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Use of spiders as characterisation and conservation tool of heathlands in the Brugge area

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USE OF SPIDERS AS CHARACTERISATION AND CONSERVATION TOOL OF HEATHLANDS IN THE BRUGGE AREA

WÉRENNE GLADYS

TRAVAIL DE FIN D'ÉTUDES PRÉSENTÉ EN VUE DE L'OBTENTION DU DIPLÔME
DE MASTER BIOINGÉNIEUR EN GESTION DES FORÊTS ET DES ESPACES
NATURELS

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A mon père,
qui m'a transmis son amour de la nature
et qui a toujours encouragé mes passions,
même les plus incongrues.

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Ce travail a été réalisé avec et pour l'Institut des Sciences Naturelles de Belgique.

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Abstract

This study analyses data on spiders collected between 2014 and 2024 by the Royal Belgian Institute of Natural Sciences (RBINS) in the Brugge region. The objectives were 1) to identify and characterise, in the regional context, a typical heathland community, 2) to situate it among other assemblages in Flanders, 3) to identify whether vegetation structure and management influence the composition of the assemblages, 4) to draw up management recommendations and 5) to establish whether monitoring is optimal. To achieve this, alpha diversity analysis (species richness, extrapolated Chao richness, Fisher alpha), functional diversity (FRic, FEve, FDiv), IndVal analysis and multivariate analysis techniques (tbPCA, CoCA, dbRDA, RLQ and fourth corner analysis) were performed. It emerged that, although the heathland community is distinct from forests and grasslands, it was not possible to identify typical species. It appears that the composition of the community undergoes change over the course of ecological succession and that the stages in question require further characterisation. Vegetation structure and, indirectly, management influence the composition of assemblages. Management appears to be either too intense or insufficient in some places to maintain a heathland community. Overall, this work confirms the importance of maintaining a mosaic of habitats at various stages of succession in order to maximise biodiversity.

Résumé

Le présent travail analyse les données relatives aux araignées collectées entre 2014 et 2024 par l'Institut Royal des Sciences Naturelles de Belgique (IRSNB) dans la région de Brugge. Les objectifs étaient 1) d'identifier et caractériser, dans le contexte régional, une communauté typique des landes à bruyère, 2) de la situer parmi d'autres ensembles de Flandre, 3) d'identifier si la structure de la végétation et la gestion influencent la composition des assemblages, 4) d'établir des recommandations de gestion et 5) d'établir si le suivi est optimal. Pour cela, une analyse de la diversité alpha (richesse spécifique, richesse extrapolée de Chao, alpha de Fisher), fonctionnelle (FRic, FEve, FDiv), une analyse IndVal ainsi que des techniques d'analyse multivariée (tbPCA, CoCA, dbRDA, RLQ et fourth corner analysis) ont été réalisées. Il ressort que, si la communauté des landes se distingue des forêts et des prairies, il n'a pas été possible d'en identifier des espèces typiques. Il apparaît que la composition de la communauté évolue au cours de la succession écologique et que les stades devraient être mieux caractérisés. La structure de la végétation et indirectement la gestion influencent la composition des assemblages. La gestion paraît trop intense ou insuffisante par certains endroits pour maintenir une communauté des landes. En définitive, ce travail confirme l'intérêt de maintenir une mosaïque de milieux à divers stades de succession en vue de maximiser la biodiversité.

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Abbreviations

- **Arabel** : *Arachnologia Belgica*, the Belgian arachnological society
- **CEP** : Cornell Ecology Programs
- **CoCA** : Co-Correspondence Analysis
- **dbRDA** : distance based Redundancy Analysis
- **FRic** : Functional Richness
- **FEve** : Functional Eveness
- **FDiv** : Functional Divergence
- **RBINS** : Royal Belgian Institute of Natural Sciences
- **tbPCA** : transformation based Principal Composant Analysis

1. Introduction

The spiders (Araneae Clerk, 1751) are the subject of increasing scientific interest. Due to the ecological requirements of certain species, they are used as bioindicators, and notably of the success of ecological restoration in conjunction with other taxonomic groups, such as Carabidae. For this reason, the Royal Belgian Institute of Natural Sciences (RBINS) is studying these arthropods in the urbanised area of Brugge. Some sites in particular ecosystems have been restored and are being monitored, mainly by pitfalls trapping. One noteworthy ecosystem in Flanders are heathlands, which provide a habitat for a number of species throughout their life cycle. In Belgium, the large-scale reclamation of heathlands dates back to the XVI$^{\text{th}}$ century. Only a small number of patches of the extensive pastoral areas that surrounded the city of Brugge remain. Given their location between major heathland complexes in Western Europe (such as the Kalmthoutse Heide) and other significant ecosystems, notably coastal dunes, these remnants are deemed to possess biogeographic interest.

The RBINS long-term monitoring near Brugge, has already yielded data for several groups over a ten year period. The present master's thesis is primarily concerned with data pertaining to spiders. The main objective is to characterise the spider communities and provide recommendations for management. Following a literature review on heathlands and spiders ecology as well as some facts about numerical ecology (Section 2), the definition of objectives (Section 3) and the methodology used to achieve them (Section 4), the results will be presented (Section 5) and discussed with some recommendations and perspectives (Section 6). A brief overview of the personal contribution will be given (Section 7) before concluding (Section 8).

2. Literature review

The aim of this section is to present a general overview and key conceptual elements pertaining to various aspects of the work. It is structured into three parts. The first one gives elements regarding the history, characterisation and prevailing management practices of heathlands. The second part concerns the taxonomic faunal group of spiders. A number of salient points to consider for management are given, with an emphasis on heathlands. Their protection status and their use as bioindicators are examined. The third part provides an outline of the study of ecological communities and the suitability of multivariate statistical methods in this field.

2.1 Heathlands

Heathlands are interesting milieux that have become rare in Europe. Their characterisation and restoration can be approached from an ecological, phytosociological, landscape, as well as cultural, archaeological or social perspective. Indeed, these formations are mainly anthropogenic in origin and were historically a functional space (Noirfalise et al., 1976) with a high cultural value (Noirfalise et al., 1976; Perigord, 1994; Marty et al., 2007; Génin et al., 2014; Ombashi et al., 2023).

2.1.1 History

The heaths distribution depends on climate and several episodes of retreat and recolonisation occurred over glaciation events with a maximum around 4000 years BP (Mahy et al., 1999;Diemont et al., 2013;Fagúndez, 2013). However, the majority of current heathlands are secondary formations, resulting from the agropastoral use of large, cleared areas with nutrient-poor soils; probably as early as the Bronze Age but more intensely from the Middle Ages onwards (Noirfalise et al., 1976; Fagúndez, 2013; Ombashi et al., 2023). Heaths are in a state of plagioclimax, in which natural succession has been prevented by human management and practices (Diemont et al., 2013). The only primary heathlands are those developing in conditions unfavourable for the development of forests, in terms of latitude, longitude and soil. These include those located along coastal cliffs and in high mountains, or, more rarely, those that result from natural forest degradation (Fagúndez, 2013; Glemarec et al., 2015).

The economic model that underpinned the management of heathlands was primarily based on grazing, predominantly by sheep, although several management practices existed across Europe over time, as described by Webb, 1998 and Diemont et al., 2013. Heathlands were typically part of what are known as "commons", i.e. areas that are exploited collectively by a community. Their decline coincides with the Industrial Revolution in the XIXth century (Diemont et al., 2013; Fagúndez, 2013). The rural exodus resulted in the abandonment of heaths. In many regions, political measures were implemented to increase the economic value of these infertile soils. Some heathlands were enhanced (Glemarec et al., 2015). In most cases, however, they were planted with forest species, which were considered at the time to be the best way to increase their value (e.g. Trochu, 1820). Nevertheless these conversions were not without resistance from locals who still relied on heathlands for their survival and perceived these reclamations as a threat. The case of Belgium was studied by Clout, 1977. Heathland management was highly diversified across the country prior to independence. Initially disappearing into private ownership, heathlands were reclaimed on a large scale after the creation of Belgium. This was facilitated by political stability, population growth, rising land prices, improved communications and wider acceptance of agricultural progress.

2.1.2 Characterisation

Heathlands are perceived primarily as expansive, infertile areas. The vegetation is open, characterised by dwarf shrubs and grasses. In a broader sense, this definition encompasses moors and grassland (Diemont et al., 2013; Fagúndez, 2013). Over time scientists have refined the definition and included botanical and pedological aspects. Among them the contribution of the British botanist C.H. Gimingham has been a reference in Europe for a long time. Today most authors concur to define a heath as a formation physiognomically dominated by dwarf perennial sclerophyllous shrubs, mostly belonging to the ericoids, and in particular to the order *Ericales*. Heaths develop on acidic, oligotrophic soils, especially those depleted in phosphorus (P). The underlying substrates are little altered or release few fertile elements, such as sedimentary rocks of the sandstone type and former natural sandy deposits in a decalcified dune context. (e.g. Diemont et al., 2013; Fagúndez, 2013; Glemarec et al., 2015; Delescaille et al., 2022). This poverty has on occasion been perpetuated by farmland practices (Webb, 1998; Diemont et al., 2013; Glemarec et al., 2015). To thrive, heathers benefit from their capacity to absorb more elements than other plants thanks to mycorrhizal symbiosis (Glemarec et al., 2015).Heaths are present worldwide and are found across a vast geographical area in Europe, extending from the Iberian Peninsula to Norway, including the British Isles. From the coast, heath occurrence is limited by the distribution of characteristic species, heathers and lings (Noirfalise et al., 1976).

