

Evaluation of recent nature development measures in the river IJzer estuary and long-term ground beetle and spider monitoring (Coleoptera, Carabidae; Araneida)

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Summary

In order to evaluate recent nature development measures, ground beetles and spiders were studied in the river IJzer estuary (Belgium), an area that has been studied for these invertebrates without interruption since 1989. Starting immediately after restoration measures, five intensive short-term pitfall trapping campaigns were performed in 2001 till 2003 along nine transects covering the entire nature reserve. About 25.000 ground beetles and spiders were identified from more than 200 species.

Assemblages, derived from these sampling campaigns, are compared between old and new habitats and sites and show quick species responses in the first years after the nature restoration measures. We observe several beetles and spiders new to the study area as well as a marked increase within the area of several target species with high conservation interest (Red data book species).

However, beetle and spider results also suggest that additional management measures will probably be necessary for a further successful development of the nature restoration area. These mainly concern problems related to the maintenance of early successional dynamic stages of great biological value as well as those related to recently observed increased sand deposits in new and old salt marshes. Further invertebrate monitoring, including population genetics, therefore is a pre-requisite for a well-founded long-term evaluation of the performed nature development measures. Such monitoring will be of much interest, both for an evidence based nature conservation management and for fundamental ecological research.

Key Words: nature development, colonization, salt marsh, coastal dunes, ground beetles, spiders, assemblages, species quality, monitoring, IJzer estuary

Introduction

In recent years, within the field of nature conservation in the region of Flanders (Belgium), an increasing amount of interest and energy has been diverted towards nature development and nature restoration projects (VAN UYTVANCK & DECLEER, 2004). The main aim of such projects in general is the restoration of natural values on degraded sites through important technical measures with a strong influence at the site or landscape level (e.g. large scale digging and soil removal or restructuring activities). Newly created situations then undergo spontaneous succession and colonization processes, with the hope that nature will develop towards an ecologically expected and interesting or actually threatened situation.

In order to evaluate and, if necessary, further manipulate the development of restored habitats or areas, it is important not only to study or monitor the structuring vegetation on manipulated sites, but also to investigate other biota which can function as umbrella species or groups for the assessment of total biodiversity in the entire study area. Invertebrates offer unmatched possibilities in this context, being speciose, generally with numerous ecological indicators and mostly useful at a multitude of spatial scales.

An important nature development project has recently been realised by the Flemish Government along the river IJzer estuary (HOFFMANN et al., 2005). In this area, most energy and restoration measures have been directed towards an important increase of the pre-existing limited surface of old salt marsh, as well as towards increasing contact zones between mud flats, salt marsh and coastal dune habitats.

Since 1990, the department of Entomology (RBINSc, Brussels) is continuously monitoring ground beetle and spider populations in the river IJzer estuary coastal dunes and salt marshes, mainly by means of uninterrupted long term pitfall trapping on several sites. From this unique study area, along the right bank of the IJzer estuary and the seaside beach front, no less than 200 spider and 140 ground beetle species are hitherto known based on these continuously performed samplings (BAERT & DESENDER, 1993; DESENDER, 1996, 2005b; DESENDER & BAERT, 1995). These long-term samplings have also been further continued since the start of the recent nature development measures in the area. From autumn 2001 onwards, we have additionally sampled terrestrial invertebrates along nine transects covering the entire area within the context of the inter-institutional 'MONAIJ' project (HOFFMANN et al., 2005). We have repeated this area-covering but short term sampling effort five times between autumn 2001 and autumn 2003. At the same time, our long term continuous sampling (complete year cycles) was ongoing along a dune transect from seaside marram dunes to inland dune grassland and moss dunes, as well as in 'old' salt marsh, 'recent' salt marsh, newly constructed dikes and on the margins of a newly created dune pond.

The following paper basically analyses, for the three years of the mentioned MONAIJ-project, the results obtained by means of these area-covering short-term beetle and spider samplings in the river IJzer estuary area. Beetle and spider assemblages and species are compared between old and new habitats and sites and in function of the time elapsed since the end of the restoration measures, in order to describe tempo and mode of colonization by these invertebrates. We also evaluate changes through time of the obtained nature conservation values by assessment of diversity and habitat specificity and an evaluation of species quality (Red data book species). Finally, we attempt to evaluate and suggest whether and which additional management measures might be necessary for further successful nature development in the area, along with further invertebrate monitoring needs in this respect.

Material and methods

Continuous sampling started already during and immediately after restoration measures and digging activities

and as such enabled us to investigate in detail the initial colonization processes of ground beetles and spiders in the study area. On longer terms this will enable us to evaluate how and at which rate a given area or habitat that was made ready for development towards a dune/salt marsh complex, evolves faunistically towards the target ecosystem.

Our area-covering samplings were performed by means of a large number of pitfall traps (three glass jam jars per sampling site; 9,5 cm diameter, with a formalin solution as fixative and emptied and refilled at fortnightly intervals). All sampling sites were arranged along nine transects covering the entire nature reserve and restoration area. Simultaneously we also installed some window traps, continuously monitoring beetle flight or spider ballooning activities, along with 10 continuously sampled sites with pitfalls (long-term study). The area-covering 'MONAIJ'-sampling campaigns lasted between two to four weeks each, during spring and autumn, starting from the autumn of 2001. On the whole, 40 sites were sampled with three traps each along nine transects (Figure 1).

This paper analyses the captures resulting from these five sampling campaigns in (1) autumn 2001, (2) spring and autumn 2002 and (3) spring and autumn 2003. On

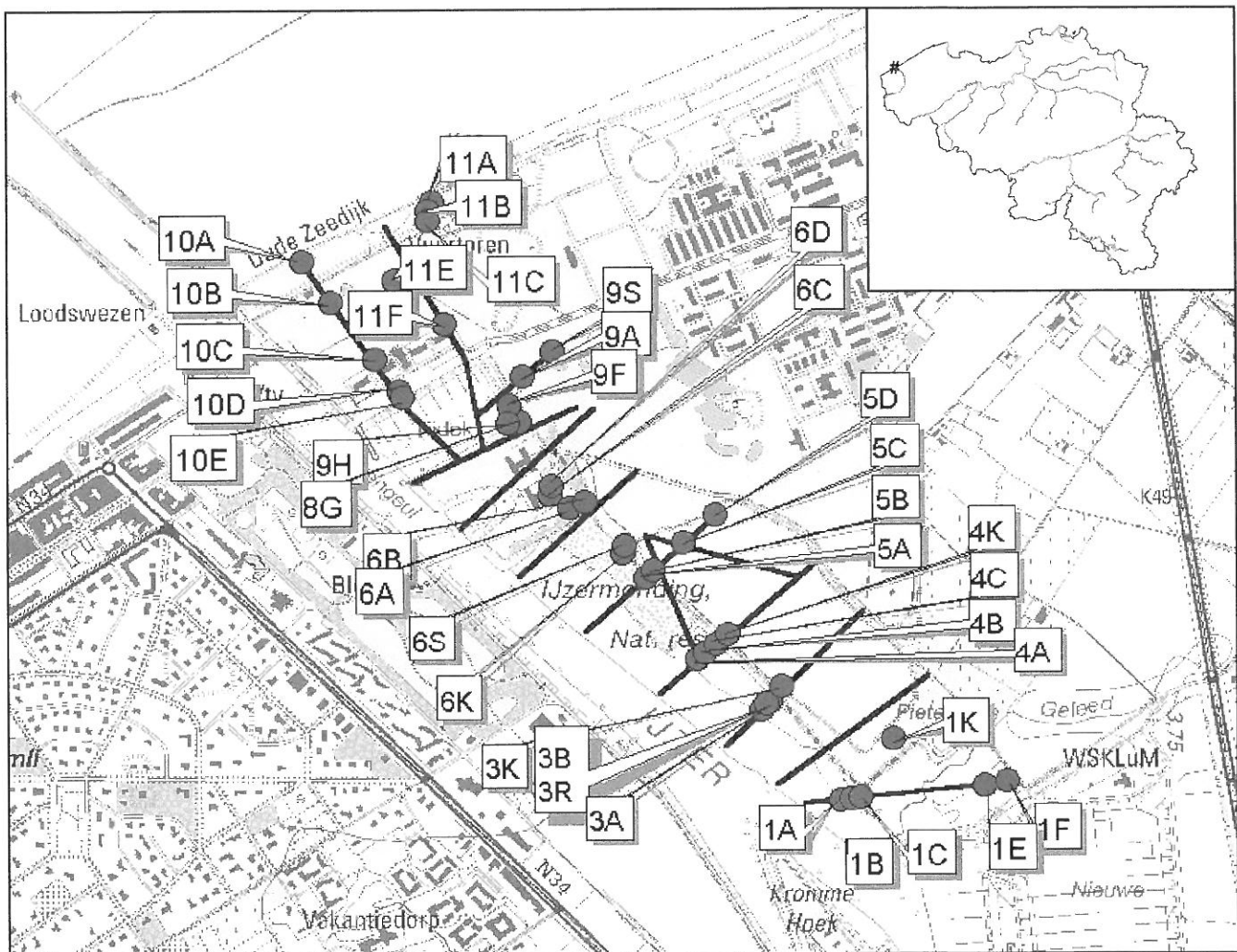


Fig.1 — Location of the 'MONAIJ' short term samplings sites for ground beetles and spiders along the river IJzer Estuary (not shown: 3D situated very close to 3R).

the whole, we collected and identified more than 25.000 individual ground beetles and spiders during these samplings, from more than 200 species.

