# The use of spiders as indicators of habitat quality and anthropogenic disturbance in Flanders, Belgium

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#### **Abstract**

A review of the last few decades of nature conservation spider research in Flanders, northern Belgium is provided. We show that spiders are very useful in site assessment and in monitoring the nature value and biodiversity of the several kinds of natural and semi-natural habitat types that occur in this region. Studies on particular species show that these spiders can be good indicators of the detrimental effects of human induced disturbances, such as fragmentation and pollution, on natural populations and ecosystems.

**Key words:** spiders, bio-indicators, habitat quality, biodiversity, anthropogenic disturbance, Belgium

## INTRODUCTION

The intent of this contribution is to provide a short review of the applied ecological research concerning spiders as bio-indicators of Flanders (northern part of Belgium) between 1975-2003. As a taxonomic group, spiders are very well suited for use as bio-indicators in studies of habitat quality in terrestrial ecosystems (Maelfait & Baert 1988ab; Maelfait 1996; Maelfait et al. 1989b). This is because spiders are a rather species rich group which occur in the majority of terrestrial ecosystems and even in some aquatic ones. Each species has its own specific requirements regarding humidity, temperature regime, litter and vegetation structure and so on. This means that slight changes in habitat quality cause important changes in the spider assemblage composition. Furthermore, small changes in the spider composition of a habitat indicate changes in the quality of that habitat. A practical reason to use spiders as bio-indicators is that they are easy to sample in a standardised manner, at a relatively low cost. We have used spider assemblage analysis to bio-indicate the natural value and the biodiversity content of a wide variety of habitat types. These investigations were, and are done within the framework of nature conservation and nature management in our region. We give an overview of the more important results for each habitat type in the Results section. On the basis of all these investigations a Red List for the spiders of our region was developed, in which a habitat characterisation was given for the threatened species. This Red List is dealt with in the Discussion and conclusions section. During more recent years, spiders were not only used as biodiversity and nature value indicators, but we also tried to understand individual species and populations. This was done in an evolutionary ecological context with much attention having been paid to interpopulation variation in life cycle patterns and other fitness related characteristics. The results of these studies are also treated under the heading for the habitat type in which the model organisms occur.

#### MATERIAL AND METHODS

Most often pitfall traps were used as sampling devices. Three or more of these cheap traps were installed per sampling site. We normally used easily available glass jam jars of half a litre. Their upper rim had a diameter of 9.5 centimetres. They were sunk into the soil so that their upper side was just below the soil surface. A 4% formaldehyde solution, with detergent to lower fluid surface tension, was added to the traps. Bottom surface-active animals are easily caught in such traps. The traps were generally emptied at fortnightly intervals over a period of one year. Because pitfall capture data not only depend on the densities, but also on the activity patterns of the captured arthropods, they have to be analysed with both these influencing variables in mind (Maelfait & Baert 1975; Maelfait 1996; Maelfait & Segers 1986). The total yearly captures of a particular species made in several habitats with the same sampling effort, gave a picture of its habitat preferences. To compare species in their distribution over several habitats, the captures of these species were all given equal weight in classification and ordination analyses. The distribution of the captures over consecutive (fortnightly) intervals of an annual cycle, gave a picture of the seasonal activity of a species. These temporal capture data provide information about the phenology, or life cycle timings of the species. Besides pitfall trapping, we have also used several other techniques, such as hand catching, sweep netting, eclectors to capture tree trunk active spiders and quadrat sampling. In the last case, we used some twenty to thirty sampling units (i.e. quadrats) of an area which varied in size depending on the body size of the spider population involved in the study (e.g. 12.5 cm X 12.5 cm for the small erigonid spiders occurring in highly fertile pastures, 50 cm X 50 cm for lycosids of nutrient poor dune grasslands), in order to obtain good estimates of numbers of individuals per square metre.

#### RESULTS

# Coastal dune spiders

Belgium has a coastline of approximately 60 kilometres. With the exception of two small salt marsh areas, this coastline is built up of a narrow zone of lime rich, quaternary sand depositions of only a few kilometres wide, called coastal dunes. Inland of this dune strip we find the polder region with intensive agriculture (Provoost & Hoffmann 1996). Especially during summer, but also during winter the fine-sanded beaches attract huge numbers of tourists. This led to an ever-increasing expansion of the tourist industry during the 20th century. Coastal villages grew and changed in a few decades to highly urbanised areas. About half of the natural dune areas present at the beginning of the 20th century have been overbuilt by apartments and hotels. The remaining natural dunes are thus highly fragmented by human settlements and road infrastructures (Vermeersch 1986).

In the mid 1970s, Professor Hublé of the Ghent University initiated investigations on the coastal spider fauna. These investigations were of a faunistic nature. It was found that the spider fauna occurring on these sandy hills and in the salt-marshes, was very special and species rich (Hublé 1975, 1976; Hublé & Maelfait 1982; Maelfait et al. 1989a; Baert & Maelfait 1999). Especially dry sandy, thermophilic habitats like marram dunes (blond dunes), moss dunes and short grazed dune-pastures, contained a lot of rare and endangered species (Maelfait et al. 1989a, 2000). These habitats are typical of subclimax situations and are maintained as such by grazing animals, like cows, horses and rabbits and also by wind dynamics. After World War II, local farmers abandoned their agro-pastoral activities. For lack of grazing, the open, thermophilic vegetations were more and more overgrown by sea buckthorn and other shrubs. Together with a decrease of the rabbit population due to viral diseases, a strong reduction and fragmentation of the grey dunes and short grazed dune grasslands took place. This meant a serious loss of the preferred habitat of many dune specific invertebrates.