Beyond these generalities, heaths encompass a diversity of plant communities that vary according to regional climate (determined by altitude, latitude, aspect, etc.), local constraints (primarily related to soil and substrate but also to factors like sea sprays, etc.) as well as anthropogenic factors and history. In Europe, phytosociologists have distinguished various vegetation formations since the 1930s (see Glemarec et al., 2015; Delescaille et al., 2022). For example, heathlands can be delimited into atlantic heaths, subatlantic and continental heaths, mediterranean heaths and (sub)alpine heaths. The water regime is another criterion frequently employed to classify vegetation as xerophilous, mesophilous or hygrophilous. Communities can also be delineated as coastal heaths, inland dry heaths or inland wet heaths. These classifications can be refined according to the dominant structuring species, namely *Calluna vulgaris* (L.) Hull and the genus *Erica* L. for western Europe. Of particular interest for the purpose of this work is the bell heather, *Erica cinerea* L. This species has evolved in drier habitats than other *Erica* (eg. *E. tetralix* L. and *E. ciliaris* Loefl.) (Snazell, 1982; Glemarec et al., 2015). In comparison, it perspires less and demonstrates an enhanced rehydration capacity. It bears a summer drying but does not tolerate flooded soils. *E. cinerea* is predominantly found in xerophilous atlantic heaths, resulting from the clearance of woodland for grazing or the regression of other types of heaths (due to erosion caused by run-offs or human activities). Conversely, a rejuvenation of these heathlands through management (eg. mowing) can transform them into oligotrophic grasslands. In the most stable heaths, lichenic carpets can develop and be abundant. This milieu is particularly exposed to fire. With regard to *C. vulgaris*, it constitutes a major structural and functional component of heaths of all kinds and stages, thanks especially to its wide ecological plasticity (Glemarec et al., 2015). The most used model to describe the dynamic of heaths is based on its biological cycle, divided in four phases (see eg. Delescaille et al., 2022) :

1. pioneering (1-2 year) with the establishment of ling,
2. building (2-4 years) with the maximal growth and flowering rates,
3. maturity (10-20 years) where growth slows down and
4. degeneration (after 20-25 years) where plants dry and heaths thin out

During the fourth phase, other plants may also develop, including those not associated with heaths. Several authors (e.g. Diemont et al., 2013; Schellenberg et al., 2020) have proposed a re-evaluation and refinement of this cyclical perspective, incorporating considerations of climatic conditions, competition with grasses, site history and edaphic characteristics.

With regard to composition, heaths are generally poor in vascular plants, in terms of the number of species. However, lichens and arthropods appear to be diverse, heathlands being particularly rich in stenoecious species (Krause et al., 2016). Their presence depends on the microhabitats formed by environmental variables, such as soil moisture, vegetation structure, the presence of watercourses, mosses, etc. (De Blust, 2005).

2.1.3 Management

Heathlands are recognised as habitats of Community interest (Conseil Européen, 1992) and cultural landscape. But most of the traditional practices that have maintained these areas have disappeared. Where they have not been reclaimed or planted, heathlands have evolved into shrub and woodland. The senescence stage, less rich in species, is more common (Krause et al., 2016). Most of the relict heaths in conservation are found in the most oligotrophic conditions, on substrates such as sandstone, shale and quartzite, and some granitic arenas. Many organisms have evolved in, and now depend on, the harsh conditions and human disturbances that characterise heathlands. Among arthropods, this is particularly true of spiders, lepidopterans, orthopterans, hemipterans, hymenopterans and various beetles (Delescaille et al., 2022). In addition, heathlands provide a range of ecosystem services such as wildfire protection, drinking water supply and carbon storage. They have a variety of other values: landscape, archaeological, social, educational, etc. The economy of the heathlands is currently based mainly on tourism and recreational activities (Diemont et al., 2013; Glemarec et al., 2015). Moreover, in order to achieve conservation objectives (as set out in the Habitats Directive), the restoration of ancient heaths is necessary. However this is not as straightforward as expected. Bakker et al., 1999 listed the main abiotic and biotic constraints to the restoration of ecological diversity in grassland and heathland communities.

In addition to the abandonment of traditional farming practices, agricultural intensification, combined with industrial and transport pollution has increased the trophic level of ecosystems and accentuated acidification. Atmospheric nitrogen deposition is of particular concern due to the acceleration of natural succession, trophic disturbance and the spread of perennial grasses such as *Molinia caerulea* (L.) Moench and *Deschampsia flexuosa* (L.) Trin. (Chapman et al., 1989, Borchard et al., 2014). While nitrogen can promote the growth of ling, it also makes it more palatable to heath beetles. Nitrogen inputs are estimated to be between 30 and 55 kg/ha/yr in grasslands and heathlands whereas the maximum level commonly cited for dry heathlands should be 10-20 kg/ha/yr (Diemont et al., 2013). Overall, however, the effects of nitrogen deposition vary according to local conditions, especially phosphorus content (Diemont et al., 2013). Other depositions, such as sulphur compounds, have also lowered the pH, threatening the development of specific plants.

Furthermore, the importance of heathland species in seed banks is not clear. Stieperaere et al., 1983 found that some species, including heathers, can survive in the soil 20 years after conversion into grassland. But in general, regeneration from the seed bank alone has little diversification. Seed banks may also contain many non-target species whose establishment and competition with target species can be facilitated by some management practices such as turf cutting (Bakker et al., 1999). Dispersal is another important issue in heaths restoration. Dispersal is defined as all the processes by which organisms leave their original population to colonise a new territory, particularly for the purpose of reproduction. The establishment of a species belonging to the regional pool in the community depends on several factors (Bakker et al., 1999): the persistence of the species in the seed bank, the fecundity and dispersal capacity of the species, the presence of dispersal agents, the distance separating the community from the nearest population of the species, the ability of the seeds to germinate and the requirements of the species. The dispersal capacity of heathland species has been reduced by fragmentation and the abandonment of traditional practices. Species with long-lived seeds are less affected by fragmentation and isolation than long distance dispersers. Nevertheless, the small size of the remnants prevents community structure and threatens genetic diversity. Invasive species can be added to these biotic factors as mentioned by Fagúndez, 2013. He also highlights the fact that climate change can exacerbate these constraints and that the interaction between factors, the history of the site and the landscape matrix must be addressed as much as individual factors.

In order to conserve heathlands, various management practices have been implemented to mimic past uses, with various impacts on biodiversity and in particular on spider communities (Bell et al., 2001, see also section 2.2) :

- Grazing : this practice appears to be the closest to past management, but this would neglect the fact that heathlands were a multifunctional landscape and that farmers got everything they could out of them in a multi-outcome scheme, which is rarely known at the local scale (Diemont et al., 2013). Furthermore, the abandonment of these areas did not mean the end of grazing everywhere. Wild herbivores such as rabbits, deer and roe deer have recolonised the heathlands in some places (see e.g. Kaae et al., 2024. For effective management, several parameters have to be considered. The type and number of grazing animals is of paramount importance. The amount and type of grazed vegetation depends on the animal, which selects plants according to their digestibility, palatability, accessibility, but also water availability, season, learned behaviours and social cohesion. The height and spatial structure of the vegetation, as well as the microclimate, are therefore influenced by the stocking rate per hectare, and in turn have an impact on the spider community. Reduced grazing favours the diversity and density of spiders, mainly of the families Gnaphosidae, Clubionidae and Thomisidae and some Linyphiidae, by increasing litter depth. Indirect effects of grazing also affect spiders. Refusals can be favoured by certain web spinners. Dungs can attract prey but can reduce the competitive advantage of heath flora. Moderate trampling may benefit some groups by creating regeneration niches. Dispersal can be improved by cattle movements. However, the impacts vary from species to species and it is difficult to generalise. In general, a balance needs to be found between over- and under-grazing (Birkhofer et al., 2015).

- Mowing and cutting : these methods have direct and immediate effects on the vegetation, the microclimate and the availability of prey, which are generally detrimental to the spider fauna. Most of the species favoured by grazing no longer benefit from cutting (Pétillon et al., 2007). However, the effects depend on the technique used, the timing, the frequency and the removal of vegetation. For spiders, it is better to limit this technique and its intensity. Spring and autumn cutting seem to be less deleterious than summer cutting but this is not clear everywhere; Lafage et al., 2014, for example, found no difference.

- Burning : more complex to control, burning damages the spider community in the short term (unless they can take refuge in an unburned area, in uninflammable debris or in the ground). Pioneer species benefit from the large bare areas created by fire. Recolonisation by other species, especially those dependent on litter, will depend on the presence of nearby reservoirs. Diversity increases over time. To be effective, burning should ideally be implemented in large connected areas, with unburned refuges, in rotation and at low frequency to allow recolonisation (Krause et al., 2016).

- Topping : by eliminating the litter, mowing the soil has similar but more significant adverse effects than mowing, in addition to increase the mobility and toxicity of heavy metals for spiders (Diaz et al., 2011).

For more effective management, these techniques can be combined as threats are multifactorial and taxonomic groups have different requirements (Damgaard et al., 2013). Coupling burning or topping over a long period (25-40 years) with other more frequent techniques in rotation (10-12 years) helps to promote overall biodiversity and deplete nitrogen (Chapman et al., 1989; Niemeyer et al., 2005; Krause et al., 2016; Delescaille et al., 2022). The success of restoration and management is highly dependent on local and surrounding conditions such as soil, site history, environment, hydrological regime, seed bank etc. which require management at a larger scale (Stieperaere et al., 1983; Bakker et al., 1999; Schellenberg et al., 2020). Management needs to be adapted to the local context and may be hampered by the small size of sites or the nature of the surrounding matrix (Delescaille et al., 2022). Management outcomes may conflict with the different uses and values of heathlands (Webb, 1998), such as carbon storage (Alonso et al., 2021; Walmsley et al., 2021). In general, heterogeneity resulting from management and the maintenance of early successional stages are the most beneficial for heath biodiversity (e.g. Stieperaere et al., 1983; Pétillon et al., 2008; Diemont et al., 2013; Delescaille et al., 2022). As part of the assessment of structure and function, the presence of various stages of ling is therefore used as an indicator of the regeneration potential of dry lowland heathlands (Delescaille et al., 2022). Other physiological variables can be used to measure plant response, as well as fauna (see below) and humus (Diemont et al., 2013).