The most important habitats that were sampled, along with the most important changes that took place in the area between 2001 and 2004 due to nature development measures are illustrated on a number of figure plates (plates 1 to 9 in appendix), while classification and sample codes per sampling campaign are regrouped in Table 1, including the discerned habitat types as further used in analyses and interpretation of results.

Based on the quantitative data for the most numerous species, after transforming data to relative densities within each species over the different individual sampling sites (i.e. equal weighting each species), DCA-analyses were performed based on the data for each separate sampling year (autumn 2001, 2002 and 2003) and for beetles and spiders separately. To prevent possible overruling noise from accidental species in these analyses, only those present with more than 10 individuals were

retained. Test runs with a more or less strict criterion nevertheless yielded a basically similar ordination result, as far as the following interpretations are concerned. In what follows, for each of these ordination analyses, species and site scores are plotted, accompanied by a graph showing an overlay of each sampling site by its habitat type (cf. Table 1).

Results and discussion

1. Assemblage analyses in old and more recent dunes, dikes and salt marshes during different sampling years

1.1. Ground beetle assemblages

In total, we identified more than 10.000 ground beetles belonging to 93 species. Beetle data were grouped per habitat type and year and documented for what concerns their species quality (Red data book species; cf.

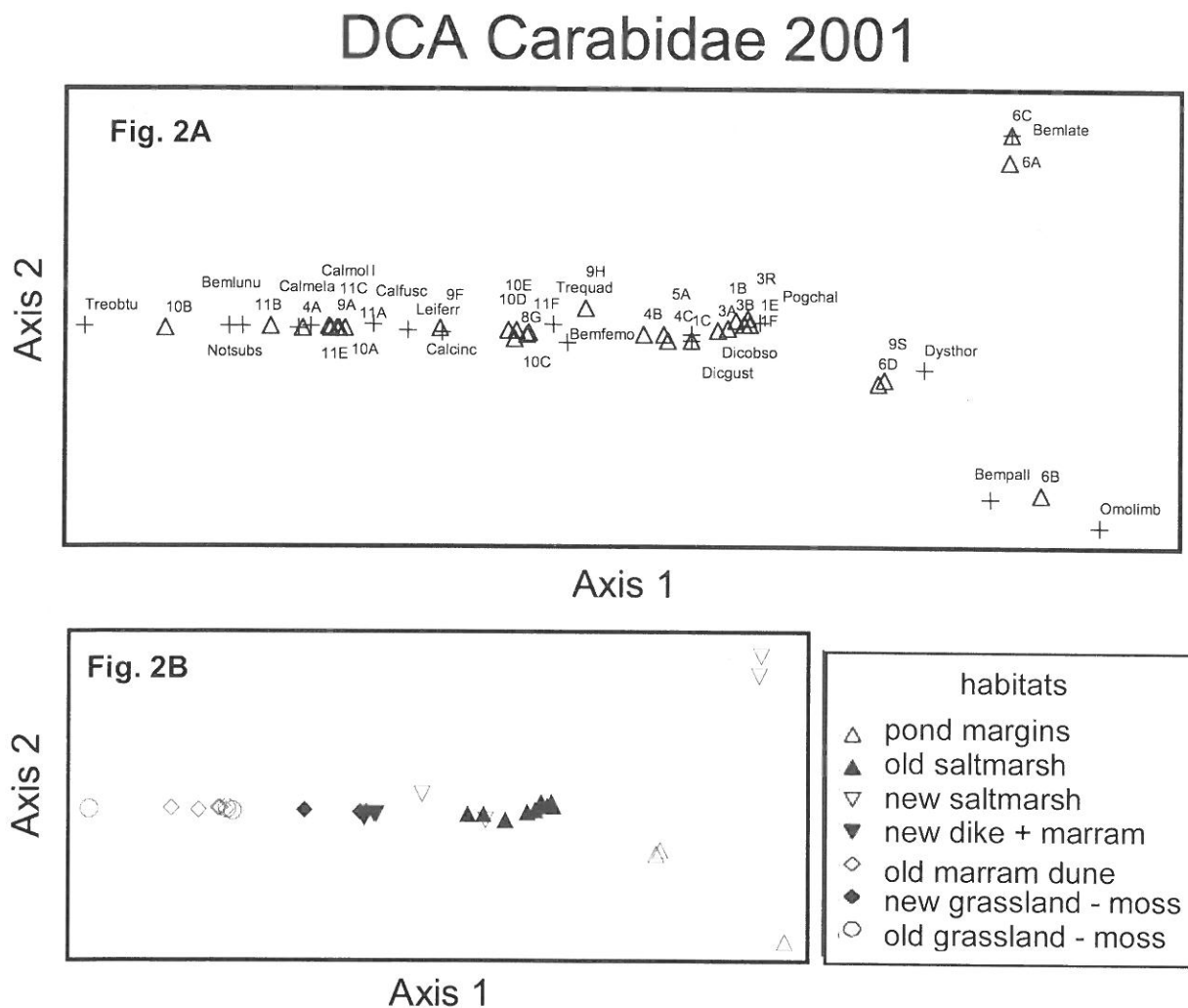


Fig. 2 — **A.** DCA-ordination (autumn 2001 sampling campaign) based on ground beetle data (sample score legends cf. Table 1; species score legends composed of three characters of genus name and four characters of species name, cf. Table 2 (appendix) for a complete species list). **B.** DCA-ordination (autumn 2001) of sampling sites based on ground beetle data with overlay of discerned habitat types.

