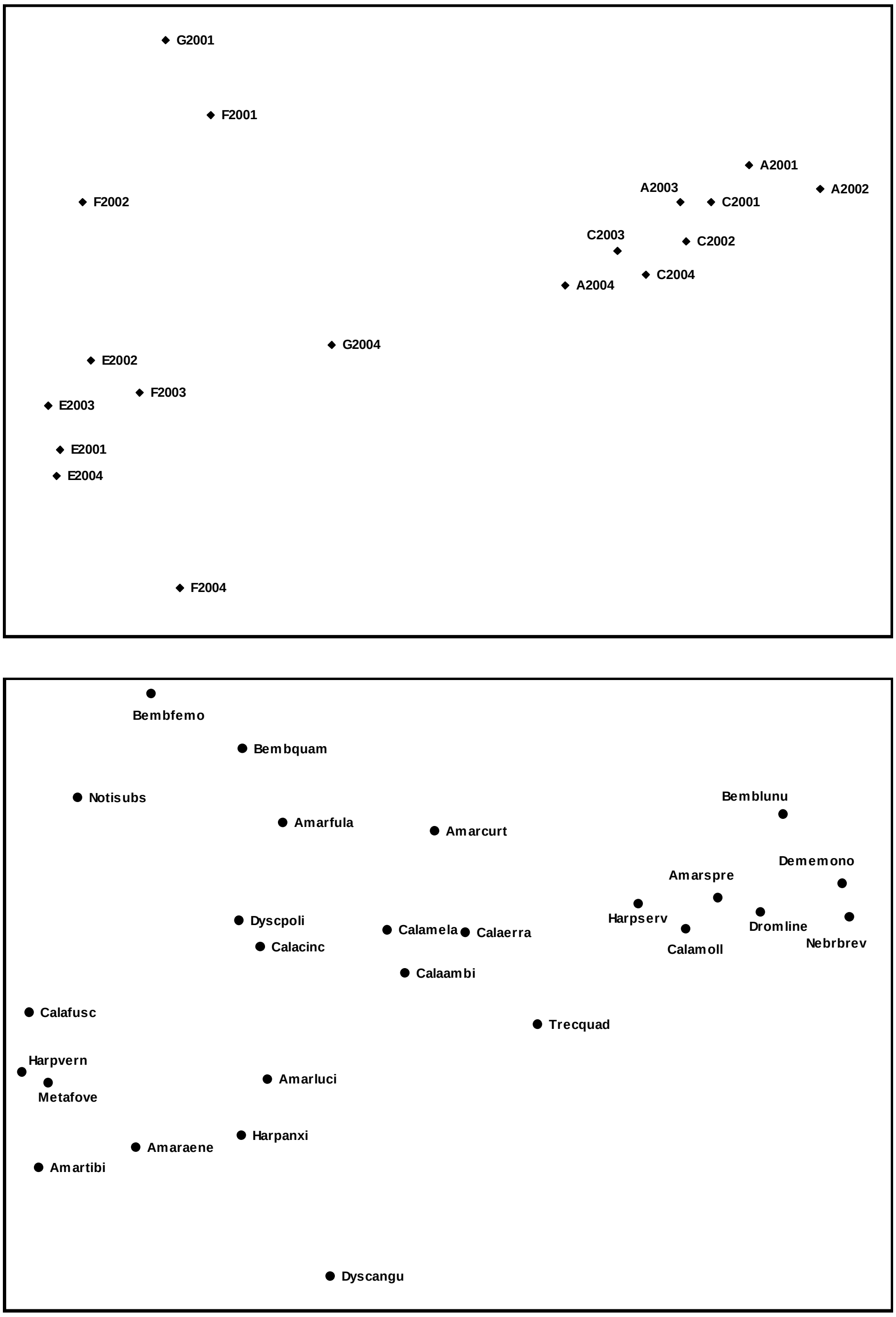

Figure 4: Scores of the year-sites (above) and the species (below) along first and second axis after DCA ordination of the spatio-temporal distribution over old and new dune sand sites of the 26 most abundant carabid beetles. For full species names of abbreviations used here: see Table 2.