2.2 Spiders

Spiders are a diverse group of arthropods with the peculiarity to be almost exclusively predatory. Taxonomically, they form the order Araneae, belonging to the class Arachnida, in the subphylum Chelicerata (Coddington et al., 1991). According to the World Spider Catalog, 2024, at the beginning of 2024, there were more than 51,000 validated species in the world, distributed in 135 families and 4,377 genera. This makes them the most diverse group of carnivorous arthropods (Nentwig, 2013). Partly as a result of this enormous diversity, the classification is highly unstable and has changed considerably over time (Coddington et al., 1991).

2.2.1 Generalities

The earliest known traces of spiders date back to the Late Carboniferous period, 300 million years ago (Nentwig, 2013). Over the course of their evolution, spiders have developed many features related to their predatory lifestyle. Foelix, 2011 and Nentwig, 2013 gave a comprehensive overview of what is known about the morphology, biology and physiology of spiders, but many aspects remain to be explored. As for Herberstein, 2011, they explored their behaviour.

Spiders can be distinguished by a number of characteristics, such as the bipartite body, the presence of a pair of chelicerae, a pair of pedipalps, spinnerets, eight pairs of locomotor legs and the absence of abdominal segmentation. A major characteristic of spiders is their ability to produce silk and use it in a variety of ways. Mating takes place in an unusual way. Indeed, the male's copulatory organs, modified structures of the pedipalps, are separated from the testes, which are located in the abdomen. The female genitalia of most of the so-called entelegyne species have evolved in concert with the male organs, resulting in a key-lock system that prevents interspecies mating. This feature is of considerable importance in araneology, as it is often the only way to identify species with certainty. Haplogyne species generally have simpler organs and hybridations are still possible. Development can be divided into three periods : embryonic, larval, and nymphal-imagal. Juveniles resemble adults. They grow and develop their organs through moulting. The lifespan is usually short, rarely exceeding one or two years in temperate regions.

Spiders disperse in two main ways, either by air or by land. The first is referred to as "ballooning" and is the most effective to cover long distances (although it is accomplished in several steps). It is carried out by means of a thread expelled from the abdomen, which is carried away by the wind (Figure 2.1). practiced by juveniles and adults of species with a mass of less than 30 mg (termed as "aeronauts"), its success depends mainly on the wind, temperature and humidity, as well as the suitability of the arrival habitat, as the ballooners have little control over their trajectory. Less is known about ambulatory dispersal.

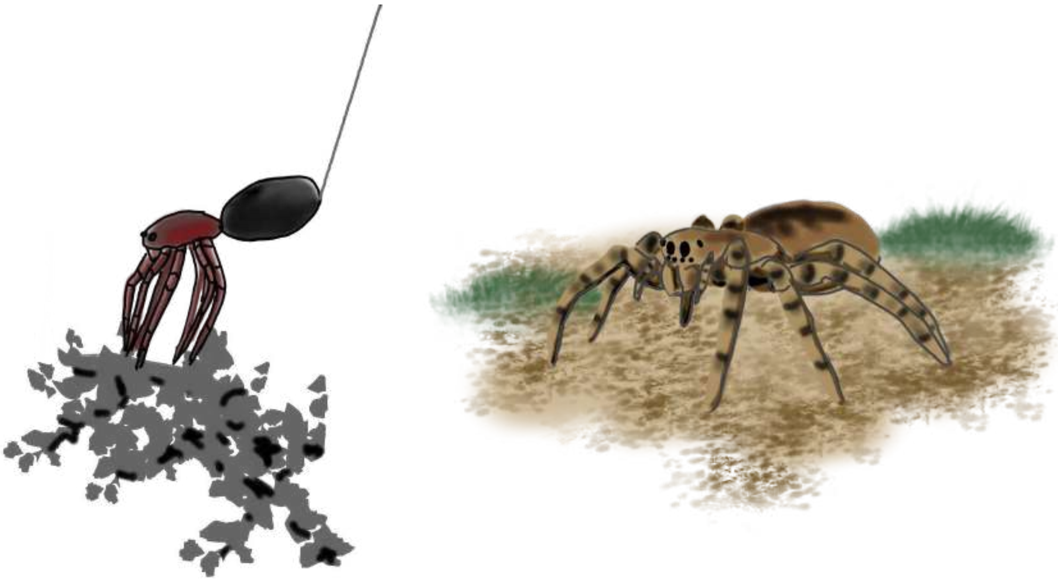


Figure 2.1: Spider dispersion. Spiders disperse in two principal ways. The first, referred to as ballooning, is achieved through the use of silk thread carried by the wind. The second, which is less well-known, is by ground.

Most species have more or less specific habitat requirements related to wetness, dryness, shade, light and temperatures. The least demanding are termed "euryoecious" while the least flexible are labelled "stenoecious". Shade and moisture are the factors that most influence community composition and ecological traits such as body size, as pointed out by Entling et al., 2007. Stenoecious species are most commonly found at the extremes of these gradients and benefit from low phylogenetic constraints. In contrast to most other groups, warm and dry environments favour large body sizes while cool and wet environments favour smaller ones. This pattern persists on a large scale, body size decreasing towards higher latitudes, at least in Europe Entling et al., 2010. Several explanations have been proposed, relating to physiology (growth rate, resistance to desiccation, etc.), biotic interactions (predatory behaviour, predation pressure, competition) and phylogeny. Latitude and longitude also appear to influence the distribution of some species. Kumschick et al., 2009 found that the peak of diversity of sheetweb spiders in Europe occurs around 55°N. The main limiting factor towards the north is energy availability, while towards the south it is mainly water resources and interactions within communities. Altitude also seems to have an influence (see e.g. Malumbres-Olarte et al., 2018). Duffey, 1993 reviewed some other factors influencing the distribution of spiders, namely landscape history, species habitat versatility, habitat fragmentation and habitat heterogeneity. He highlighted the difficulty of habitat characterisation due to the lack of preference of widespread species that occur in many habitats but also due to so-named "diplostenoecism" (the fact that the species is present in few but very different habitats) and the rarity (low abundance) of certain specialised species. Dispersal capacity also plays a role at this scale (Martín-Devasa et al., 2024).

For heaths, the main factors influencing the composition of spider communities were reviewed by Bell et al., 2001. The most important is habitat structure. It affects both abiotic and biotic aspects. Spiders generally do not show strong host-plant associations, but the physiognomy and architecture of vegetation are important for hunting (e.g. horizontal and vertical surfaces are used differently by jumping spiders), courtship (and notably the transmission of vibrations), oviposition, overwintering and so on. Some characteristics are correlated with spider diversity : vegetation tip height, vegetation height, vegetation density, and proportion of bare ground. The choice of microhabitats may differ according to developmental stage, sex, etc. The state of the vegetation (particularly in terms of succession) is also important (Figure 2.2), for example when building a retreat. Older heaths are richer in woodland species (see eg. Borchard et al., 2014). Litter layer and other physical features also play a role Duffey, 1993. The presence of a species also depends on its mode of dispersal, prey availability and composition, and microclimate (mainly temperature and humidity).

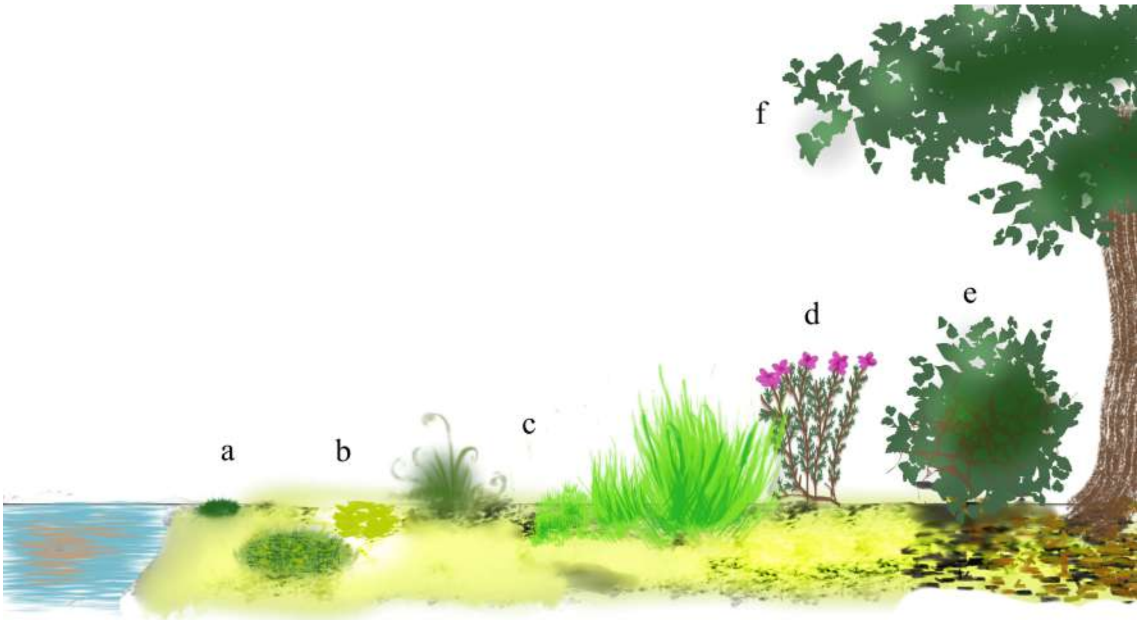


Figure 2.2: Influence of vegetation. The physiognomy and architecture of vegetation exert an influence on the composition of spider communities. The spatial organisation, proportion of bare soil, soil texture and nature of the litter contribute to the heterogeneity of the environment. a: mosses, b: lichens, c: herbaceous plants and grasses, d: heather, e: thickets, f: trees.