From the second half of the 1980s, we started investigations on the effect of nature management and hydrology on the spider fauna of the nature "De Westhoek", an important dune nature reserve at the French-Belgian border. This research confirmed the findings of Hublé, in that the most interesting spider assemblages were found in the open habitats without shrubs (Baert & Desender 1993; Bonte & Hendrickx 1997; Bonte et al. 1999, 2000b). We also found that high levels of groundwater extraction for tourist needs during the summer threaten the spiders' typical open wet habitats (Maelfait et al. 1997). Important for the hibernation and thus the survival of many spider populations occurring in these short vegetations are islets of higher, rougher vegetation with litter accumulation (Maelfait et al. 1997; Bonte et al. 2000a). Such patches of rough vegetation should be left over in case of a mowing management. Our studies, together with those of our botanist colleagues, led to a change in the management of several of the larger dune nature reserves. A management regime of year round grazing with cattle, horses and donkeys was started in the 1990s, with the major aim being to keep vegetation open and free of shrub encroachment.

Recently all the available community structure data were compiled and analysed (Bonte et al. 2002c). The main factor determining the spider species composition was the transition from nude sand over short vegetation to shrubs and forest development. Also very important was the dry-wet gradient, including aerial humidity. A third important determining factor was the degree of disturbance of the soil cover, by grazing animals or wind blown sand depositions. This analysis also confirmed that although the total species content of the four major habitat types (dune shrubs, dune grasslands, dune slacks and grey dunes) were comparable (i.e. between 25 and 40 species), the content in typical dune living spiders was much higher in the dune grasslands and grey dunes than in the other two habitat types (Bonte et al. 2002b; Fig. 1). In these grey dunes, not so much the total species richness, but the richness in typical species was dependent on the surface of the open, dry habitat types (Fig. 2). In addition, some typical species were dependent on litter rich vegetation for their juvenile development, and were found to seasonally and diurnally migrate between the grey dune and the dense vegetation

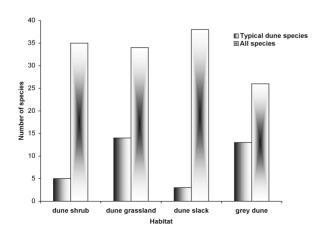


Fig. 1. The total number of spider species (right) and the number of dune spider species (left) encountered in each of the major dune habitat types.

(Bonte et al. 2000a). In Fig. 3 it can be seen that the densities of the juvenile gnaphosid spider Haplodrassus dalmatensis (L. Koch, 1866) were quite high during the whole season in the shrub litter, while adults rarely occurred. During summer these adults were found on the sun-exposed grey dunes where reproduction took place. A comparable pattern was observed for Typhochrestus digitatus (O.-P. Cambridge, 1872). From late spring until early autumn, juveniles of this erigonid spider occurred in high densities in the litter layer of the creeping willow (Salix repens) shrub. In autumn they became adult and remained in the cover of the shrub until early spring, at which time they moved to the open ground of the grey dune to reproduce. In grey dunes, we also found an invasive occurrence of a Mediterranean erigonid spider, probably as a result of global warming (Bonte et al. 2002a).

A model organism, which has received some attention, is the lycosid Pardosa monticola (Clerck, 1757). It is quite understandable that this cursorial spider of open, thermophilic, short grassy vegetation and moss dunes, experienced the dunes as a highly fragmented environment (Bonte & Maelfait 2001). It can find its preferred habitat only sporadically, in between stretches of bare sand and shrub. The patches of suitable habitat for this species are islets in a sea of unfavourable, uninhabitable environment. In two years, 1998 and 2000, during the reproductive season (i.e. May and June), a large number of habitat patches thought to be suitable for P. monticola, were thoroughly searched (Fig. 4). The smaller patches were never occupied, or were only occupied during one season. Current research is focusing on the metapopulation dynamics and life history variation of this and other species of dune-living spiders (Bonte et al. 20003a, b,c,d).

## Heathland spiders

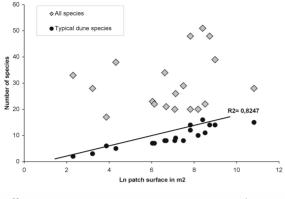
Heathland is a semi-natural habitat characterised by dwarf scrubs like *Calluna vulgaris* in the dry places and *Erica cinerea* on wet sites.