DCA Carabidae 2002

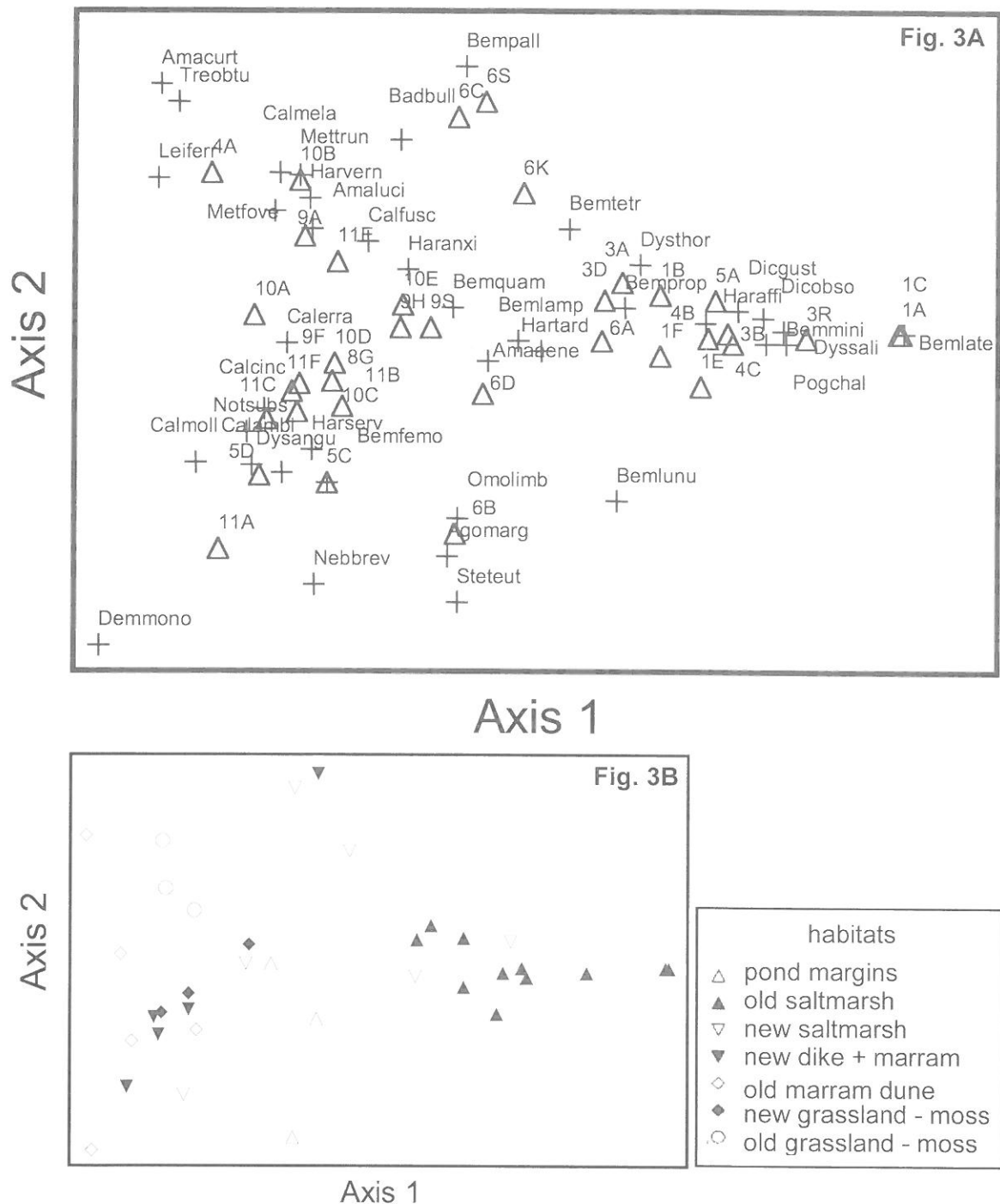


Fig. 3 — **A.** DCA-ordination (2002 spring and autumn sampling campaign) based on ground beetle data. **B.** DCA-ordination (2002) of sampling sites based on ground beetle data with overlay of discerned habitat types.

DESENDER et al., 1995). All species and their abundance (recalculated to an equal number of 15 traps) in the different main habitats during the sampling years 2001-2003 are given in Table 2 (appendix), ordered according to Red data book status (species threatened to a specified degree compared to non-threatened species) and habitat preference.

Ground beetle ordination results are summarized on Fig. 2A (2001 species and site scores), Fig. 2B (2001, with habitat type overlay), Figs. 3A and 3B (id., for 2002), Figs. 4A and 4B (id., for 2003).

From these results we can discriminate different groups of sites based on their ground beetle assemblages (for 2001, and largely also for 2002 and 2003). These

DCA Carabidae 2003

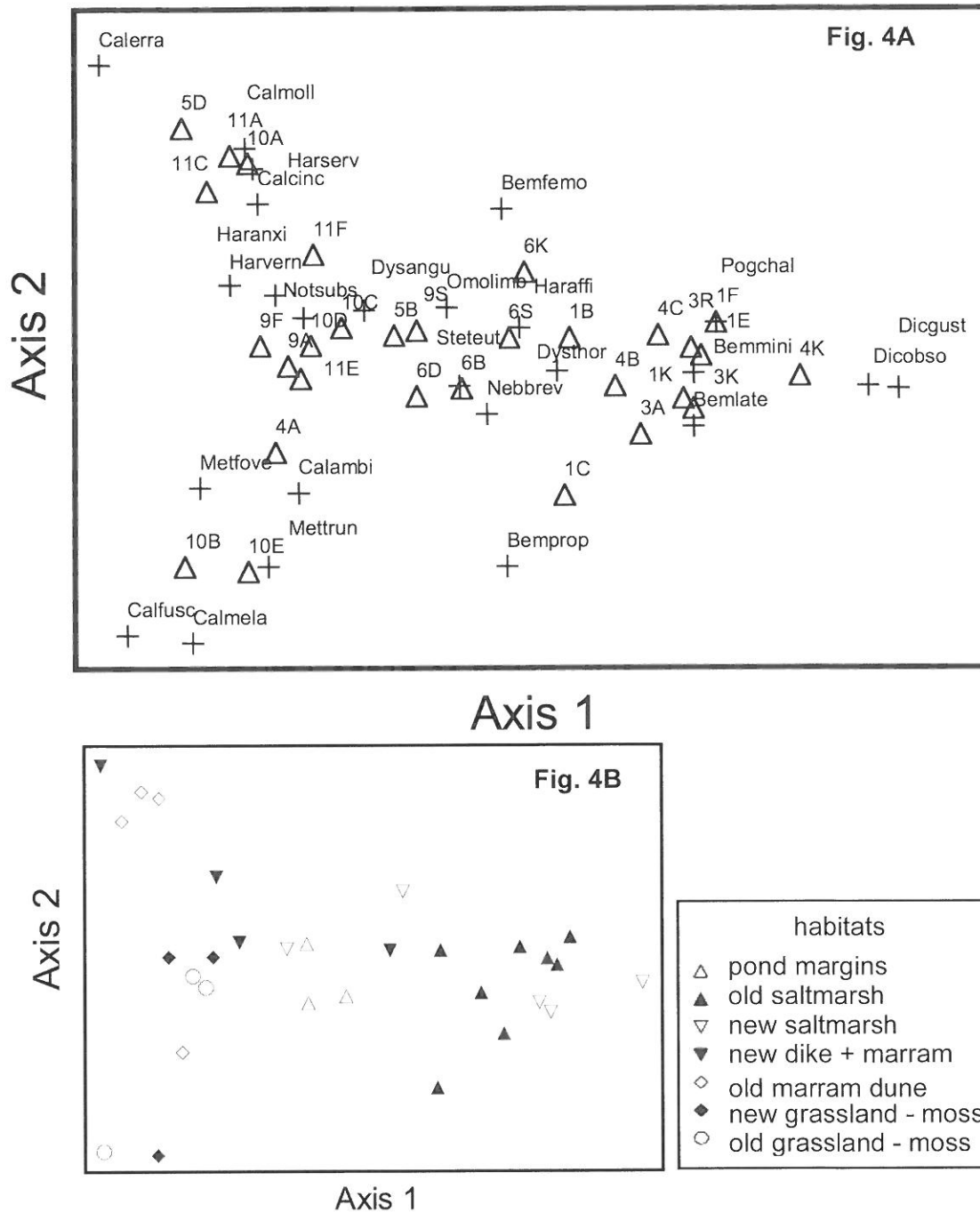


Fig. 4 — **A.** DCA-ordination (2003 spring and autumn sampling campaign) based on ground beetle data. **B.** DCA-ordination (2003) of sampling sites based on ground beetle data with overlay of discerned habitat types.

groups and typical species are described and discussed hereafter against the background of knowledge from earlier studies on dune and salt marsh beetle assemblages in our region (DESENDER; 1996, DESENDER et al., 1992) or from The Netherlands (TURIN, 2000).

A) Marram dunes and dune grasslands. In this habitat group, seaside marram dunes (codes 10A, 11A-B-C) with the typical and abundant ground beetle *Calathus mollis*

(Red data book category: rare) can be further distinguished from moss dunes and dune grasslands (4A, 9A, 10B, 11E) with *Trechus obtusus* (common), *Calathus cinctus* (vulnerable) and *Calathus fuscipes* (a eurytopic and drought-preferring beetle). Several other typical dune-inhabiting Red data book ground beetles occur in these habitats in small numbers: *Demetrias monostigma* (rare), *Amara eurynota* (vulnerable) en *Harpalus vernalis* (threatened).