Consequently, management practices affect spider communities by modifying the structure of vegetation in space and time (see subsection 2.1.3). Although the results vary site to site, composition is poorly diversified and often dominated by a small number of species, mainly aeronauts with r strategies and associated with bare ground where management is very intensive (Toft et al., 2024). Communities are more complex and diverse (both in terms of species and functions) with low-intensity management, which creates more niches. In general, however, there is no perfect management and practices do not affect all spider species in all situations in the same way.

As for Snazell, 1982, he studied the preferences of some heathland species in Dorset, England. It appears that most of them prefer microhabitats characterised by moderate conditions and a few by more extreme ones. The phenology of species, an important ecological trait, has been studied in the same environment by Merrett, 1967, 1968, 1969.

The differences in phenology reduce interspecies competition, particularly between species with close habitat preferences.

2.2.2 Status and protection

Like many other taxonomic groups, spiders undergo a loss of diversity, reflected in particular in shifts in the ecological traits of communities (Toft et al., 2024). The greatest threat is habitat loss and degradation. Intensive agricultural practices affect spiders through environmental degradation and impacts on insects, the main prey of spiders (Nyffeler et al., 1994; Seibold et al., 2019). Climate change, pollution, and invasive species also play a role. The case for heaths and associated habitats is less clear and depends on local conditions. In the case of insects associated with early successional stages of ecosystems in the UK, Thomas et al., 2015 found that heathland species were less affected than woodland species, possibly due to better habitat protection status. In addition, heat-preferring species have increased near their northern limits. Spiders could follow the same patterns. Although Gajdoš et al., 2000 found no evidence of decline in a heathland community over 20 years, a similar recent study in coastal dunes Toft et al., 2024 showed faunistic impoverishment. The dominance of some species, mainly euryoecious, has increased while stenoecious and geographically restricted species are becoming rarer, the proportion of aeronauts and hygrophilous species is more important, and some species show a phenological shift towards earlier activities.

Despite this, spiders are under-represented in policies and conservation tools, as shown in the review of spider conservation in Europe by Milano et al., 2021. Only one species was retained in the Bern Convention and benefits from protection under the Habitats Directive. Few countries include spiders in their national and sub-national legislation (178 species listed in 19 European countries at the time of the study). This taxonomic bias remains in the extinction-risk assessment. Few European regions have drawn up a red list of spiders. In Belgium Maelfait et al., 1998 established one for the Flemish region based on the 1994 IUCN criteria and those used in Germany, but it has not been revised since. More generally, risk assessment in Europa suffers from a lack of standardisation and information, sometimes of a taxonomic nature. The term "rare" also raises difficulties, as a lack of knowledge of the biology and ecology of species can make a species appear rare when it is not (this notion has already been discussed by Bristowe, 1933).

As the most important threat is habitat loss, an effective conservation measure for spiders is the protection of large areas of good quality habitats. Smaller areas can also play a role as Theron et al., 2020 showed that remnant vegetation in agricultural matrices can support spider diversity, including rarer and range restricted species.

2.2.3 Study and use in ecological evaluation

The study of spiders involves capture. Different techniques are used depending on the purpose of the research, the biology and ecology of the species. Duffey, 1972 has given an overview. For this part Canard, 1981 compared the main, and complementary techniques used in heathlands. The aspects considered were :

- the degree of disturbance,

- the completeness of the collect and
- the time required for sampling and sorting

The sampling techniques compared were:

- Sight hunting : capture of all the spiders that the observer can see, there are several modalities depending on the area surveyed, sampling, etc.
- Collection box : a sample of turf is collected and analysed in the laboratory
- Branch sampling : branches are collected and analysed in the laboratory
- Beating : the vegetation, especially bushes and trees, is shaken and the animals are collected in nets
- Sweeping : vegetation is crossed with a sweeping net
- Ground trapping : mainly pitfalls, also known as Barber trap, basically a container buried to ground level and filled with "wetting" liquid and preservative

Of these techniques, pitfalls are most often preferred because of their ease of implementation, low cost, ability to study time series and phenology and the possibility to obtain statistically significant numbers of captures (e.g. in Snazell, 1982). However, precautions have to be taken to guarantee their effectiveness. It is preferable to include protection from rain and to avoid capturing non target groups, such as amphibians and micromammals. Disturbances are locally limited. However, the potential impact on the studied species may be significant depending on their lifestyle, epigeic spiders being more susceptible (Brown et al., 2016), and the sampling time (e.g. during the reproductive period). The structure of the surrounding vegetation and soil, as well as weather conditions, influence the number of individuals captured. Certain families are more likely to be caught : Lycosidae, Gnaphosidae, Clubionidae, Dysderidae, and to a lesser extent Thomisidae, Theridiidae, Linyphiidae and Agelenidae (Duffey, 1972). This may lead to a bias in community studies as the pitfalls are mainly representative of cursorial species. Their ability to represent relative abundance is also debated, as in Topping et al., 1992. It is thought that this provides more information about activity, which is not constant from one species to another. For example, the number of catches may vary as a result of mate searching, postcopulatory dispersal of females, oviposition sites searching and hunting, but can not be attributed with certainty to any behaviour.

As ecosystems are subject to a variety of pressures, spiders have proven to be valuable bioindicators in many contexts, such as ecotoxicological studies of heavy metals and pesticide contaminations (Maelfait et al., 1997; Nentwig, 2013. Spiders can similarly be useful in conservation ecology. As many restoration projects have been implemented across Europe, the need to assess and monitor restoration success has been raised. Spiders, together with other arthropod groups, are used as indicators of restoration and management success, notably in heathland and grassland ecosystems (see eg. Gajdoš et al., 2000; Perner et al., 2003, Pétillon et al., 2006; Cristofoli et al., 2010; Borchard et al., 2014; Hacala et al., 2020, Bach et al., 2024 and Toft et al., 2024 as well as Solascasas et al., 2022 for a review).

2.3 Statistical methods in community ecology

Community ecology is a branch of ecology that studies the assemblages of living organisms in time and space in a given environment. It has benefited from advances in statistical methods and the ever-increasing power of computers.

2.3.1 Community ecology : scope

According to Vellend, 2010 community ecology, or synecology, is "the study of patterns in the diversity, abundance, and composition of species in communities, and of the processes underlying these patterns", grouped in four categories : selection, drift, speciation, and dispersal. Diversity is an equally broad concept, and the main contribution to its formalisation is that of Whittaker, 1972. He introduced the concepts of alpha (site scale), beta (between sites) and gamma diversity (landscape scale), which are widely used today and commonly measured by indices.

In addition to species richness, evenness, abundance and composition, the diversity and evolution of ecological traits such as dispersal pattern, body size or phenology are increasingly used (e.g. Lambeets et al., 2009; Mouillot et al., 2013; Kędzior et al., 2020). Traits have been strictly defined by Violle et al., 2007 as "any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organization." Because they are subject to selection, they are meaningful in explaining the presence of species. For example, small species with high dispersal abilities first appear after disturbances. Trophic relationships are also used, as the abundance of carnivorous species is favoured by complex ecosystems. The nature of these traits, their differences among organisms and their distribution within an ecosystem is called functional diversity (de Bello et al., 2021).

Despite the existence of a multitude of schools that have developed as many methods, the difficulty of spatial and temporal delimitation of species assemblages and the difficulty of conducting manipulative experiments on a large scale (Gauch, 1982), from a practical point of view, the field studies attempt to shed light on three main aspects (Duffey, 1972):

- the identity and number of species present in a habitat,
- the abundance and variation of each species,
- habitat preferences and ecological tolerances to environmental factors.

It is impossible to give a complete answer, and all ecological surveys have to make compromises depending on the objectives, the resources available, the object of study, etc. For example, it is almost impossible to know the true population size of moving animals and including estimates in the analysis makes them uncertain (Gauch, 1982).

2.3.2 Multivariate analyses in community ecology

In order to characterise a community, synecology usually involves sampling it. This first stage is of paramount importance and determines the analyses that can be carried out. The accuracy, homogeneity, efficiency and size of the data influence the quality of the studies. A sample that is too small weakens the analyses, which are then difficult to interpret, while a sample that is too large represents a waste of energy and time, as well as the unnecessary sacrifice of living organisms (Jongman et al., 1995).

A common type of study is to characterise a community at a given location and relate it to quantitative environmental factors (Gauch, 1982; Vellend, 2010; Dray et al., 2012). The so-called Q mode of the analysis is the study of pairs of objects, based on the similarity/dissimilarity between the pairs. The comparison of descriptors, based on the dependence between them is the R mode Borcard et al., 2018. The data collected for these purposes are in the form of matrices :

- Sampling x species,
- Sampling x environmental variables and
- Species x traits

However, the ecological data have certain characteristics that are worth remembering (Jongman et al., 1995; Borcard et al., 2018). Surveys mainly consist of semi-quantitative, presence-absence or abundance data. Depending on the context of the study, the absence of a species may be as important as its presence. The relationship between species and environmental factors is in most cases non-linear and the correlation between species is generally strong. The same applies to environmental variables, which can confound the interpretation of analyses. These data are also poorly suited to the statistical tests developed in experiments. The information contained in the dataset may also be indirect Gauch, 1982. In this context, multivariate analysis is highly appropriate. In particular, the number of data items can be very large, which leads to representation problems.