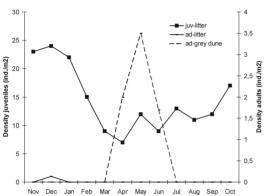
Both wet and dry habitats were found to harbour a very rich spider fauna (Jocqué 1986; Maelfait et al. 2000). Where they occur in our region, heathland vegetation is kept young and vivid through the rather intensive management of mowing or intensive grazing. This is done mainly to prevent these dwarf scrub communities being colonised and overgrown by grasses, such as Molinia. In our region growth of these grasses is stimulated through the deposition of airborne nitrogencompounds originating from our intensive agriculture. Only regular mowing or grazing by sheep can prevent these grasses overgrowing the Calluna heathlands. This rather intensive management, however, has the disadvantage that Calluna heather only rarely becomes old and dies off. We found that mosaics of old heather with a thick litter layer, alternating with open patches where Calluna died off, provided an optimal combination for a lot of typical heathland spiders and other arthropods (Maelfait et al. 1990a). The litter rich patches offer shelter in winter and the open patches are suitable for reproduction during the summer.

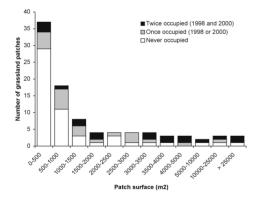
On a southerly exposed motorway verge an interesting heathland-like spider fauna was found (Baert & Maelfait 1988). It is important that such exceptional road verges are well managed to conserve their biodiversity.

# Spiders of field edges

Flanders' agriculture is intensive, with very high inputs of fertilisers and pesticides. As long as compulsory purchase of land have not been issued, parcels are usually of one or a few hectares. In the more traditional rural landscapes, there are quite a number of hedges, field roads and field margins in between the fields. During the 1980s we assessed the possible role of these unused edges of arable land and of pastures (Maelfait & De Keer 1990; Maelfait & Desender 1995; Maelfait & Tanghe 1996). We found that the spider assemblages that occurred on arable land and on







intensively grazed pastures were dominated by springtail and aphid-consuming small spiders, such as *Erigone* and *Oedothorax* species, *Tenuiphantes tenuis, Bathyphantes gracilis,* and so on. A few larger spiders, such as *Pachygnatha degeeri, P. clercki, Pardosa palustris* and *P. amentata* also occur in high numbers. Field margins were found to have a higher diversity and three categories of spider species were

Fig. 2. The total number of species and the number of typical grey dune species collected by means of equal sampling efforts in patches differing in surface area of that dune habitat type.

**Fig. 3.** Haplodrassus dalmatensis: number of juveniles and adults per m² in the litter layer of a patch of shrub vegetation (juv-litter: solid line with squares and ad-litter: dashed line) and the densities of the adults in an adjacent grey dune (ad-grey dune: solid line), where they reproduce during summer.

Fig. 4. Pardosa monticola: occurrence of that species in patches of suitable habitat of different size classes in the reproductive season of 1998 and/or 2000.

known to occur there. First of all, there was a series of species which would not be able to survive in the agricultural landscape if these less intensive strips were not present. These species are not yet rare in our region but may become so if there is a further loss of non-crop habitats in the countryside, e.g. *Pardosa nigriceps*, *P. pullata*, *Alopecosa pulverulenta*. We also found that these margins may also have

played a role in the overwintering of the species living in the crop fields and the populations of the pastures during summer. Adults and subadults of Oedothorax fuscus, O. retusus, O. apicatus and Bathyphantes gracilis seemed to retreat into these field margins during winter months. As a third category, we also captured a few individuals of species which normally only occurred in natural areas, like forest, marshes, heathlands and so on. It is still unclear whether these individuals were representatives of low density, marginal populations or whether they were incidental captures of nearby, thriving populations. Whichever the case, these captures highlighted the possible role of field margins and road-side verges as corridors between natural areas.

## Forest spiders

The exploitation of forested areas in Western Europe began some 5 to 7 thousand years ago. These anthropogenic influences lead to a reduction in total forest cover, the conversion of natural forests to simplified monocultures of mainly exotic tree species and a severe fragmentation of the remaining forests. These fragments are isolated from each other by intensively exploited agricultural land, industrial areas, roads and urban settlements. Nowadays, semi-natural woodlands in Flanders cover only about 3% of the region and are small in size. Total forest cover with the inclusion of plantations of exotic tree species is about 8%. The average forest area amounts to 19.2 ha, but almost 70% of the forests are less than 10 ha and 14% are even less than 1 ha (Tack et al. 1993). Particularly in the northeast, the forests there consist of coniferous plantations. These were planted at the beginning of the 20th century as a source of timber for coal mine exploitation. Their plantation caused the a lot of heathland. Our studies on the spider assemblages of forest habitats that were started in the 1970s, are still ongoing depending on the availability of project funding (Maelfait & Baert 1978; Segers & Maelfait 1988a,b; Maelfait et al. 1990b, 1992, 1995; De Bakker et al. 2001; Hendrickx et al. 2001; Gurdebeke et al. 2003b). A few years ago, we had the opportunity to sample 56 forest stands of 40 forests distributed over the major geographical units of our region. In agreement with the variation in spatially auto-correlated environmental variables like soil texture, soil fertility and tree cover, there was a pronounced differentiation in the composition of the spider assemblages living in the litter layers of these forests (De Bakker et al. 2000, 2002). The deciduous forests on loamy soils were by far the most interesting because of their natural value. In the best of these forest plots, more than 40% of the individuals caught belonged to stenotopic forest species.