B) Habitats of newly created, restored or developed sites (dikes, dunes, salt marsh as well as banks of freshwater habitats). Here, we observe a large number of ground beetle species (and spiders, see further) which are typical indicators for strongly **disturbed habitats**, more specifically for cultivated fields and ruderal sites on light soil. *Trechus quadristriatus* and *Bembidion femoratum* (illustrated on Plate 10) indeed prefer poorly vegetated disturbed sand to sandy loam soils, such as on cultivated fields, but also occur in rather wet situations such as highly dynamic riverbanks. In addition, an important number of Red Data book species are also found in these new or restored habitats. These include many typical dune and salt marsh species, occurring in the immediate surroundings, but also several special 'newcomers' for the study area such as *Bembidion pallidipenne* (near-extinct in Flanders) and *Bembidion argenteolum* (threatened). Another typical species for first stages of riparian or dune slack habitats is *Omophron limbatum*, preferring unvegetated margins of fresh or brackish water bodies of high quality, including early stages of succession of coastal dune slacks. The three last-mentioned species are also illustrated on Plate 10.

These species nowadays only persist in very few nature reserves of our region, but are typical pioneer species from coastal freshwater-brackish waterside habitats on sandy soil, such as dune slacks and dune-salt marsh transitions. Such species in general possess an excellent dispersal power (cf. DESENDER, 1989a) and apparently successfully and rapidly colonized the new habitats that became available in our study area. To survive in the long run, these ground beetle species need relatively continuously present dynamics at ecosystem level. Indeed, the results for 2002 and 2003 suggest that at least some of these species only occurred or were abundant during or immediately after the restoration measures took place, quickly disappearing after that initial stage. This aspect will be treated in more detail based on our continuous monitoring data (complete year cycles with ground beetle succession data) in a forthcoming paper (DESENDER et al., in prep.).

C) Sampling sites on mud flats and salt marshes (a.o. with the halobiontic and rare *Dicheirotichus obsoletus*). Within this group of samples, a further distinction can be made between, on the one hand, **salt marshes on heavy soil** (clay) with indicator species such as the halobiontic *Pogonus chalceus* (rare) and *Dicheirotichus gustavii* (rare) and, on the other hand, more **sandy salt marsh and newly created (sandy) transition zones between dunes and mud flats**, with the peculiar carabid *Bembidion laterale* (probably endangered), a species that can occur in high numbers on the upper zones of mud flats as well as in tidal marks along estuaries.

The ordination based on ground beetle data from 2002 shows much more diverse species groups, which is mainly a consequence of adding spring data. In general, however, we observe the same habitat groups based on beetle assemblages as for 2001, but in this case there are even more species typical for each of the discriminated

assemblages. In 2003, the target habitat 'new salt marsh' clearly shows already more similarities to the 'old salt marsh' fauna. A large proportion (but not all species, see further) of the typical salt marsh species from this estuary apparently has been able to colonize rather quickly the newly created or restored habitats. A similar conclusion is obtained for dune target habitats.

1.2. Spider assemblages

On the whole we identified more than 15000 spiders from 125 species. Spider data were also grouped per habitat type and year and documented for what concerns their species quality (Red data book species; cf. MAELFAIT et al., 1998). All species and their abundance (recalculated to an equal number of 15 traps) in the different main habitats during the sampling years 2001-2003 are given in Table 2 (appendix), ordered according to Red data book information (species threatened to a specified degree compared to species near the border of their distribution area and non-threatened species).

Spider ordination results are summarized on Fig. 5A (2001 species and site scores), Fig. 5B (2001, with habitat type overlay), Figs. 6A and 6B (id., for 2002), Figs. 7A and 7B (id., for 2003).

From these results we can discriminate different habitat groups based on their spider assemblages (for 2001, and largely also for 2002 and 2003). These groups and their most typical species are described and discussed hereafter, taking former knowledge on spider assemblages from dunes and salt marshes in our region into account (BAERT & MAELFAIT, 1999; BONTE et al., 2002a,b, 2003a,b, 2004a,b; MAELFAIT et al., 1997, 2000, 2004).

A) Marram dunes (codes 4A, 10A, 11A, 11B and 11C). Except for three ubiquitous aeronautic species (*Bathyphantes gracilis*, *Lepthyphantes tenuis* and *Erigone atra*) this habitat also harbours large numbers of the typical (threatened) dune species *Agroeca cuprea*. Also numerous are two other Red Data Book species, bound to dune habitats, *Alopecosa barbipes* and *Pelecopsis nemoralis*. Besides, *Haplodrassus dalmatensis* and *Pardosa nigriceps* are also abundant on these sites.

B) Dune grasslands (9A, 10B en 11E). Except for the same already mentioned three ubiquitous and ballooning species (*Bathyphantes gracilis*, *Lepthyphantes tenuis* and *Erigone atra*) this is the typical habitat of *Argenna subnigra* (threatened), whereas *Ozyptila simplex* and *Pardosa monticola* also were numerous here.

C) Habitats of newly created, restored or developed sites (dikes, dunes, salt marsh as well as freshwater habitats). Here, we observe some very abundant spiders typical for all kinds of disturbed situations (*Oedothorax* and *Erigone* species, cf. MAELFAIT et al., 2004). Because of their pronounced aeronautic behaviour such species can easily and rapidly colonize these newly created habitats. Promising is the appearance of *Arctosa perita* in the dike planted with marram grass (8G).

D) Sampling sites on mud flats and salt marshes. These are dominated by the typical species *Allomengea*

DCA Araneae 2001

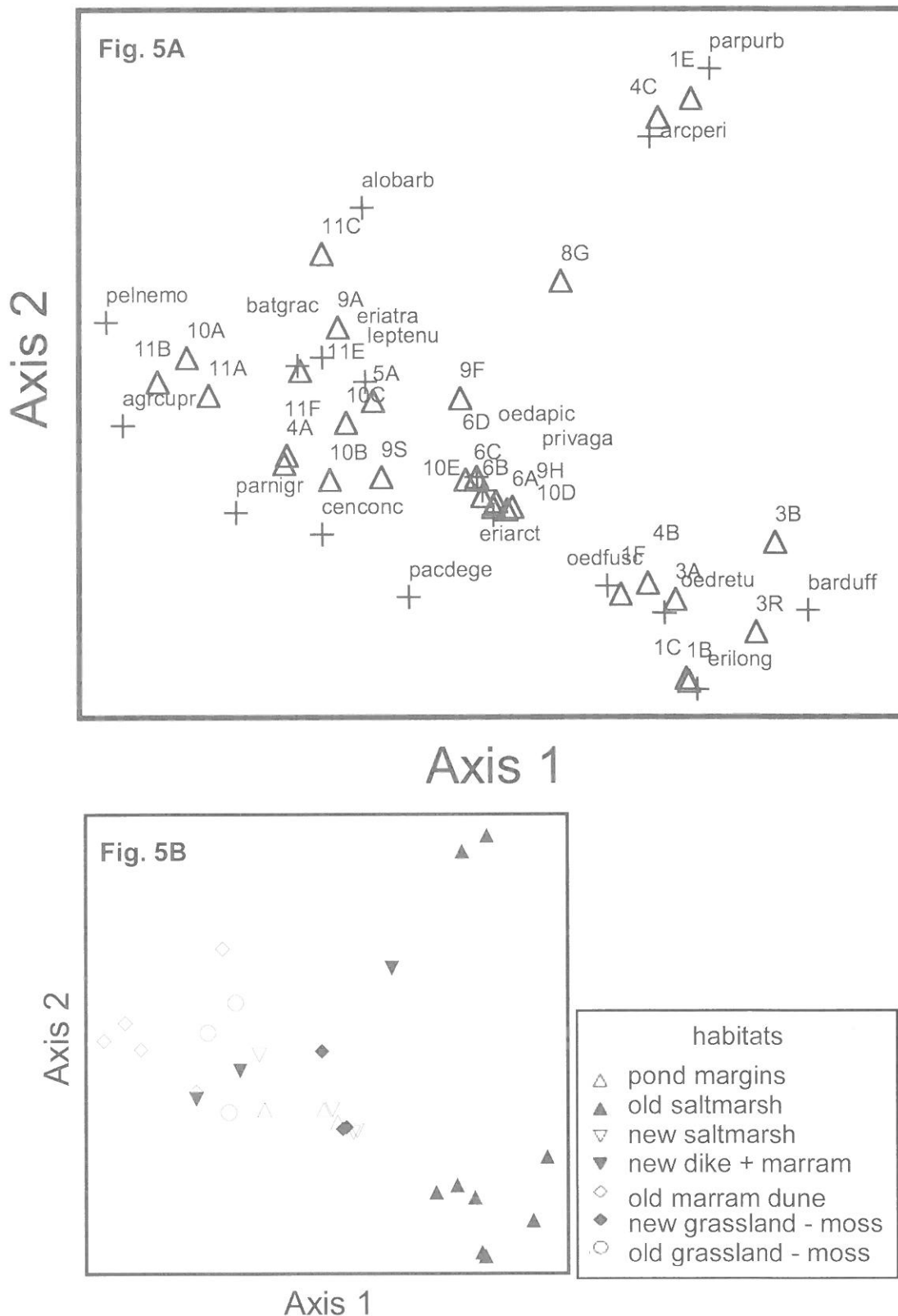


Fig. 5 — **A.** DCA-ordination (autumn 2001 sampling campaign) based on spider data (sample score legends cf. Table 1; species score legends composed of three characters of genus name and four characters of species name, cf. Table 2 (appendix) for a complete species list). **B.** DCA-ordination (autumn 2001) of sampling sites based on spider data with overlay of discerned habitat types.