On the basis of these ordinations, but also derived from the captures made in the old dune sites during the five years before the construction of new dune sand habitats, the year-sites and species are ordered in Table 1 (spiders) and Table 2 (ground beetles). The median values of the five yearly captures before 2001, i.e. from 1996-2000, in dune sampling sites A, C and E are mentioned in Tables 1 and 2. To obtain a more convenient arrangement of the results (and the discussion), each species was attributed to one of the Classes 1a to 3c (Column "Class" in Tables 1 and 2) according to its spatio-temporal distribution over the year-sites. However, when considered needed, idiosyncrasies of particular species are also taken into account.

Table 1: Yearly capture rates of the most abundant spider species per sampling year-site, ordered and grouped according to the DCA ordination of Fig. 2 and the capture rates made in the old dune habitats in the five years before 2001 (median value of 5 yearly capture rates in columns E, C and A). Red-listed species based on Maelfait et al. (1998). Code: abbreviation for species name as used in figure 3. Class: explained in text.

Code	Spider species	G2001	G2004	F2001	F2002	F2003	F2004	E2001	E2002	E2003	E2004	C2001	C2002	C2003	C2004	A2001	A2002	A2003	A2004	E	C	A	Class	Red list
eriarct	Erigone arctica	96	5	182	3548	1800						8				39	51	1					1a	-
oedfusc	Oedothorax fuscus	103		86	352	23		4	14	7	1	2	1	1		2	5		2	2			1a	-
oedretu	Oedothorax retusus	8		24	75	6		1				1				2	6		1				1a	-
oedapic	Oedothorax apicatus	253		283	626	8	1	1	2	1	1	2	2			23	119		7	1		1	1a	-
privaga	Prinerigone vagans	4	1	10	25	5			2		2					1	2						1a	-
miliner	Collinsia inerrans	6	2	8	21	4	2		1			3				4	3						1a	-
dipconc	Diplostyla concolor	6	3	11	18	29	10	2		1	1	1			1	3	6	1				1	1b	-
meirure	Meioneta rurestris	6	43	6	44	7	26	1			2	5		2	1					1	1		1b	-
pormicr	Porrhomma microphthalmum	6	4	6	10	7	13	3			2				1	1	4	1	1	1			1b	-
pelpara	Pelecopsis parallela	2	57		85	518	889		5		3												1b	-
erident	Erigone dentipalpis	56	10	118	711	188	101	96	177	16	23	6	1	1	1	3	7			83	1	1	1c	-
batgrac	Bathyphantes gracilis	45	7	64	112	17	35	14	43	3	12	2	9		3	44	54	9	13	6	11	21	1c	-