More detailed investigations were done on a species typical for good forest conditions, including Coelotes terrestris (Segers & Maelfait 1990). Females of this funnel web spider can attain a body length of about 1 centimetre, while males are generally slightly smaller. It is widespread species in north-western Europe, where it can be common in deciduous, mixed and coniferous forests. In our region it is largely restricted to the forests of the loam and loamy sand geographical subregions. Coelotes terrestris lives in a tubular, silklined burrow under stones and logs, and within moss and leaf litter. It feeds on beetles, mainly carabids, dipterans and other arthropods. The males have a pronounced activity peak in September, when mating occurs. A first brood is produced in May and a second can be produced in July. The young stay with the mother and are fed by her until they have undergone three moults. Their long-distance dispersal capabilities can be assumed to be poor, since the young are already quite large and heavy when they start dispersing, so that ballooning is probably no longer possible. To assess the population genetic effects of forest fragmentation, we chose Coelotes terrestris as a model organism because it is so strongly forest habitats (Maelfait Hendrickx 1998; Gurdebeke et al. 2000; Gurdebeke & Maelfait 2002; Gurdebeke et al. 2003a, b). A first attempt to reveal the population genetic structure of this species was made by using allozyme electrophoresis. Only the enzyme PGI, however, showed good interpretable variation. Nevertheless, we observed significant differences between many pairwise comparisons of population allele frequencies, implying a high degree of genetic isolation between the spider populations inhabiting the forests. The larger forests had three alleles, while most of the smaller forests had only two alleles. We also looked at allele frequencies of PGI in Coelotes terrestris occurring in ten other forests dispersed over our region. Most of these forests were different from each other in the frequency of the alleles coding for that enzyme. Some, however, were not. Using the PCR technique we investigated the DNA banding patterns produced by Random Amplified Polymorphic DNA, RAPD. showed that all 10 populations were significantly different in their genetic constitution. There was no relationship between the geographical distance between the populations and their genetic similarity. Forest fragments only 2 kilometres apart differed as much from each other as forests much further apart. This implied that even populations in very nearby forests were genetically isolated from each other. This may lead to adaptation to local environmental conditions.

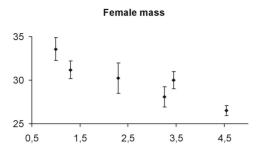
# Spiders of marshes along a tidal river

Halfway through the 1990s, we started investigations on the spider fauna occurring in marshes along the river Scheldt. This large river rises in northern France, flows through Belgium and discharges into the North Sea in the Netherlands. It remains tidal for some 140 kilometres up to the sluices of Ghent. Salt marshes occur occasionally along the Dutch Scheldt. A few brackish tidal marshes are still present between the Dutch border and the city centre of Antwerp, in between the port installations of that city. Upstream of the Antwerp city centre and onto Ghent, there are several freshwater tidal marshes. We sampled 40 of

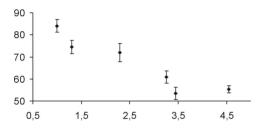
these marshes for their spiders. The spider assemblage composition changed drastically along the fresh- to salt-water gradient (Hendrickx et al. 1998a,b; Desender & Maelfait 1999). These salt marshes were found to have few species, but those that were present were considered to be very rare and included *Pardosa agrestis purbeckensis* and *Baryphyma duffeyi*. The freshwater tidal marshes were more species rich and included special species such as *Donacochara speciosa* and *Tmeticus affinis*. *Pirata piraticus* was also discovered, which occurred in large numbers in freshwater and brackish marshes.

In the mid 1990s we did some prospective sampling of all kinds of invertebrates in the marshes along the Scheldt. We determined their body content of heavy metals, such as Cu, Zn, Pb and Cd. The non-essential metal Cd was often present in high concentrations (Maelfait 1996; Maelfait & Hendrickx 1998; Tojal et al. 2002). Like woodlice, lumbricids and slugs, spiders were accumulators of these heavy metals (Hendrickx et al. 2003a). This made them good candidates as bio-indicators for the flow of ecotoxic substances, such as heavy metals from the soil through the food chain. We measured concentrations of heavy metals present in the body of Pirata piraticus together with concentrations in the soil and the litter layer present on the sites where the animals were collected. There was no straightforward relationship between body burden and the soil and litter concentrations. This implied that measuring body concentrations in organisms living in polluted environments was not a redundant activity. These concentration measurements were at least complementary to soil concentration measurements.

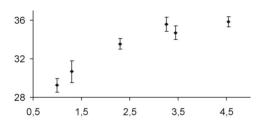
We compared life history characteristics of six populations occurring on a gradient of exposure to three heavy metals (Cu, Zn and Cd). This degree of contamination of the six populations is shown along the x-axis of Fig. 5; details of how this exposure rate was determined are given in Hendrickx et al. (2003b). As can be seen, the mean size of the breeding females



#### Clutch size



## Egg size



#### Clutch mass

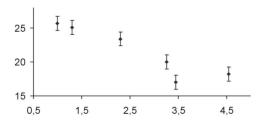


Fig. 5. Pirata piraticus: female mass (mg dry weight), clutch size (number of eggs), egg size (100 X mm³) and total clutch mass (mg dry weight) versus degree of exposure of population to the heavy metals Cu, Zn and Cd.