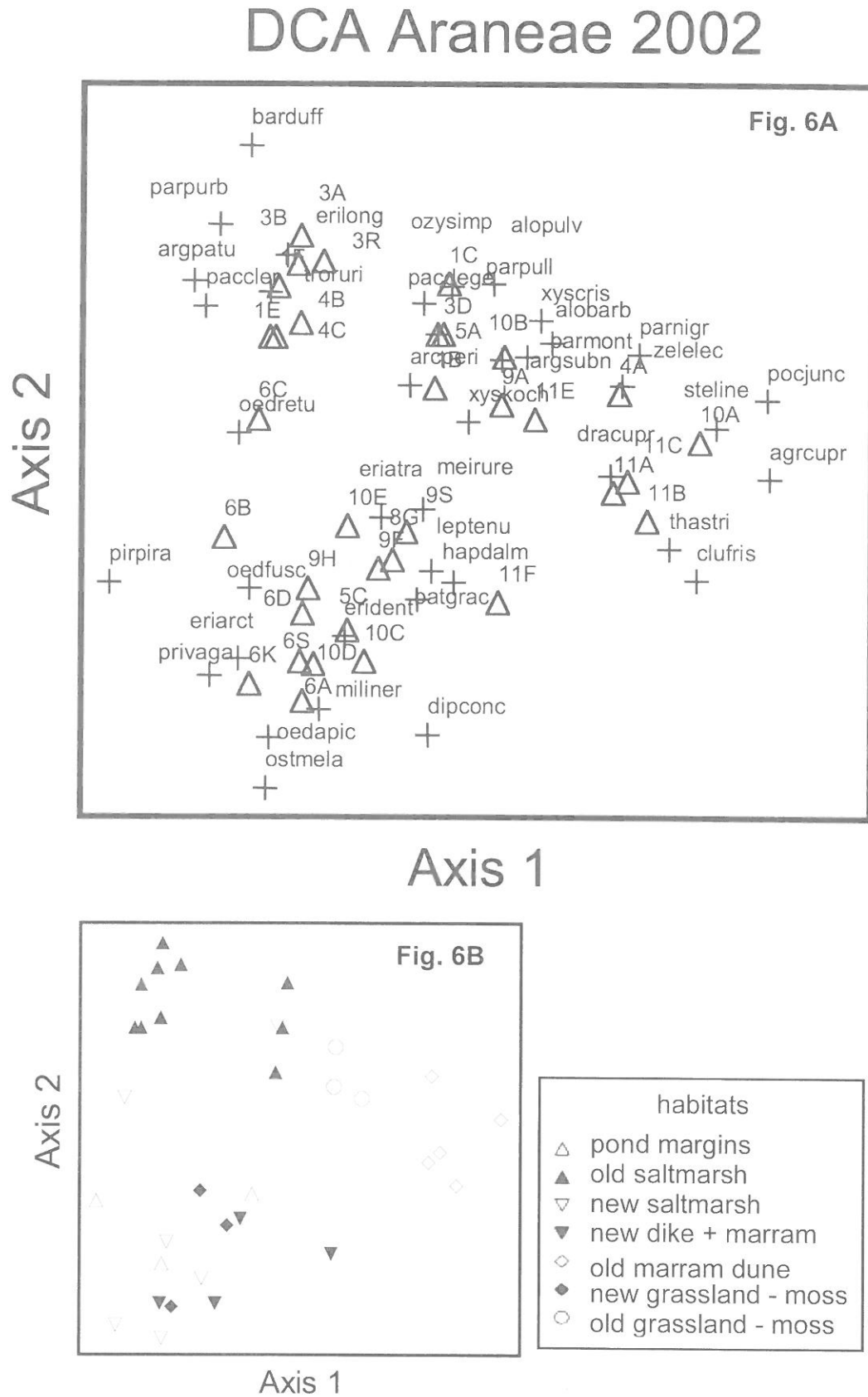


Fig. 6 — A. DCA-ordination (2002 spring and autumn sampling campaign) based on spider data. B. DCA-ordination (2002) of sampling sites based on spider data with overlay of discerned habitat types.

DCA Araneae 2003

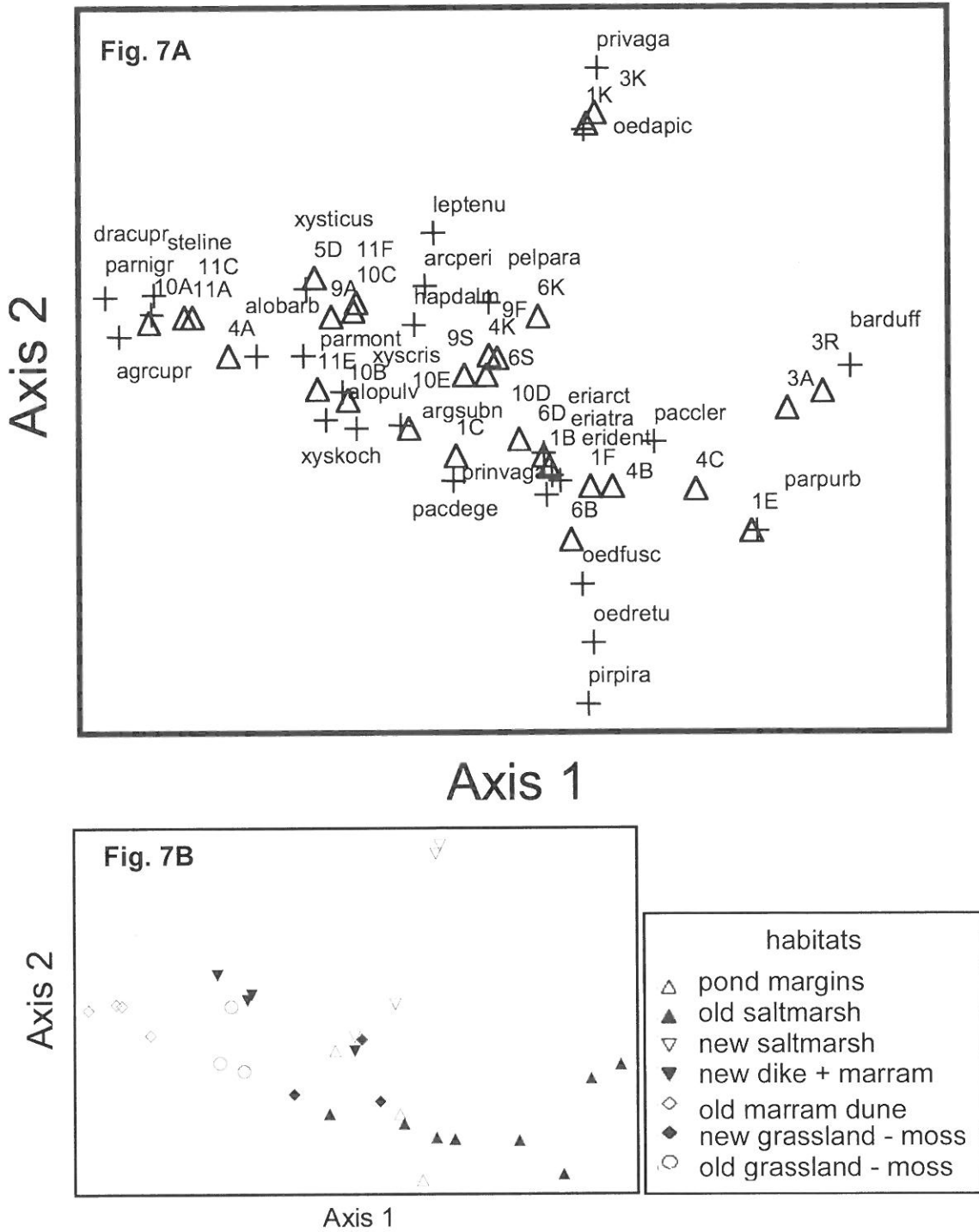


Fig. 7 — A. DCA-ordination (2003 spring and autumn sampling campaign) based on spider data. B. DCA-ordination (2003) of sampling sites based on spider data with overlay of discerned habitat types.

scopigera, *Argenna patula*, *Pardosa purbeckensis*, *Erigone longipalpis* and *Baryphyma duffeyi* (cf. BAERT & MAELFAIT, 1999).