Multivariate analysis is generally justified when the number of individuals or variables is greater than 10 or 15 Gauch, 1982. More generally, an analysis involves taking into account the particularities of the dataset in terms of its variability, i.e. :

- relationships: this is the part of the variability that the researcher is interested in, those that allows the interpretation of species assemblages and the influence of environmental variables;
- noise: the variation among samples may be due to phenomena not directly studied (local disturbances, organism activity, etc.), chance, measurement artefacts, etc. Ideally, this part is avoided in the analyses;
- redundancy: the data from different samples may be similar, or even be identical in terms of composition. This is due to the large number of samples taken in relation to their inherent variability. It is by synthesising these redundancies that the analyses can produce summarised and interpretable results;
- aberrant data: one sample or species may be very different from the others, for example, due to disturbance or heterogeneity

Multivariate analyses are used to summarise information, reduce noise, highlight relationships and identify outliers. They allow community data to be linked to other types of data, such as environmental variables. They are also used to improve the modelling and representation of communities Gauch, 1982. Some of their components, such as the inertia of certain ordinations, can be interpreted in terms of alpha and beta diversity, in relation to commonly used indices (Simpson, Shannon, etc.) (Pélissier et al., 2003). Multivariate analyses are numerous and not all are adapted to the specific objectives of a study. The choice of a particular method must be carefully considered and should take into account several aspects, from accuracy and robustness to data and computer memory sobriety (Gauch, 1982). The human factor plays an important role in the choices made. One of the aspects to be taken into account when choosing a technique is whether it involves defining parameters or making methodological choices. In this case, the degree of subjectivity is greater, although no technique is completely objective. The evaluation of techniques is mainly based on comparison with models, obtained by mathematical reasoning or simulation using data with a known structure. At the same time, the study of a community is an iterative process of refinement that may require the use of several techniques (e.g. ordination in the exploratory phase followed by classification) (Gauch, 1982; Jongman et al., 1995).

The main methods used are multivariate regression, ordination and classification. Multivariate regression is a generalisation of univariate regression. In ecology, it is mainly used to study the distribution of species along a gradient. It can be used to model communities and then provide a means of comparison for evaluating multivariate analysis methods (Gauch, 1982). Ordinations are used to summarise the information in a dataset by representing the relationships between species and sites along orthogonal gradients of compositional variability in a space of reduced dimensions. In the case of constrained (or canonical) ordinations, the organisation of variability in specific composition is conducted according to environmental factors. The result is presented in the form of a graph, usually two-dimensional, in which species or sites are ordered along axes, with similar objects being closer together than dissimilar ones (, (Gauch, 1982; Jongman et al., 1995; Dray et al., 2012). While reducing dimensions facilitates representation and communication, data projection comes at the expense of fidelity to data structure. Objects are visualised in a plane, whereas in reality they are located in a three-dimensional space. However, this is not a problem when data structuring is reduced (Borcard et al., 2018). The principle of classification is to group similar entities into the same groups, based on their values for variables. Classification often involves the researcher in the implementation of the technique, and the results are therefore partly a manifestation of the researcher's representations (Jongman et al., 1995).

3. Objectives

3.1 Context

Near Brugge RBINS has carried out monitoring at several restored sites in different habitats, mainly heathlands with *E. cinerea*. Different taxonomic groups are being studied, including Carabidae, Hymenoptera, Staphylinidae and Araneae. However, some have not yet been analysed in detail. This work focuses on data from Araneae.

3.2 Objectives

The general aim of the work is to characterise the spider communities in the restored sites and to assess the evolution of the typical heathland community according to the characteristics of the sites in order to provide management recommendations. This includes several specific objectives:

1. To compare the data from the surveys carried out on the restored sites with each other and with references (red lists, literature reviews, etc.) in order to characterise, if possible, a typical heathland araneological community in terms of species composition, alpha diversity, indicator species, functional diversity, habitat preferences in the context of the region and to assess its evolution.

2. Compare the communities near Brugge with nearby heathlands, dunes and grasslands in Flanders.

3. Determine if management practices and vegetation structure influence the species composition and abundance of the sites and, if possible, determine the variables influencing the success of recomposition (number of typical species).

4. Identify the management method(s) best suited to safeguarding the typical araneological community of heathlands (species composition).

5. Assess the adequacy of the monitoring, by checking whether the pooled data from three traps is comparable to that from individual traps, and whether year-round monitoring is necessary.

4. Material and methods

4.1 Study area

The data come from several restored sites near the city of Brugge. These are distributed between the municipalities of *Brugge*, *Oostkamp*, *Zedelgem*, *Jabbeke* and *Oudenburg* (Figure 4.1, for more detailed maps, see Appendix A1). At each site, pitfalls have been set at several sampling points, identified by a code. In the next parts of the work, the following terms will be used :

- Location for the place where a monitoring was carried out (e.g. : Roksem, ...)
- Station for the placement of 3 traps within the location, written with an alphabetical code (e.g: A, B, KM, KO, ...) referring to a place (eg. BB = "Beisbroek Bos")
- Sample for the combination of the station and the monitoring year in which the traps were collected, written with the year in Roman numerals next to the station code (e.g. : A.III, B.III, KM.I, KO.II, ...).

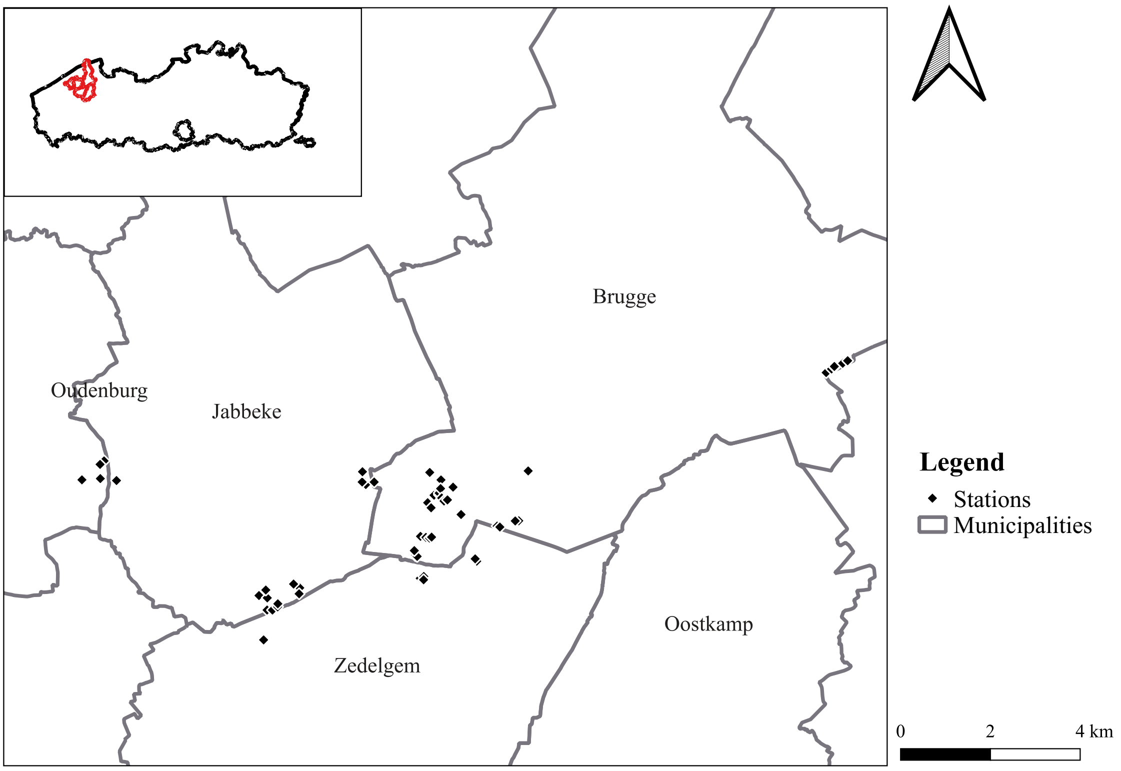


Figure 4.1: Location of capture stations in the study region. The stations are located in the Brugge region, Belgium. The points correspond to the geographical location of the central pitfall (on 3 traps) of each station; box: location of the municipalities concerned in the Flemish Region.

The study area belongs to the Atlantic bioregion, in a largely urbanised matrix with the city of Brugge and the E40 road dividing the landscape. The region was long dominated by heathlands. Some aspects of its characteristics and history are given in De Blust, 2005. Belgium has three main heathland districts linked to climatic gradients : Ardennes, Campine and Flanders. The Brugge region belongs to the latter. Additionally, it represents a transition zone between the complexes of the Kempen, northern France and southern England. (Stieperaere, 1969). The vegetation in this region includes species with a more southerly distribution. *Erica cinerea* can be locally abundant in heathlands and can dominate *C. vulgaris* (inspiring Stieperaere with the *Ericetosum cinereae* phytosociological subassociation), but also along paths and in conifer plantations. Its germination is favoured by the high temperatures that occur, for example, in soils with coarse humus and strong sun exposure, or after burning.

The soils are mainly sandy or sandy-loam, overlying a layer of Pleistocene sand. The heaths were part of the "commons" and are the result of deforestation, grazing for manure and wool production and resources extraction (humus, fodder, etc.). As a result, the soil of this region typically evolved into a post-podzolic soil (plaggeptic haplohumod), with a Bh/fe horizon crumbled by microbial activity (De Blust, 2005).

The heathlands began to disappear with a reclamation movement that started in the XIth century, initially led by private owners and some physiocratic personalities (Van Acker, 1960). Communally managed heathlands were only preserved for a while due to the resistance of local communities. Of the heathland area in 1775, barely 1% remained in the early 2000 (Piessens et al., 2005). The remnants are highly fragmented and isolated, with a rescue-effect (i.e. the closeness of patches allows species to disperse between them and prevent extinction) revealed by Piessens et al., 2004. Stieperaere, 1969 found that between 1950 and 1970, the distribution of the bell heather had shrunk by 35%, with the main remaining areas being around Sint-Andries and Zedelgem.