eriatra	Erigone atra	56	18	172	414	95	49	260	448	58	113	2	3	1	1	2	15	3	3	321	8	7	1c	-
leptenu	Tenuiphantes tenuis	52	93	63	168	23	120	22	57	8	51	15	10	1	20	89	120	27	99	19	49	97	2a	-
hapdalm	Haplodrassus dalmatensis	7	72	4	24	48	66	15	36	12	17	15	25	22	9	18	2	1	8	67	21	4	2a	yes
cenconc	Centromerita concinna	2	98	2	6	12	26	33	63	11	33	26	17		3	23	2	1		47	9	4	2a	-
xyskoch	Xysticus kochi		27		11	6	18	54	51	57	69	12	25	15	12	18	7	5	9	14	10	3	2a	-
dracupr	Drassodes cupreus		16		2			1	3	2	4	3	10	11	13	1	2	4	3	1	25	2	2a	-
alobarb	Alopecosa barbipes	2	11		2		3	13	20	23	15	4	7	10	15	10		2	2	6	32	2	2a	yes
steline	Stemonyphantes lineatus		47	1	3	1	5	10	6	3	5	32	83	31	22	141	267	64	67	5	7	27	2a	-
pelnemo	Parapelecopsis nemoralis		5		1	1	6	3	3	2	7	23	19	3	6	14	56	13	46	15	158	73	2a	yes
arcperi	Arctosa perita	20	7	3	10	14	8	1			1	8	15	7	2	4	3	2	3	2	3	6	2b	yes
cerroma	Styloctetor romanus		3		1	1	6		2	1		98	35	18	13	10	3	2	3	1			2b	yes
pacdege	Pachygnatha degeeri	4	2	2	3	3	2	23	5	11	2	1				2				2			2c	-
zelelec	Zelotes electus	1	10			2		16	16	12	10	1	2		4					15	6		2c	yes
parmont	Pardosa monticola	9	31	3	3	12	20	96	87	90	193			2	4		1		1	17			2c	yes
typdigi	Typhochrestus digitatus	1	3	1	2	2	14	7	14	10	108									14			2c	-
walmono	Walckenaeria monoceros					1		22	34	20	31	9	14	6	1	9	11	6	3	39	21	18	3a	-
agrcupr	Agroeca cuprea		1	1				14	3	3	7	7	10	7	3	20	10	15	35	5	11	20	3a	yes
parnigr	Pardosa nigriceps	1	1		3			12	3	6		1	6	11	11	5	1		4		3	1	3a	-
zellong	Zelotes longipes									1	2	2	3	13	9			3	6		1	1	3b	yes
sitdist	Sitticus distinguendus				1							1	3	3	2	1		24	10		2		3b	yes
agrlusa	Agroeca lusatica		1								2	2	5	1	6		8	4	38	1	6	3	3b	yes
clufris	Clubiona frisia								1			13	14	4	11	25	13	26	12		13	18	3b	yes
waluni	Walckenaeria unicornis											3				2	7	14	16			2	3b	-
pocjunc	Pocadicnemis juncea							2	2		1	2	2	7	7	27	41	14	18	1	2	26	3b	-
phifall	Philodromus fallax											19	1	1		14	27	3				1	3b	yes
tisvaga	Tiso vagans	1		1				29	11	9	19												3c	-
xyserra	Xysticus erraticus							17	17	9	21									5			3c	yes
xyscris	Xysticus cristatus					2	2	17	15	27	23		2	2	2	1	1	1	1	11			3c	-
tricito	Trichopterna cito		1				1	39	20	36	61		1		1	1				22		1	3c	yes
argsubn	Argenna subnigra					5		20	19	37	41		1				1	1		24			3c	yes