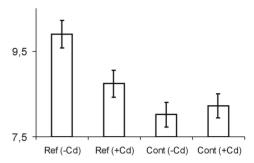


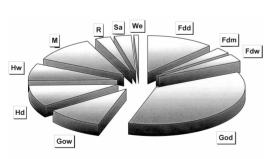
Fig. 6. Pirata piraticus: body mass of young (dry weight in mg) after eight weeks rearing in the laboratory respectively descending from parents of a contaminated (Cont) and a reference site (Ref) after having been fed with Cd contaminated (+Cd) and uncontaminated (-Cd) fruit flies.

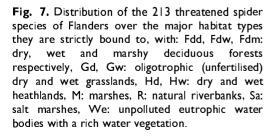
(female mass in Fig. 5) was smaller in the contaminated populations. The number of eggs produced by a female of a given size (clutch size in Fig. 5) was higher in the less exposed populations compared with the number of eggs produced by a female of the same size in the more contaminated populations. The eggs were however larger in the heavily contaminated populations, which means that the clutch mass was not that different between the populations. The interpopulation variation of life cycle characteristics in Pirata piraticus was most probably caused by natural selection with heavy metal contamination as the dominant selection pressure, as shown in results of laboratory rearing of this spider (Hendrickx, unpublished results). Progeny from animals collected on a heavily Cd contaminated site grew slower than animals from a reference population (Fig. 6). However, their body mass (dry weight in mg) after eight weeks of growth was not lower when fed with Cdcontaminated fruit flies rather than with uncontaminated flies. Young with parents from a reference site differed in that respect. In contrast with the animals from the reference site, spiders from the contaminated site seemed to be adapted to the presence of that toxic metal in their food.

## DISCUSSION AND CONCLUSIONS

On the basis of the results from spider sampling in all habitat types of our region, we were able to develop a Red List for the spider fauna of Flanders (Maelfait et al. 1998). This proved to be a very useful tool in many site assessment and monitoring studies. This is so because whilst compiling the list we tried to understand why species are or were becoming so rare in our region. Of the approximately 700 spider species in Belgium, about 600 occur in the northern part of the country, in Flanders, of which half are rare. Approximately one quarter of these 300 species are rare because Belgium lies at the northern, southern or western limit of their geographical distribution range. Here, they are occasionally encountered in several habitat types. Species at the northern limit of their distribution were more frequently observed during recent years (e.g. Bonte et al. 2002a). More interesting for site assessment and monitoring are the remaining 213 of these rare species. These species are rare because the habitats they are strictly bound to are rare, in other words because these habitats are threatened. Natural and semi-natural habitats that have

largely disappeared or that were greatly reduced in their occurrence and area in our region, especially during the last century, are (between brackets: abbreviation as used in Fig. 7): dry, wet and marshy deciduous forests (respectively: Fdd, Fdw, Fdm), oligotrophic (unfertilised) dry and wet grasslands (Gd, Gw), dry and wet heathlands (Hd, Hw), marshes (M), natural riverbanks (R), salt marshes (Sa) and unpolluted eutrophic water bodies with a rich water vegetation (We), the natural habitat of Argyroneta aquatica and Dolomedes plantarius. The relative number of species bound to each of these major habitat types is given in Fig. 7. The use of the Red List in applied nature conservation research is straightforward. Finding for instance in a forest one or more species strictly bound to particular dry deciduous forest conditions means that the site is of importance for nature conservation and should be managed appropriately. In Fig. 8, a simple application of the Red List is illustrated . A wetland nature reserve of about two hundred hectares near the city of Ghent, called the Bourgoyen, was thoroughly sampled for its spider fauna. To obtain an idea of the completeness of the spider fauna





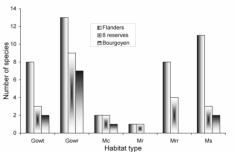


Fig. 8. Number of spider species respectively bound to wet oligotrophic grasslands with tussocks (Gowt), wet oligotrophic grasslands with rough vegetation (Gowr), marshes dominated by Carex (Mc), reed marshes (Mr), rough reed marshes (Mrr) and marshes with Sphagnum (Ms) in (from left to right): the whole of the region of Flanders, in eight wetland reserves in the vicinity of Ghent and in Bourgoyen, one of these eight reserves.

of this wetland reserve, we determined the number of species strictly bound to threatened wetland habitats types represented in the reserve. As can be seen, species bound to reed marshes and rough reed marshes (Mr and Mrr) were absent. Because the managers of the reserve wanted to obtain a wetland fauna as complete as possible, we recommended that the area of these habitat types should be enlarged in this reserve. Raising the level of the groundwater was known to have this effect. Later, these management measures were taken.

We have shown that spiders are not only useful in assessing biodiversity and nature value, but that they can also be good indicators of the effects anthropogenic disturbance, such as fragmentation and heavy metal pollution.