The sampling stations are grouped along the first DCA-axis in three main clusters:

1° sites of the old marram dunes together with the new dike planted with marram grass;

2° sites from the old grasslands with new dune grasslands;

3° sites from the salt marsh relic with those from newly developed marshland.

These three groups largely overlap for autumn 2001 (the first sampling campaign after the nature development measures), somewhat less for 2002 and nearly not anymore for the sampling during 2003. This means that the spider fauna of the newly developed sites gradually starts to be similar to the remnant target habitats.

2. Diversity, habitat specificity and the fate of Red data book species in restored and newly created habitats

The spring and autumn results are summarized for all ground beetles and spiders for respectively 2001, 2002 and 2003 in Table 2 (appendix). Therein, all species and their abundance (brought back to an equal number of 15 traps) are regrouped in the different main habitats during each sampling year and ordered according to Red data book status (species threatened to a particular degree compared to species near the (northern) border of their distribution area and non-threatened species) as well as according to their optimal habitat (regrouped into the main categories dry poor grassland (Gsd), humid-wet sandy areas (Gsn), riparian sandy habitats (Oz), brackish and salt marshes (Szb) and disturbed habitats (D)). Because the timing and length of the sampling campaign was not the same over the years, the given numbers are only comparable within each year, implying some caution in interpretations between years.

Several threatened species from dry sandy areas (Gsd-species in Table 2), that used to be restricted to old marram dunes (OH) and old dune grasslands, clearly expanded their local occurrence through colonization of newly created or restored dry sandy habitats (DH, ND, KW). Examples among ground beetles are *Calathus mollis* and *C. cinctus* and among spiders *Arctosa perita*, *Argenna subnigra* and *Haplodrassus dalmatensis*. This could also apply to the carabids *Harpalus vernalis*, *H. servus*, *Amara lucida* and *A. tibialis* as well as the spiders *Agroeca cuprea*, *Clubiona frisia*, *Pardosa monticola*, *Thanatus striatus* and *Cheiracanthium virescens*. Future monitoring will enable to conclude whether or not the individuals observed in these new habitats are making up a permanent (well-established) population or, alternatively, only a temporary population as a result of source-sink effects from adjacent high-quality habitats. Such effects could especially manifest themselves in years with high abundance of particular species. For the (constantly wingless) ground beetle *Demetrias*

monostigma as well as the spiders *Alopecosa barbipes*, *Trichopterna cito*, *Zelotes electus*, *Pelecopsis nemoralis*, *Ozyptila atomaria*, *Metopobractus prominulus*, *Xysticus erraticus* and *Ceratinops romana*, apparently the newly created habitats are not sufficiently nearby and/or did not yet have the appropriate ecological conditions to allow their successful colonization at the time of sampling.

Restored and newly created habitats also resulted in the appearance of some species, new to the study area, or at least gave rise to the development of large populations of formerly only sparsely occurring species. Examples are the rare carabids *Dyschirius angustatus* and *Calathus ambiguus* and the spider *Ozyptila sanctuaria*. At the moment it is unclear if and to what level these thermophilic invertebrates from partly open sandy soil will remain abundant during the further evolution of the restored area. Again, further monitoring is essential to evaluate these future developments. Many other species from dry sandy areas were only observed in low numbers during these sampling campaigns and are therefore not further discussed here.

Two threatened carabid species, typical for humid and wet sandy habitats (Gsn-species), expanded considerably their population in the area due to the nature development activities: *Dyschirius politus* and *Bradycellus distinctus*. The spider *Robertus arundineti* also colonized these newly created habitats. Nevertheless, in these cases also, the long-term persistence of these species in the nature reserve is still uncertain because they are bound to unstable humid sandy sites, without much vegetation.

Several highly interesting species from sandy riparian situations or early dune slack stages (Oz-species) quickly appeared as completely new to the area: examples are the ground beetles *Bembidion pallidipenne*, *B. argenteolum*, *Chlaenius vestitus* and *Acupalpus brunripes* and the spider *Pardosa agrestis*. The first-mentioned beetle is extremely rare in our country and until recently only was known from very few coastal locations. The beetle appears to colonize nearly exclusively the first unvegetated stages of brackish-fresh water riparian sites such as dynamic early stages of dune slacks. It needs constantly present dynamics and turnover in order to maintain a long-term surviving metapopulation structure. At present, this ground beetle species has already disappeared nearly completely from the study area again, which could have important implications for options concerning future nature conservation management.

Several rare or threatened species from mud flats and salt marshes (Szb-species), the ground beetles *Pogonus chalceus*, *Dicheirotichus obsoletus*, *D. gustavii* and *Bembidion laterale*, immediately expanded their populations in the newly created salt marsh areas (see also higher DCA-results for 2003). This is not the case for the species *Dyschirius salinus* and could be due to a lack of sufficient clay in the substrate of the new marshes. This beetle indeed is adapted to a very fine-structured salty substrate and avoids sandy sediments (DESENDER, 1989a; TURIN, 2000). The relatively high abundances of *Dicheirotichus obsoletus* and *Bembidion laterale* on newly created sites (in contrast to the congeneric species

D. gustavii, typical for heavier soils) also points into the same direction as these beetles clearly prefer a sandier substrate as compared to other salt marsh or halophytic carabids. Also for typical salt marsh spider species, the restored areas apparently are not yet sufficiently well developed. Presumably, these spiders will only be able to establish populations when the vegetation will be sufficiently developed and at a further stage than the primary *Salicornia-Suaeda* vegetation type.

Striking is the abundant appearance of the Southerly distributed spider *Diplocephalus graecus* on the dike with clay topsoil (BONTE et al., 2002b). Among the ground beetles, *Bembidion nigropiceum*, a wingless species with a remarkable biology, was observed for the first time in our country in the strongly disturbed zones at the basis of a newly created dike (DESENDER, 2005a). It seems probable, however, that this interstitially living species has already disappeared from the area again.

As can be further derived from Table 2, massive numbers of small spider and beetle species, adapted to highly disturbed situations, were observed immediately after digging activities had been finished in the area. Many of these species are well-known also from eutrophic riversides, road verges and cultivated fields, where they mainly prey on springtails. Their rapidly expanding populations on disturbed sites also radiated towards the old marram dunes and dune grasslands, especially obvious in 2002, already less so from 2003 onwards.

The remaining group obviously contains many species found in newly created habitats, e.g. the high incidence of the marshland spider *Pirata piraticus* in freshwater upwelling zones. Interestingly, the dike covered with clay was not (yet?) colonized by *Pelecopsis nemoralis* but by its sister species *Pelecopsis parallela*, adapted to more nutrient-rich situations.

3. Conclusions, future conservation management and suggestions for continued monitoring

In the first three years after the nature restoration measures, our results on invertebrates are hopeful and interesting, firstly because of the findings of several species new to the study area (including a ground beetle and a spider new for the Belgian fauna, cf. DESENDER, 2005a; BONTE et al., 2002b), secondly because of the marked increase within the area and/or the colonization in new or restored habitats of several target species of high conservation interest (typical and/or Red data book species). However, we obviously have documented the very first stages only of the development of these new sites in the river IJzer Estuary during these 'MONAIJ' project sampling campaigns in 2001-2003.