Class 1a species appear in site G and F in 2001, occur in high numbers in F in 2002 and 2003 (G not sampled in these two years) and disappear (or almost so) in 2004. All spider species of this group show the pattern as exemplified for *Erigone arctica* (Fig. 5). During the years of high abundance in G and F, these species also appear in considerable abundance in A, but also in E and C, where these species were virtually absent during the five years before the creation of the new dune sand habitats F and G.

Table 2: Yearly capture rates of most abundant carabid beetle species per sampling year-site, ordered and grouped according to the DCA ordination of Fig. 2 and also on the basis of the capture rates in the old dune habitats during five years before 2001 (median value of 5 yearly capture rates in columns E, C and A). Red-listed species based on Desender et al. (1995). Code: abbreviation for species name as used in figure 4. Class: explained in text.

Code	Carabid species	G2001	G2004	F2001	F2002	F2003	F2004	E2001	E2002	E2003	E2004	C2001	C2002	C2003	C2004	A2001	A2002	A2003	A2004	E	C	A	Class	Red Data Book
Bembfemo	Bembidion femoratum	170	1	80	73				1								3	1					1a	-
Bembquam	Bembidion quadrimaculatum	8		15	10	3			5							3		1						-
Amarfula	Amara fulva	6	15		3	13	3	1				1				1								-
Dyscpoli	Dyschirius politus	2	20		12	33	1											2	2				1b	yes
Dyscangu	Dyschirius angustatus	5	25	5	25	63	74						3	3	3	5	3	8	15					yes
Nebrbrev	Nebria brevicollis		3	2					2	1		1	4	1	1		49	3	1			1		-
Notisubs	Notiophilus substriatus	1	16	23	113	67	3	25	29	13	23	1				1	1			5			1c	-
Trecquad	Trechus quadristriatus	4	11	7		4	15			1	4		1		2	8	1	6	21		6	16		-
Calacinc	Calathus cinctus	52	112	56	106	75	133	241	215	26	54	30	37	17	1	13	30	28	3	221	13	1		yes
Calaambi	Calathus ambiguus	9	339	20	14	43	36	1	4	7	13		15	14	9	1	2	2		19	2			yes
Calamela	Calathus melanocephalus	1	3	4	2	3	1	8	7	6	9		3	3	1		3	5	1	3	1	1		-
Calaerra	Calathus erratus	2	410	3	6	23	3	9	20	21	29	4	11	26	7	2	6	46	3	27	71	10		-
Calamoll	Calathus mollis	37	1243	22	28	30	79	280	154	38	53	772	641	729	329	529	434	944	330	89	200	75	2a	yes
Harpserv	Harpalus servus	8	65	5	4	14	5	2	4	1	6	21	20	52	51	2	17	18	27	7	43	9		yes
Amarluci	Amara lucida	4	34	2	1	7	14	33	30	9	47	1		4	2	1	4	5	18	13	1	2		yes
Harpanxi	Harpalus anxius	5	89	6	25	63	59	45	36	23	33	4	2	3	9	1	3	4	13	17	25	15		-
Amarcurt	Amara curta	2	5	2	3	1		5	9	4	5	1				1	1	6	10	5	1			-
Dromline	Dromius linearis		4	1		2		1		1		5	10	3	3	9	12	13	7		3	1	2b	-
Dememono	Demetrias monostigma		2									9	3	2	1	17	37	18	9		3	1		yes
Amaraene	Amara aenea	2	35	5	19	28	36	23	21	8	45					1	1	3		11	1	1		-
Calafusc	Calathus fuscipes	2	32	7	61	45	21	96	189	224	131			6		1			1	32	1			-
Harpvern	Harpalus vernalis	7	7	6	7	24	9	133	64	64	93			2			1		1	45	4	1	2c	yes
Metafove	Metabletus foveatus	2	14	13	12	11	20	151	45	19	33	2						1		77	10	1		-
Amartibi	Amara tibialis		1			8	4	34	13	10	29							2	1	3				yes
Amarspre	Amara spreta							4									3	21	10				3b	-
Bemblunu	Bembidion lunulatum	9		12	17	5	1	5	3			12	5	3		126	84	105	18		2	15		-

As the 1a species, the 1b species did not have populations in the old dune habitats before 2001. In contrast to the former class, the species of 1b built up viable populations by 2004 in the new sites. This is especially the case for the spider *Pelecopsis parallella* and the ground beetle *Dyschirius angustatus* in site F.

Class 1c species occurred before 2001 in the old dune habitats, especially in the dune grassland E. In F they display the same year-to-year variation as the 1a species, except that the class 1c species have established populations in 2004 in G and/or F. Class 2a contains species that occurred before 2001 and during the period 2001-2004 in A, C and E. These species were able to colonise G and/or F during that 4-year period. The species making up the class 2b are spiders and carabids of the fore-dune ridge that succeeded in the colonisation of one or both of the new sites.

Class 2c species are inhabitants of habitats like site E (stabilised grey dunes) that succeeded to colonise G and/or F.

Classes 3a, 3b, and 3c are species of the fore-dunes and/or dune grassland (A and C and/or E) that were not able to colonise the newly created habitats.