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### REFERENCES

- Baert, L. & Maelfait, J.-P. 1988. Araignées des versants d'exposition Nord et Sud d'une autostrade en tranchée dans une colline sableuse. Bulletin de la Société des Sciences en Bretagne 59, 17-24.
- Baert, L. & Desender, K. 1993. De Spinnenfauna van het militair domein te Lombardsijde (Araneae). *Nieuwsbrief van de Belgische Arachnologische Vereniging* 8(1), 15-20.
- Baert, L. & Maelfait, J.-P. 1999. The spider fauna of the Belgian salt marshes. *Bulletin de l' Institut royal des Sciences Naturelles de Belgique*, Entomologie 69, 5-18.
- Bonte, D. & Hendrickx, F. 1997. Aanvullende gegevens omtrent de spinnenfauna van enkele duingebieden aan de Belgische Westkust. *Nieuwsbrief van de Belgische Arachnologische Vereniging* 12(2), 33-43.
- Bonte, D., Hoffmann, M. & Maelfait, J.-P. 1999. Monitoring van het begrazingsbeheer in de Belgische kustduinen aan de hand van

- spinnen. Nieuwsbrief van de Belgische Arachnologische Vereniging 14(1), 24-36.
- Bonte, D., Maelfait, J.-P. & Hoffmann, M. 2000a. Seasonal and diurnal migration patterns of the spider (Araneae) fauna of coastal grey dunes. *Ekologia* 19(4), 5-16.
- Bonte, D., Maelfait, J.-P. & Hoffmann, M. 2000b. The impact of grazing on spider communities in a mesophytic calcareous dune grassland. *Journal of Coastal Conserva*tion 6, 135-144.
- Bonte, D. & Maelfait, J.-P. 2001. Life history, habitat use and dispersal of a dune wolf spider (*Pardosa monticola* (Clerck, 1757), Lycosidae, Araneae) in the Flemish coastal dunes (Belgium). *Belgian Journal of Zoology* 131(2), 145-157.
- Bonte, D., Criel, P., Baert, L. & De Bakker, D. 2002a. The invasive occurrence of the Mediterranean dwarfspider *Diplocephalus graecus* (O.-P. Cambridge, 1872) in Belgium (Araneae: Linyphiidae): another southern invertebrate expanding to the north? *Belgian Journal of Zoology* 132(2), 131-133.
- Bonte, D., Dekoninck, W. & Pollet, M. 2002b. Duinstruwelen als habitat voor insecten en spinnen. *De Levende Natuur* 103(3), 95-97.
- Bonte, D., Baert, L. & Maelfait, J.-P. 2002c. Spider assemblage structure and stability in a heterogeneous dune landscape. *Journal of Arachnology* 30, 331-343.
- Bonte, D., De Blauwe, I. & Maelfait, J.-P. 2003a. Environmental and genetic background of tiptoe-initiating behaviour in the dwarfspider *Erigone atra*. Animal Behaviour 66, 167-177.
- Bonte, D., Lens, L., Maelfait, J.-P., Hoffmann, M. & Kuijken, E. 2003b. Patch quality and connectivity influence spatial dynamics in a dune wolfspider. *Oecologia* 135, 227-235.
- Bonte, D., Criel, P., Van Thournout, I. & Maelfait, J.-P. 2003c. Regional and local variation of spider assemblages (Araneae) from coastal grey dunes along the North Sea. *Journal of Biogeography* 30, 901-911.
- Bonte, D, Vandebroecke, N., Lens, L. & Maelfait, J.-P. 2003d. Low propensity for aerial

- dispersal in specialised spiders from fragmented landscapes. *Proceedings Royal Society London B* 270, 1601-1607.
- De Bakker, D., Maelfait, J.-P., Hendrickx, F., Van Waesberghe, D., De Vos, B., Thys, S. & De Bruyn, L. 2000. A first analysis of the relatonship between forest soil quality and spider (Araneae) communities of Flemish forest stands. *Ekologia* 19(3), 45-58.
- De Bakker, D., Maelfait, J.-P., Baert, L. & Hendrickx, F. 2001. Spider diversity and community structure in the forest of Ename (Eastern Flanders, Belgium). Bulletin van het Koninklijk Belgisch Instituut voor Natuurwetenschappen, Entomologie 71, 45-54.
- De Bakker, D., Maelfait, J.-P., Desender, K., Hendrickx, F. & De Vos, B. 2002. Regional variation in spider diversity of Flemish forest stands. In: *European Arachnology* 2000 (S. Toft & N. Scharff eds.), pp. 177-182. Aarhus University Press, Aarhus.
- De Keer, R., Alderweireldt, M., Decleer, K., Segers, H., Desender, K. & Maelfait, J.-P. 1989. Horizontal distribution of the spider fauna of intensively grazed pastures under the influence of diurnal activity and grass height. *Journal of Applied Entomology* 107, 455-473.
- Desender, K. & Maelfait, J.-P. 1999. Diversity and conservation of terrestrial arthropods in tidal marshes along the river Scheldt: a gradient analysis. *Biological Conservation* 87, 221-229.
- Gurdebeke, S., Neirynck, B. & Maelfait, J.-P. 2000. Population genetic effects of forest fragmentation in Flanders (Belgium) on *Coelotes terrestris* (Araneae: Agelenidae) as revealed by allozymes and RAPD. *Ekologia* 19(3), 87-96.
- Gurdebeke, S. & Maelfait, J.-P. 2002. Pitfall trapping in population genetics studies: finding the right "solution". *Journal of Arachnology* 30, 255-261.
- Gurdebeke, S., Maelfait, J.-P. & Backeljau, T. 2003a. Contrasting allozyme and RAPD variation in spider populations from patchy forest habitats. *Genetica* 119, 27-34.