4.2 Data

4.2.1 Collect of spider data

Monitoring started in 2014. Data collection is currently in its eleventh year. To date, a total of 106 samples are available from 77 stations, some of which have been monitored for several years. However, some have not been sampled for a full year. Finally, 65 stations and 91 samples were analysed for this work (see Appendix A2). Two stations, KM and KO were monitored more intensively, for 10 and 9 years respectively.

At each sampling point, three Barber traps (pitfalls) are placed along a straight line, 5 metres apart and marked by a stick with a coloured strip. The trap is a glass jar buried up to the rim, in a hole stabilised by a plastic tube. It is filled between a third and a half with a preservative, consisting of a 3.5% formaldehyde solution combined with a small amount of detergent to reduce surface tension. To prevent bycatches of small mammals, reptiles and amphibians, a small fine-mesh is fixed over the pitfall with metal stirrups (Figure 4.2). The traps are set for a year, from April to April. They are emptied fortnightly and the contents sorted and identified. For some samples, other capture techniques, such as sweeping and pan trapping were used, but only the data from the pitfalls were analysed.

(a) (b)

Figure 4.2: Typical pitfall assembly. (a) The PVC plastic piece fixes the hole and holds the glass jar filled with a preservative to collect terrestrial invertebrates. The mesh prevents bycatches and the stick helps to locate the trap. (b) The trap is left for a year, buried up to the rim.

Four other datasets, obtained through a comparable methodology, were used for objective 2. The first, from the Arabel database, consists of 13 dune, heathland and grassland stations sampled in 2005-2006. The second, from Dekoninck et al., 2000, contains 12 stations sampled in 2000-2001, in the Ghent region. The third includes samples from four dune and grassland stations monitored near Nieuwpoort over three years, from 2001 to 2003 Hoffmann et al., 2005. The fourth is composed of four dune and grassland surveys from 2013-2014, also near Nieuwpoort.

4.2.2 Environmental data

In addition to species data, for each sample, data on location (essentially municipality and latitude-longitude with the central trap as a reference), management and vegetation characteristics were collected and are detailed in Appendix A3.

Information on management refers to the methods used in terms of tillage and grazing. There is three tillage methods: deforested but without topsoil removal (1), no topsoil removal (2) and topsoil removal (3). Alongside non-grazing (1) and mowing (2), grazing has been further categorised according to the type of herbivore and the duration of the grazing period : temporary grazing by sheep and permanent grazing by rabbits (3), Galloway grazing (4), permanent grazing by sheep and rabbits (5), temporary grazing by donkeys (6), grazing by donkeys and sheep (7). The vegetation was characterised as follows. The plant cover (% of the soil) of different species *Calluna vulgaris*, *Erica cinerea*, *Erica tetralix*, *Molinia caerulea*, *Agrostis sp.* , as well as lichens, mosses and the proportion of bare sandy soil were estimated in 1m² around each trap and pooled to obtain a value per sample. In addition, the cover of grasses (cover of *Molinia caerulea* + cover of *Agrostis sp.*) and non-grass herbs was calculated. The cover of *Cytisus sp.* was estimated directly at the sample level, i.e. in a 50x50m square. The proportion of canopy cover (from shrubs and trees) and litter were also estimated at the sample level. For the forest floor, litter consists of tree leaves and small sticks, for grassland of dead dry grasses and for heathland of plant residues. The presence and quantity of dead wood was also categorised at the sample level. Each sample was classified into a habitat category, based on the vegetation in the immediate vicinity of the traps : "Heathland", "Dune/heathland", "Humid heathland", "Nutrientpoor grassland", "Forest" (Figure 4.3).

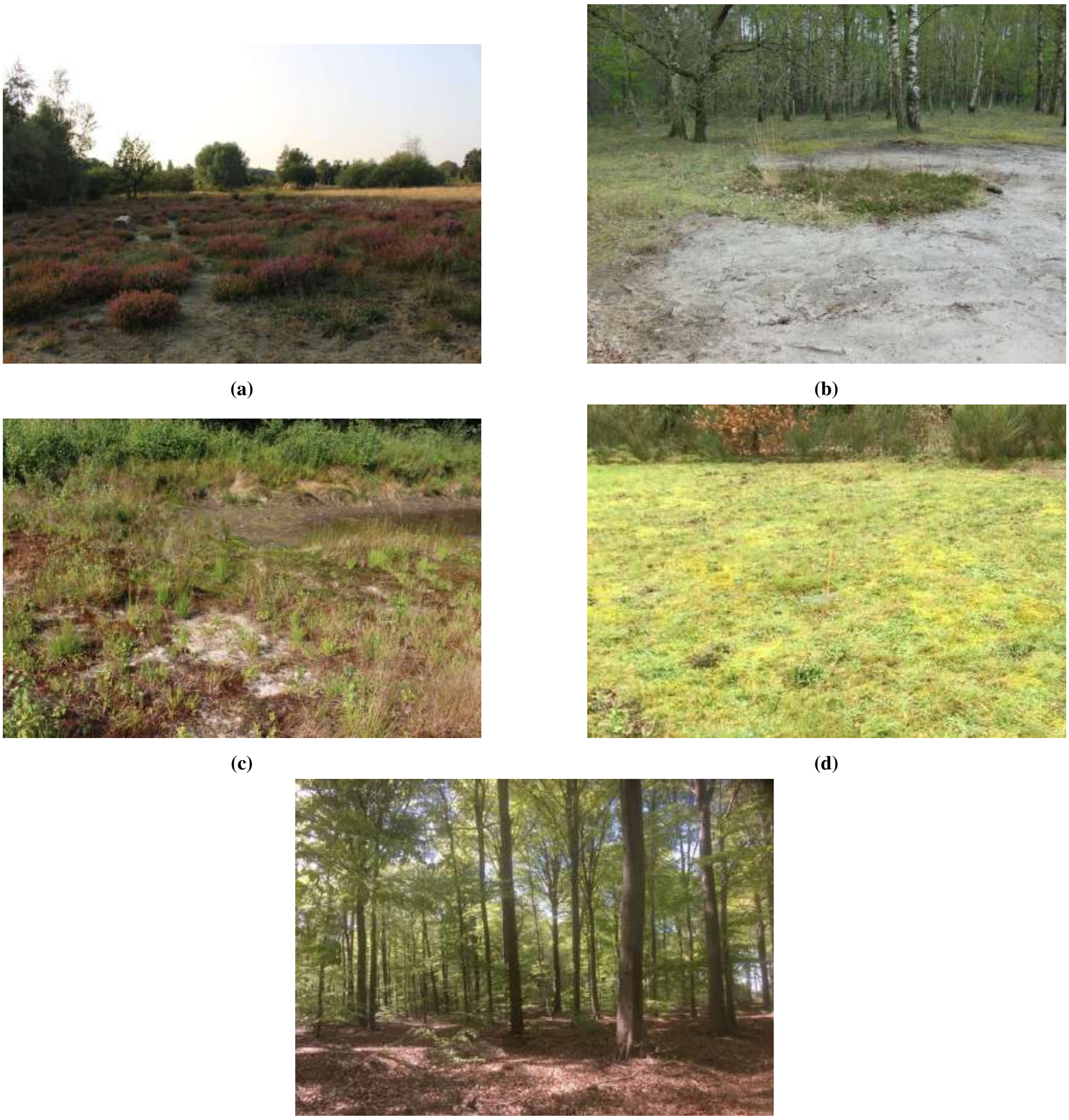

(a)
(b)
(c)
(d)
(e)

Figure 4.3: The five habitat categories studied. Example of a station for each category. **(a)** Heathland, station WB in 2018; **(b)** Dune/heathland, station ZK in 2014; **(c)** Humid heathland, station SF in 2018; **(d)** Nutrientpoor grassland, station SNC in 2021 and **(e)** Forest, station VL10 in 2020. © W. Dekoninck

4.2.3 Ecological features

Some important traits for understanding the functional diversity of spiders have been selected (Cristofoli et al., 2010, Buchholz et al., 2013, Gossner et al., 2015, Toft et al., 2024). They are not measured directly on the sampled individuals, so they are not traits in the sense of Violle et al., 2007. Clear lists of traits of spiders in Western Europe are not available, so proxies from general studies have been used. The values for each feature can be found in the Appendix A4.

The ballooning tendency is taken from Bell et al., 2005, supplemented by Blandenier, 2009 and the World Spider Traits Database (WSTD), `https://spidertraits.sci.muni.cz/` (Pekár et al., 2021). Taking into account taxonomic updates, species for which neither the species nor the genus was listed were assigned a value of 0, species for which the genus was listed but not the species were assigned a value of 0.5 and species for which the name was listed were given a value of 1. For the first two categories, the score was increased if the species was present in Blandenier, 2009 and Pekár et al., 2021. Light and humidity preferences were taken from Entling et al., 2007, the hunting guild from Cardoso et al., 2011. A heathland affinity was calculated for each species based on Hänggi et al., 1995, by dividing the number of heathland habitats where the species was recorded by the total number of habitats in which it occurs. The minimum and maximum sizes of females and males are taken from Roberts, 1985, 1987. A phenological class according Schaefer, 1977 was assigned to each species on the basis of activity graphs from the samples and those taken from the Spider and Harvestman Recording Scheme website : `https://srs.britishspiders.org.uk/` (British Arachnological Society, 2024). In temperate zones, the annual cycle of spiders is characterised by the reproduction period(s) and the overwintering stage. A species is said to be eurychronous (class 1) if its development is long and individuals can be observed throughout the year. All development stages are likely to overwinter. In stenochronous species, the adults are visible for a certain part of the year, with several modalities : some species have their reproductive period from spring to summer and overwinter as nymphs (class 2), other reproduce in autumn (class 3) and the eggs pass the winter and some are winter-active spiders (class 4). Diplochronous species have for their part two distinct reproductive periods (mainly spring and autumn) and overwinter as adults (class 5).