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A continued monitoring of the main old and new habitats of this nature reserve therefore is without doubt a prerequisite for a well-founded long-term evaluation of the performed nature development measures. Moreover, further monitoring is of high fundamental scientific interest against the background of our long-term data on beetles and spiders since more than 17 years, sampling which is still continued without interruption on several sites in this estuary. This should enable us in the future to make a clear distinction between directed changes in the area (mainly as a consequence of ecological processes, accompanying measures for conservation management) and changes due to year-to-year population dynamic fluctuations (whether stochastic or not) in carabid beetle or spider populations.

Another important aspect that was not yet taken into account in the current monitoring concerns population genetics of a number of target invertebrate species. To this end we have formerly studied, i.e. within the context of the regional project VLINA96/01, a number of ground beetles, spiders and terrestrial amphipods for their genetic diversity and differentiation in salt marshes from our region, including the river IJzer Estuary (cf. DESENDER, 1985, 1989a,b; DESENDER et al., 1998; DESENDER & VERDYCK, 2001). It would therefore be of much interest to repeat such studies in the future, for species that occurred earlier in the area or not, in order to compare population genetics from newly created or restored populations to those from the old salt marsh relic or to those from other areas. Such population genetic information not only might enable to trace the origin of colonizing species, but is also of major importance to judge population viability in the long run.

Finally, since several years now, we have observed an ongoing increase of sand depositions in the area, also in the old salt marsh relic. Observed ground beetles and spiders in the newly created marshes also suggest a preponderance of sand instead of silt in newly deposited sediments. It seems therefore self-evident that on short as well as on longer terms additional measures will be necessary in the area to alter or reverse this evolution, which could otherwise bring about the loss or at least cause a serious threat for several typical and very rare invertebrates.

Acknowledgements

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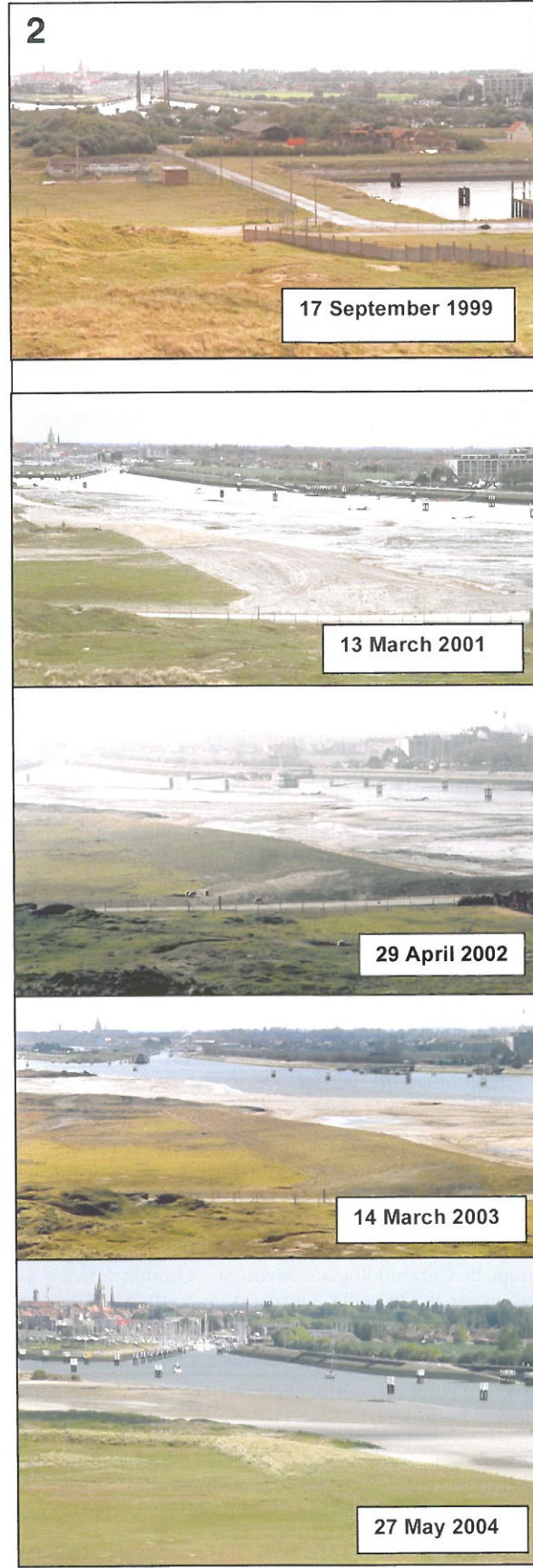
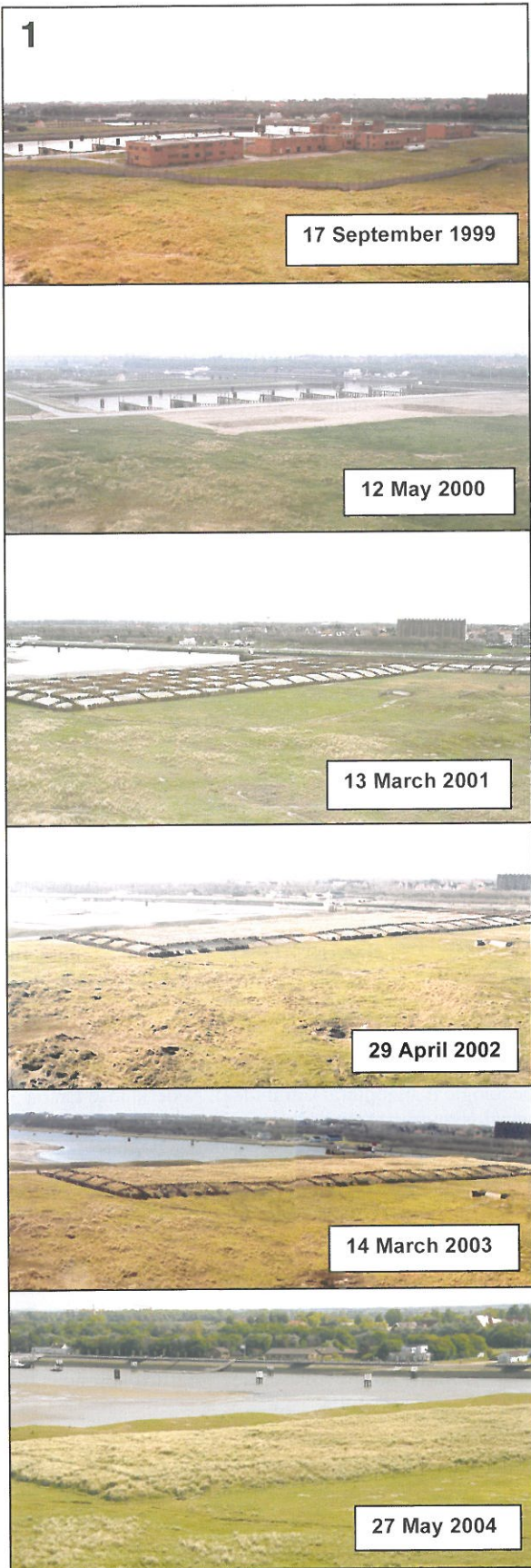


Plate 1 — Pictures of the most important changes that took place along transect 10 and 11 (observed from the top of the lighthouse, cf. Fig. 1, next to 11B).
Plate 2 — Main changes along transect 8, 9 and 11.