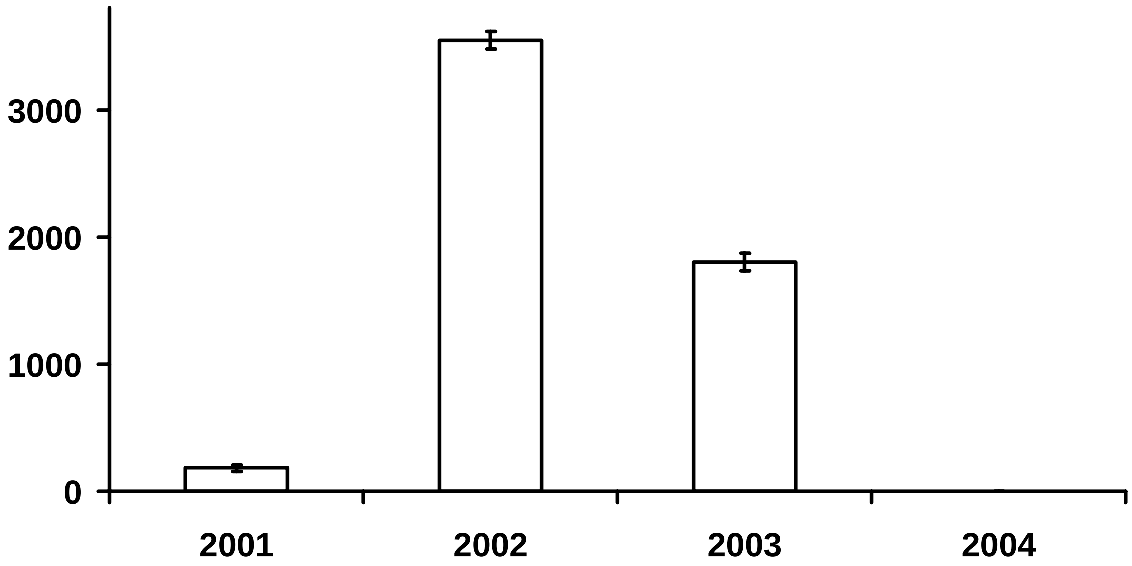

Figure 5: Yearly capture rates (+- 95 % confidence intervals) of the spider Erigone arctica in the newly created dune sand site F.

3 Discussion

All spider species of classes 1a and 1b, with the exception of *Pelecopsis parallella*, are small linyphiid spider species known to be good aeronautic dispersers. These species occur in high densities in unstable, poorly vegetated, temporal habitats such as regularly inundated riverbanks, arable land, intensively exploited hayfields, and pastures (Bell et al. 2005, Bonte et al. 1998, 2002, 2004, De Keer & Maelfait 1987A, B, 1988, 1989, Maelfait & De Keer 1990, Maelfait et al. 2004). Their colonisation capacities are well illustrated by their rapid massive appearance in G and F. While the species of class 1b, which appear a bit later than 1a species, have populations in 2004 in G and F, the 1a species already disappeared again. The vegetation apparently attained a too high ground cover by that year for such species. *Pelecopsis parallella*, a species of which there are no observations of aerial dispersal, found especially in F a very suitable habitat. It is this far more widely distributed species and not its rare sister species of dry dune habitats *Parapelecopsis nemoralis* that colonised the new sandy habitats G and F.

The spider species of class 1c are excellent aerial dispersers with a wide distribution, including man-made habitats. They differ from the class 1a species because they need low vegetation (grasses, low herbs) to attach their webs used to catch prey. In addition, the carabid *Notiophilus substriatus* is a species bound to short grassy vegetations (Desender et al. 1995, Turin 2000). These species are also quite abundant in E. This suggests that colonising individuals in G and F could as well have come from these old dune habitats as from nearby agricultural land.

All the carabids of 1a, 1b, and 1c are also good aerial dispersers, i.e. full-winged (macropterous) species with well-developed flight muscles (Desender 1989, 2000). As for the spiders, all these species, with the exception of two *Dyschirius* species, are widely distributed species in disturbed habitats. The two *Dyschirius* species are red-listed and are bound to more or less humid, patches of sand devoid of vegetation (Desender et al. 1995), as occurring in young dune slacks, a rare habitat type along our coast. As can be seen in Table 2, they were doing very well in at least of one of the two new habitats in the period 2001-2004. However, as observed in the captures of 2005 and 2006 (Desender, pers. comm.) this was only a temporary situation. It is expected that the species will again locally become extinct when highly dynamic, open sand situations cannot be kept in the area due to expected vegetation succession (cf. Desender ET AL., this volume).