4.3 Analyses

All the analyses were performed using the R language (version 4.2.0 (2022-04-22) "Vigorous Calisthenics" © 2022 The R Foundation for Statistical Computing) on the RStudio integrated development environment (version 2023.09.1 + 494). The main packages used for the analyses were *vegan*, *BiodiversityR*, *iNext*, *fundiversity*, *cocorresp*, *ade4* and *indicspecies*. Graphs were generated using *ggplot2*. A full list of R packages used can be found in section 8.

4.3.1 Exploratory data analysis (EDA) and pretreatments

Before analysing the data, the species nomenclature was updated and harmonised for all years in accordance with the version of the World Spider Catalogue in force at the beginning of the master thesis (February 2024) and the checklist of spiders of Belgium (Bosmans et al., 2017). Only one species, *Zelotes pumilus* which has now been split into two separate species, both found in Belgium, was kept as *Zelotes pumilus s.l.*. Another, *Pardosa proxima*, has been grouped with *Pardosa tenuipes* (see Isaia et al., 2018).

In the subsequent analyses, only adults of species identified with certainty are included. Four spiders identified only at genus level and seven individuals of uncertain identification were excluded. As pitfalls trapping doesn't directly inform on spider abundance, but rather activity (Topping et al., 1992), analyses were also performed with only presence-absence. As some species can be only migrant in a habitat, another turn of the analysis was performed with only species present in at least 5% of the samples, except for the diversity alpha analysis. In this case, the presence of rare or migrant species remains informative about the composition of the community or the influence of the landscape.

4.3.2 Objective 1

In order to characterise and isolate a "heathland community", diversity analyses (beta, alpha and functional) were carried out to see if the spider community of samples categorised as "heathlands" diverges from other categories. The isolation of indicator species was also performed.

Beta diversity

To examine the position of the samples in relation to each other, transformation-based Principal Components Analysis (tbPCA), a linear unconstrained ordination, was performed. Firstly with all the samples and highlighting the habitats, then with a decomposition by habitat and finally by considering only the KM and KO time series. By transforming the species matrix, tbPCA allows the use of PCA, a powerful technique but not well suited to species data Borcard et al., 2018. Here, the Hellinger transformation was retained. This reduces the importance of species with high abundance Borcard et al., 2018, justified here by the fact that the most abundant species are not necessarily the most important for the habitat. Moreover this reduces the horseshoe effect. The influence of habitat categories was evaluated by PERmutational Multivariate ANalysis of VAriance (PERMANOVA) and a pairwise comparison test.

Alpha diversity

The distribution of occurrences of species and families was explored. Then the species richness was calculated per sample. An accumulation curve was constructed for each habitat. As sampling underestimates true richness, the total richness was extrapolated. Firstly using a non-parametric approach with Chao's index, with a correction for small samples. Secondly, to compare habitats, a parametric approach was used by calculating the Fisher's alpha index, which is independent of the number of samples. Differences between means by habitat were assessed by a general linear mixed model with station as a random effect. To examine and compare diversity, dominance and evenness between habitats, Hill numbers (q) of order 0 (species richness), 1 (the exponential of Shannon's entropy) and 2 (the inverse of Simpson's concentration) were calculated. For each number, a Hill curve was constructed per habitat, and the missing parts of the coverage were extrapolated or interpolated. Since the habitat samples were not of equal size, the numbers were calculated based on sample coverage, which means that the assemblages can be compared based on equal completeness (Chao et al., 2014).

Functional diversity

Functional diversity was then assessed according to Mason et al., 2005, using indices of functional richness (FRic, corresponding to the amount of functional space filled by a group of species by means of a convex hull), evenness (FEve, representing the regularity of the abundance distribution in the corresponding space) and divergence (FDiv, the part of abundance represented by the species with the most extreme values of traits), on the Gower distance matrix species x traits, weighted by species activity.

Indicator species

The rankabundance (in this cas, rank of activity) was plotted for each habitat category. For each type of habitat, the indicator value of the species was calculated using the IndVal method (Dufrêne et al., 1997), first for each habitat separately and secondly taking into account combinations of habitats (De Cáceres et al., 2010). This method is based on a classification. An index is calculated that combines an estimate of the specificity (maximum when the species is present in only one group) and the fidelity (maximum when the species is present in all the samples of the said group) of each species to each class of the typology. The indicator value of a given species is its highest observed IndVal value. Statistical significance is assessed by randomisation. The presence of indicator species on the Red List of Spiders of Flanders Maelfait et al., 1998 was checked. The species listed as "rare" only on the basis of the geographical repartition and those whose statute was not unclear were not considered, as the geographical range may have changed due to the climatic warming.

4.3.3 Objective 2

Another tbPCA with Hellinger transformation was performed, including samples from Kalmthout, Ghent and Nieuwpoort.

4.3.4 Objective 3

Several types of analyses were carried out to determine the influence of the different environmental variables. Firstly, the influence of the vegetation structure was assessed using an asymmetric Co-correspondence Analysis (CoCA), an canonical ordination method that aims to represent two communities sampled at the same sites. The plant community was defined as the explanatory matrix. Secondly, a distance-based Redundancy Analysis (dbRDA), a constrained ordination, was performed with tillage and grazing modalities as constraining variables. Given that both grassland and woodland encompass modalities that were not applied in the other habitats, the analysis was conducted exclusively on the three heathland types. The distance used was the Hellinger distance with a Lingoes correction to reduce the type I error (Borcard et al., 2018). Significance was assessed by a permutation test. For this analysis, only the heathland, dune/heathland and humid heathland complex is taken into account. In fact, management methods are unevenly distributed across the habitat categories, with grassland and woodland managed differently from heathland.

4.3.5 Objective 4

A combination of a RLQ analysis and fourth corner analysis was performed on the three heathland types to see which traits are influenced by environmental variables, following the workflow described by Dray et al., 2014. Separate ordinations were performed on the three matrices: a Correspondence Analysis (CA) for the site x species matrix (L), and a Hill-Smith analysis for the site x environmental variables matrix (R) and for the species x ecological features matrix (Q). These are combined by the RLQ analysis. The importance of the L-Q and R-L relationships is evaluated through a random test utilising a permutation model that permutes both rows and columns. This model, the sixth of six possible models, is based on the general assumption that variables and traits are independent. In essence, it is a combination of two other models applied sequentially:

model 2 (H0: species composition is independent of environmental variables) and model 4 (H0: species composition is determined by environmental variables independently of traits). The fourth corner analysis aims to test the significance of the parameters resulting from the calculation of an ecological features x environmental variables matrix (D). For these analyses, 45 species with missing values for ecological traits, out of the 224 that comprise the three habitats were removed.

4.3.6 Objective 5

The efficiency of monitoring was analysed on two points. Firstly, the need to monitor a whole year was assessed by plotting the number of individuals captured over time and by characterising the activity periods of species in order to isolate a period of maximum frequency. A period of activity is defined by pooling the numbers of individuals caught per month, as long as the interval between two occurrences does not exceed two months. Secondly, to check the correspondence between the results obtained at sample level and those from individual traps, the pitfall data from the thirty samples with the most heterogeneous environment (Dekoninck, pers. comm.) were projected *post hoc* onto the tbPCA resulting from objective 1.

5. Results

5.1 Objective 1

A summary of the analyses is provided in Table 5.1. It is indicated whether a difference between habitats was detected and, if so, which categories were involved.

Table 5.1: Summary of the principal outcomes achieved in relation to objective 1. (H : Heathlands, D/h : Dune/heathlands, Hh : Humid heathlands, Npoorg : Nutrientpoor grasslands, F : Forests)

Analysis	Test	Difference	Pairs	Adjusted p-value	Illustration
Families occurrence	/	/	/	/	Figure 5.1
tbPCA	/	Yes	/	/	Figure 5.2
PERMANOVA	Pairwise multilevel comparaison	Yes	All	All < 0.05	Table 5.2
Species richness (samples)	/	/	/	/	Figure 5.4
Accumulation curves	Confidence interval	Yes	H-D/h H-Ng	/	Figure 5.5
Chao's index	/	/	/	/	Table 5.3
Fisher's alpha	LMM	Yes	H-F Ng-F	0.0103* 0.0229*	Figure 5.6
Hill numbers curve	Confidence interval	Yes	/	/	Figure 5.7
FRic	LMM	Yes	H-F D/h-F hH-F Ng-F	5.56e-05 *** 0.00615 ** 0.02725 * 7.47e-05 ***	Figure 5.8a
FEve	LMM	Yes	H-Ng D/h-Ng F-Ng	1.97e-05 *** 0.0363 * 0.0208 *	Figure 5.8b
FDiv	LMM	No	/	/	Figure 5.8c
Rankabundance	/	/	/	/	Figure ?
IndVal	/	/	/	/	Table 5.4

The species matrix is characterised by proportion of absences (i.e. 0 values), which account for 82% of the data. The number of individuals ranges from 0 to 535, for a total of 64 856 individuals belonging to 252 species. The majority of species are present at low frequencies (59% of species occur in less than 10% of samples), while a few are highly abundant, occuring in the majority of samples (five species present in 90% of samples). Twenty-height families are present. The majority of species (42%) belongs to the *Linyphiidae* family, followed by *Lycosidae*, *Theridiidae*, *Gnaphosidae*, *Salticidae*, *Thomisidae* and *Clubionidae*. The remaining families comprise less than 10 species (Figure 5.1).