- Gurdebeke, S., De Bakker, D., Vanlanduyt, N. & Maelfait, J.-P. 2003b. Plans for a large regional forest in eastern Flanders (Belgium): assessment of spider diversity and community structure in the current forest remnants. Biodiversity and Conservation 12, 1883-1900.
- Hendrickx, F., Maelfait, J.-P. & Desender, K. 1998a. Arthropodes terrestres le long de la Bas-Escaut et de la Meuse. *Notes Fauniques de Gembloux* 35, 70-82.
- Hendrickx, F., Maelfait, J.-P., Muylaert, W. & Hoffmann, M. 1998b. Spider distribution patterns along the tidal river Scheldt (Belgium). In: *Proceedings of the 17th European Colloquium of Arachnology* (P. Selden ed.), pp. 285-292. British Arachnological Society, Edinburgh.
- Hendrickx, F., De Cock, K., De Bakker, D. & Maelfait, J.-P. 2001. Differences in geographic distribution and habitat of some cryptic species in the *Pardosa lugubris* group (Araneae: Lycosidae) in Belgium. *Belgian Journal of Zoology* 131(2), 61-66.
- Hendrickx, F., Maelfait, J.-P. & Langenbick, F. 2003a. Absence of cadmium excretion and high assimilation result in cadmium biomagnification in a wolf spider. *Ecotoxicol*ogy and Environmental Safety 55(3), 287-292.
- Hendrickx, F., Maelfait, J.-P., Speelmans, M. & van Straalen, N.M. 2003b. Adaptive reproductive variation along a pollution gradient in a wolf spider. *Oecologia* 134, 189-194.
- Hublé, J. 1975. Arachnofauna van strooisel onder duinstruweel van de Belgische Westkust (soortenlijst). *Biologisch Jaarboek Dodonaea* 43, 146-150.
- Hublé, J. 1976. Bodemspinnen van duinmoeras en helmduinen in het staatsnatuurreservaat 'De Westhoek' (soortenlijst). *Biologisch Jaarboek Dodonaea* 44, 226-230.
- Hublé, J. & Maelfait, J.-P. 1982. Analysis of the spider fauna from a North and a South facing slope of a coastal dune (Belgium). Faunistisch-Ökologische Mitteilungen 5, 175-189.

- Jocqué, R. 1986. Etude de l'aranéofaune d'un gradient d'humidité dans une bruyère campenoise (Belgique). Mémoires de la Société royale belge d'Entomologie 33, 93-106.
- Maelfait, J.-P. & Baert, L. 1975. Contribution to the knowledge of the arachno- and entomofauna of different woodhabitats. Part I. Sampled habitats, theoretical study of the pitfall method, survey of the captured taxa. *Biologisch Jaarboek Dodonaea* 43, 179-196.
- Maelfait, J.-P. & Baert, L. 1978. Contribution to the knowledge of the arachno- and entomofauna of different woodhabitats. Part III. Araneidae: Erigoninae. Bulletin et Annales de la Société royale belge d'Entomologie 114, 107-118.
- Maelfait, J.-P. & Segers, R. 1986. Spider communities and agricultural management of meadow habitats. In: *Actas X Congreso Internacional de Aracnologia, Jaca/Espana 1986*. I (J. Barrientos ed.), pp. 239-243. Imprenta juvenil, Barcelona.
- Maelfait, J.-P. & Baert, L. 1988a. Les araignées sont-elles de bons indicateurs écologiques? Bulletin de la Société des Sciences en Bretagne 59, 155-160.
- Maelfait, J.-P. & Baert, L. 1988b. L'usage pratique des araignées en tant qu'indicateurs écologiques. *TUB-Dokumentation Kongresse und Tagungen* 38, 110-118.
- Maelfait, J.-P., Desender, K. & De Keer, R. 1988a. The arthropod community of the edge of an intensively grazed pasture. *Münstersche Geographische Arbeiten* 29, 115-117.
- Maelfait, J.-P., Desender, K., De Keer, R. & Pollet, M. 1988b. Investigations on the Arthropod fauna of grasslands. In: *Environmental management in agriculture. European perspectives* (J.R. Park ed.), pp. 170-177. Belhaven Press, London.
- Maelfait, J-P., Alderweireldt, M., Desender, K. & Baert, L. 1989a. Lycosid spiders of the Belgian coastal dunes and saltmarshes. Bulletin et Annales de la Société royale belge d'Entomologie 125, 327-332.
- Maelfait, J-P., Desender, K. & Baert, L. 1989b.