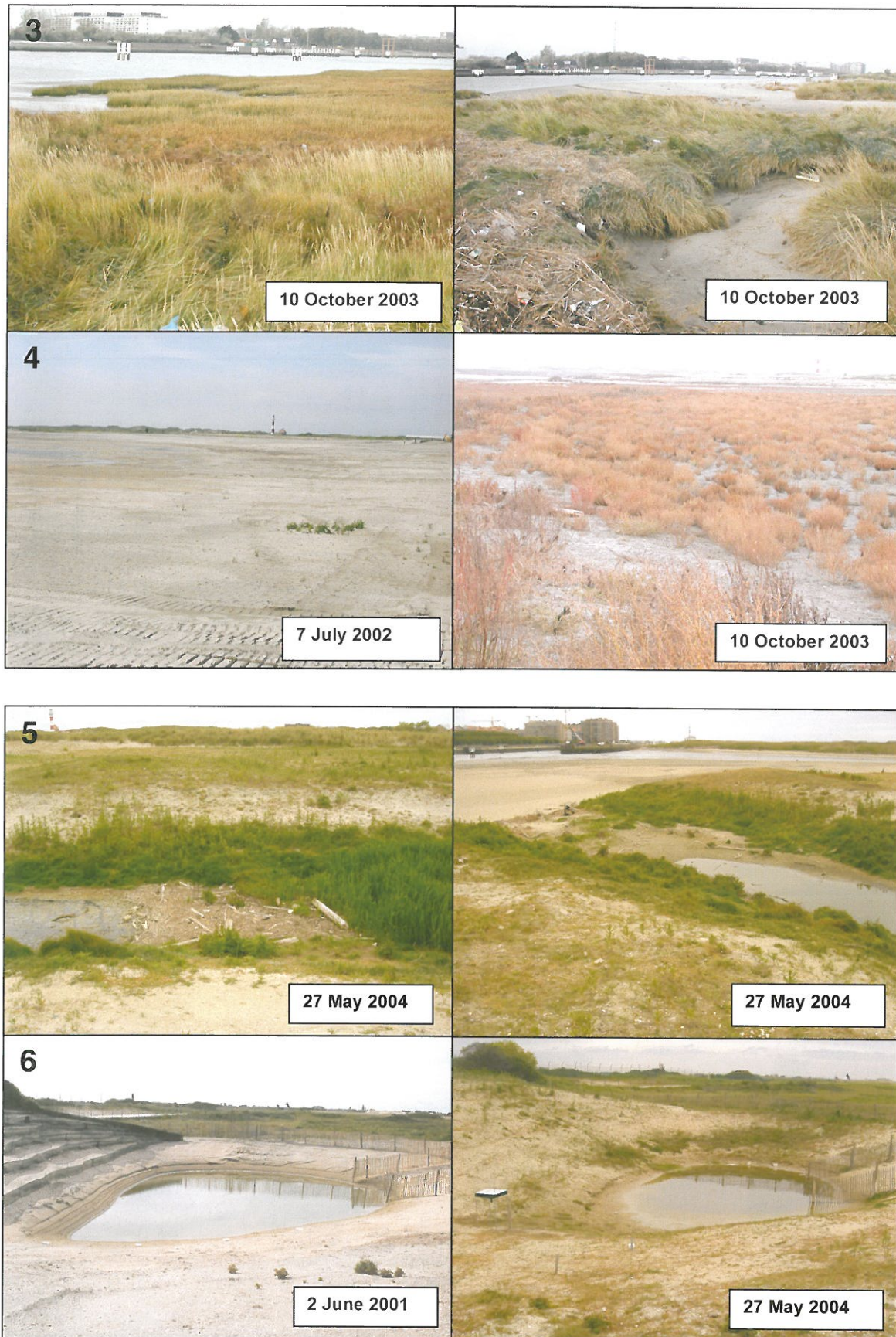


Plate 3 - 6 — Plate 3 shows some views of the old salt marsh, to the right one can observe a zone with recent sand deposits, Plate 4 shows the depression where main digging activities were performed along transect 1 to 5, and its evolution to new lower salt marsh, Plate 5 shows new small freshwater ponds originating from an upwelling of groundwater at the base of a newly created dike (cf. fig. 1, 6B and 6D) and Plate 6 illustrates the newly created brackish dune pond - dune slack on transect 9 (9S).

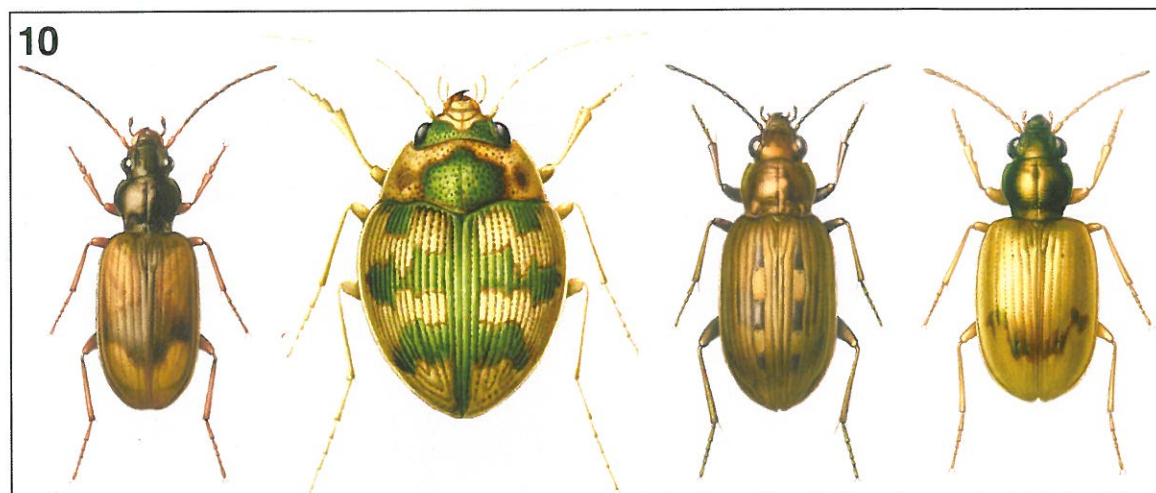
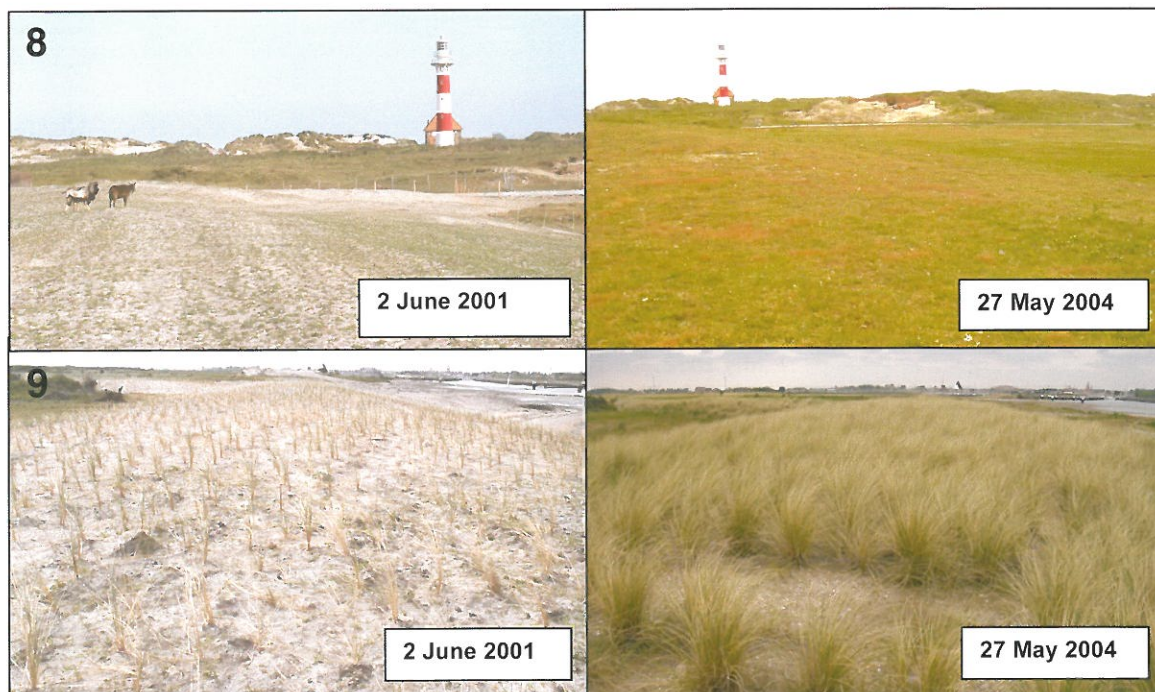


Plate 7 — Photographs of the long-term study transect, sampled continuously since 1990 for spiders and ground beetles from seafront marram dunes (11A-11B-11C) to dune grassland with mosses and lichens (11E).

Plate 8 — Illustrates the sandy dike with clay top soil and grassy vegetation (9F).

Plate 9 — Shows the same dike in a zone covered with sand and planted with marram grass (8G).

Plate 10 — Ground beetle indicator species for some newly created or restored sites: from left to right: *Bembidion femoratum* (disturbed open sites), *Omophron limbatum*, *Bembidion argenteolum* and *Bembidion pallidipenne* (early stages of dune slacks, margins of dune pond).