The relatively high numbers caught in C, E and especially in A of several species of the classes 1a and 1b in 2001 and 2002 are most probably the result of an overflow of the rapidly growing populations in F (and presumably in G, not sampled in 2002). Mass effects (Leibold et al. 2004, Leibold & Miller 2004) by species with a high aerial dispersal propensity, i.e. by ballooning spiders and flight by carabids with fully developed hind wings (and functional flight muscles) appear to have been important in the first year of the restoration process. During the first year, newly created habitats acted as a sink for dispersers coming from highly productive source populations in their vicinity, such as agricultural habitats, a dredging sludge dump area of several hectares excavated during the sampling campaign and possibly also from the dune grasslands. Later on, the newly created habitats became a source of individuals of good dispersing species immigrating in the long existing sites. The presence of these species does not seem to have caused damage or lasting changes in the assemblage composition of old dune sites as these fugitive species disappeared again by 2004 and as no other former occurring species were lost (Figs. 3, 4, and columns A, A2001 to A2004 of Tables 1 and 2). These results confirm the strong effect that dispersal ability may have on spider (meta-) community composition of grey dunes (Bonte et al. 2004, Bonte et al. 2006). Here we observe that this effect rapidly fades away once nearby local disturbances come to an end.

As the species of class 1a and *Meioneta rurestris* (1b), the 1c species showed a sharp decline in numbers between 2002 and 2003. This decimation has probably been caused by the relatively harsh conditions of the winter 2002-2003 (Fig. 2) to which these species appear to be susceptible. Such high winter mortality can also be observed for several other species and sites, e.g. for the spider *Tenuiphantes tenuis* at all sites. Why particular species appear to be more vulnerable to harsh winter conditions than others would require investigations that are more detailed. This striking influence of climate and possibly other general stochastic environmental factors implies that the estimation of the distance-to-target of developing and restoring assemblages can best be done by sampling them simultaneously with the assemblages of the target habitats.

Of the remaining 29 spider and 18 carabid species, respectively 14 and 16 were able to colonise the new habitats after 4 years (classes 2a, 2b and 2c of tables 1 and 2), while 15 spider and 2 carabid species failed to do so (classes 3a, 3b and 3c of tables 1 and 2).

Colonisation was most successful for species with a wider distribution in dune habitats, i.e. species occurring in E, C, and A (classes 2a and 3a); for spiders: 8 species out of a total of 11 could colonise, for carabids: 9 out of 9. Colonisation was less successful for spider species of the dune grasslands like E (classes 2c and 3c: spiders: 4 out of 9, carabids: 5 out of 5). The new habitats did not yet seem suitable enough for or could not be reached yet by several species of the fore-dunes (2b and 3b): only 2 out of 9 spider species and 2 out of 4 carabids could invade the new sites.

Overall, by 2004, 16 out of the 18 typical dry dune carabid species of the area could establish populations in the new dune-like sites created by the nature restoration project, while this was only the case for 12 out of 29 typical dry dune spiders. For seven endangered spider species (column Red Data Book in table 2) one or both new habitats appeared suitable enough to be permanently colonised. However, for 9 other spider species of the Red Data Book this was not or not yet the case. For carabids, all 8 Red Data Book species were typical dry dune carabids of the area established populations and two new Red Data Book species came in, at least temporally (see above).

This leads to the conclusion that the newly created dune-like habitat can be considered a valuable enlargement of the natural habitats for several typical dune living species, mostly carabids, to lesser degree spiders. Of especially this last taxonomic group, the more specialised dry dune species could not install populations in the new habitats. Further monitoring will be required to evaluate if this situation gradually improves or if additional nature restoration and/or management measures will have to be considered.

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