- Some examples of the practical use of spiders and carabid beetles as ecological indicators. In: *Proceedings of the Symposium "Invertebrates of Belgium"* (K. Wouters & L. Baert eds.), pp. 437-442. Royal Belgian Institute of Natural Sciences, Brussels.
- Maelfait, J.-P., Jocqué, R., Baert, L. & Desender, K. 1990a. Heathland management and spiders. *Acta Zoologica Fennica* 190, 261-266.
- Maelfait, J.-P., Segers, H. & Baert, L. 1990b. A preliminary analysis of the forest floor spiders of Flanders (Belgium). *Bulletin de la Société européenne d'Arachnologie* 1, 242-248.
- Maelfait, J.-P. & De Keer, R. 1990. The border zone of an intensively grazed pasture as a corridor for spiders (Araneae). *Biological Conservation* 54, 223-238.
- Maelfait, J.-P., Desender, K., Pollet, M., Segers, H. & Baert, L. 1992. Carabid beetle and spider communities of Belgian forest stands. In: *Proceedings 4th European Congress of Entomology/XIII. Internationale Symposium für die Entomofaunistik Mitteleuropas, Gödöllö*, 1991 (L. Zombori & L. Peregovits eds.), pp. 187-194. Hungarian Natural History Museum, Budapest.
- Maelfait, J.-P. & Desender, K. 1995. Field margins as refuges and potential corridors for arthropods in the Flemish agricultural landscape. *Field Margins Newsletter* 5, 7-9.
- Maelfait, J.-P., De Knijf, G., De Becker, P. & Huybrechts, W. 1995. Analysis of the spider fauna of the riverine forest nature reserve 'Walenbos' (Flanders, Belgium) in relation to hydrology and vegetation. In: Proceedings of the 15th European Colloquium of Arachnology (V. Ruzicka ed.), pp. 125-13. Institute of Entomology, Ceske Budejovice.
- Maelfait, J.-P. 1996. Spiders as bioindicators.
  In: Bioindicator Systems for Soil Pollution (N. M. van Straalen & D.M. Krivolutsky eds.),
  pp. 165-178. Kluwer Academic Publishers,
  Dordrecht.
- Maelfait, J.-P. & Tanghe, M. 1996. Field margins: research and conservation in Belgium. *Field Margins Newsletter* 6/7, 3-4.

- Maelfait, J.-P., Baert, L. & Desender, K. 1997. Effects of groundwater catchment and grassland management on the spider fauna of the dune nature reserve' De Westhoek' (Belgium). In: Proceedings of the 16th European Colloquium of Arachnology, Siedlce, Poland (M. Zabka ed.), pp. 221-235. Szkolny Rolniczo-Pedagogicznej, Siedlce.
- Maelfait, J.-P., Baert, L., Janssen, M. & Alderweireldt, M. 1998. A Red List for the spiders of Flanders. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie 68, 131-142.
- Maelfait, J.-P. & Hendrickx, F. 1998. Spiders as bio-indicators of anthropogenic stress in natural and semi-natural habitats in Flanders (Belgium): some recent developments. In: *Proceedings of the 17th European Colloquium of Arachnology* (P. Selden ed.), pp. 293-300. British Arachnological Society, Edinburgh.
- Maelfait, J.-P., Baert, L., Bonte, D. & Hendrickx, F. 2000. The richness and paucity of the spider fauna of the Belgian coast. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie 70, 97-107.
- Provoost, S. & Hoffmann, M. 1996. Ecosysteemvisie voor de Vlaamse kust. Deel 1 ecosysteembeschrijving. Instituut voor Natuurbehoud, Brussels.

- Segers, H. & Maelfait, J.-P. 1988a. A comparative study of the spider communities of different woodland habitats. TUB-Do-kumentation Kongresse und Tagungen 38, 154-160.
- Segers, H. & Maelfait, J.-P. 1988b. Faunistical observations on the spider fauna of the Zoniën forest (Belgium). *Bulletin de la Société des Sciences en Bretagne* 59, 205-206.
- Segers, H. & Maelfait, J.-P. 1990. Field and laboratory observations on the life cycle of *Coelotes terrestris* and *C. inermis* (Araneae: Agelenidae). *Bulletin de la Société européenne d'Arachnologie* 1, 314-324.
- Tack, G., Van Den Bremt, P. & Hermy, M. 1993. Bossen van Vlaanderen: een historische ecologie. Davidsfonds, Leuven.
- Tojal, C., Hendrickx, F., Tack, F.M.G., Maelfait, J.-P., Bogaert, N., Willems, K., Vernaillen, P., Mertens, J. & Verloo, M. 2002. Heavy metal concentrations in the spiders *Pirata piraticus* (Clerck, 1757) and *Clubiona phragmitis* (C.L. Koch, 1843) along the Scheldt Estuary (Belgium). *The Scientific World Journal* 2: 978-982.
- Vermeersch, C. 1986. De teloorgang van de Belgische kust. Ruimtelijke planning. Van Loghum Slaterus, Antwerpen.