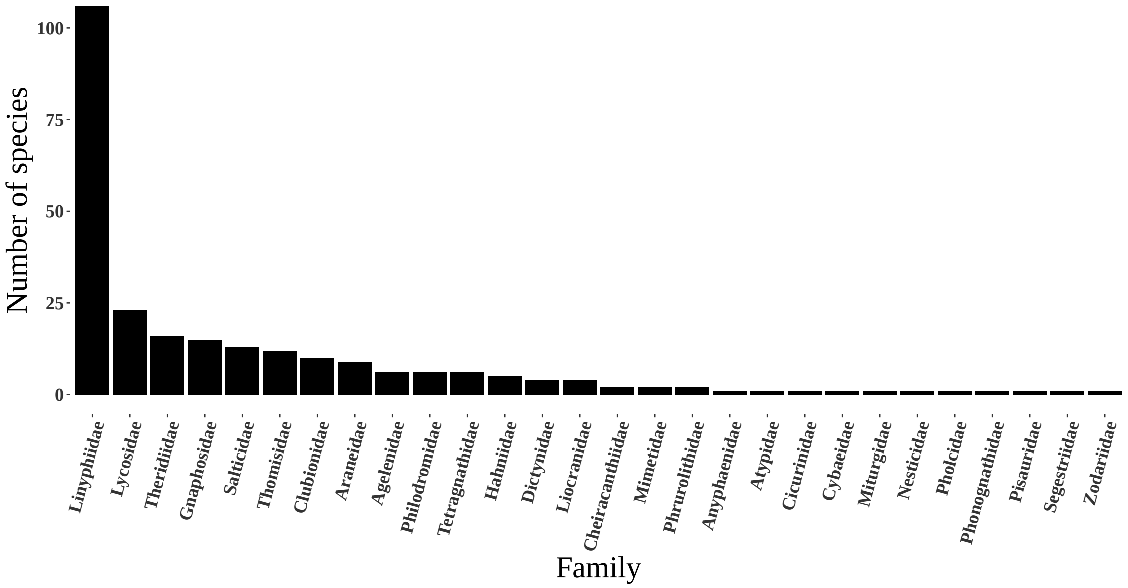


Figure 5.1: Family richness. Occurrence of families for all samples

The tbPCA is illustrated in Figure 5.2. The first two axes account for 20% and 15% of the total variance respectively. The ordination of the presence-absence data and that of the data without rare species do not differ. The PERMANOVA revealed highly significant differences between the habitats (p-value : 0.0405 *). In the pairwise multilevel comparison, only the difference between heathlands and humid heathlands has a lower level of significance (Table 5.2). Figure 5.3 depicts the tbPCA with solely the KM and KO time series.

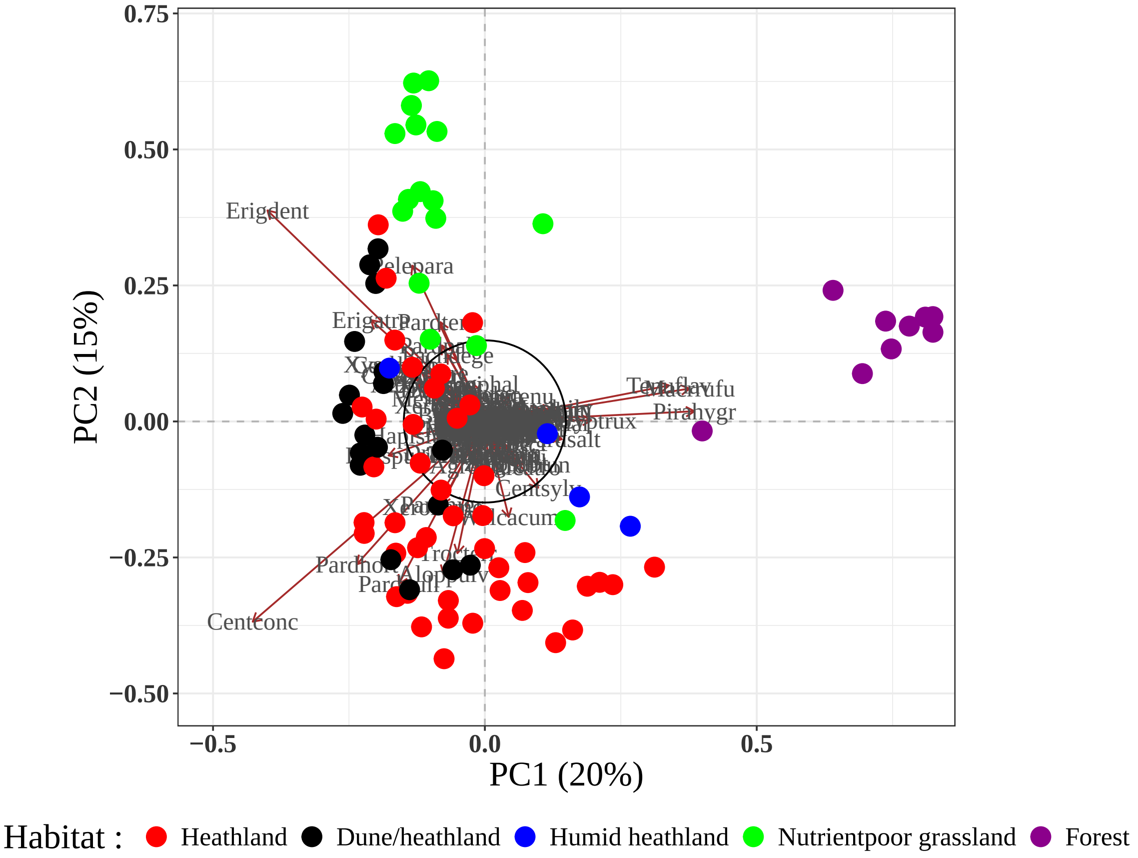


Figure 5.2: tbPCA ordination of the samples x species matrix. A principal component analysis (PCA) was conducted on species data that had been transformed using the Hellinger transformation. The figure is presented with the scaling 1 (i.e. the distances among sites are approximate representations of the Euclidean distance between them in multidimensional space). The first two axes account for 20% and 15% of the total variance respectively. The species name was abbreviated in accordance with the CEP standard, comprising the first four letters of the genus and the first four letters of the specific epithet.

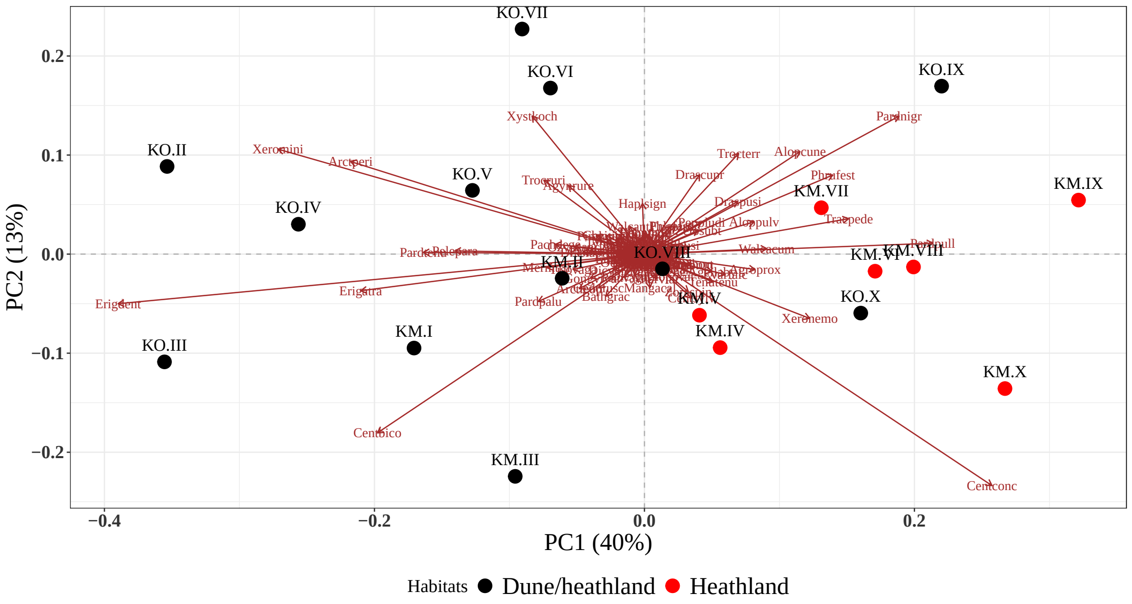


Figure 5.3: tbPCA performed on KM and KO samples. The same methodology as that employed in Figure 4.4 was utilised (Hellinger transformation, scaling 1).

Table 5.2: Evaluation of differences between habitats by pairwise multilevel comparison. Each habitat is compared with each of the other. The comparison was performed on the Hellinger distance matrix with 9999 permutations. Adjusted p-values were obtained after a Holm correction.

pairs	Df	SumsOfSqs	F.Model	R2	p.value	p.adjusted	sig
Dune/heathland vs Heathland	1	0.9352514	5.092934	0.07824097	0.001	0.010	*
Dune/heathland vs Forest	1	3.4826894	22.021691	0.45857800	0.001	0.010	*
Dune/heathland vs Nutrientpoor grassland	1	1.7190181	10.396045	0.23956205	0.001	0.010	*
Dune/heathland vs Humid heathland	1	0.7693797	5.330123	0.20243441	0.001	0.010	*
Heathland vs Forest	1	3.5772901	17.168663	0.25560525	0.001	0.010	*
Heathland vs Nutrientpoor grassland	1	2.3687806	11.478524	0.16762224	0.001	0.010	*
Heathland vs Humid heathland	1	0.4056354	1.954873	0.04163301	0.033	0.033	.
Forest vs Nutrientpoor grassland	1	3.0984660	14.674067	0.38950047	0.001	0.010	*
Forest vs Humid heathland	1	1.3708703	6.202743	0.36056711	0.001	0.010	*
Nutrientpoor grassland vs Humid heathland	1	0.8128420	3.874865	0.17713779	0.005	0.010	*

As illustrated in Figure 5.4, there is a variation in richness among samples. The most species are found in TG.II (Heathland) (68), while the fewest are found in VL11.VII (Forest) (27).

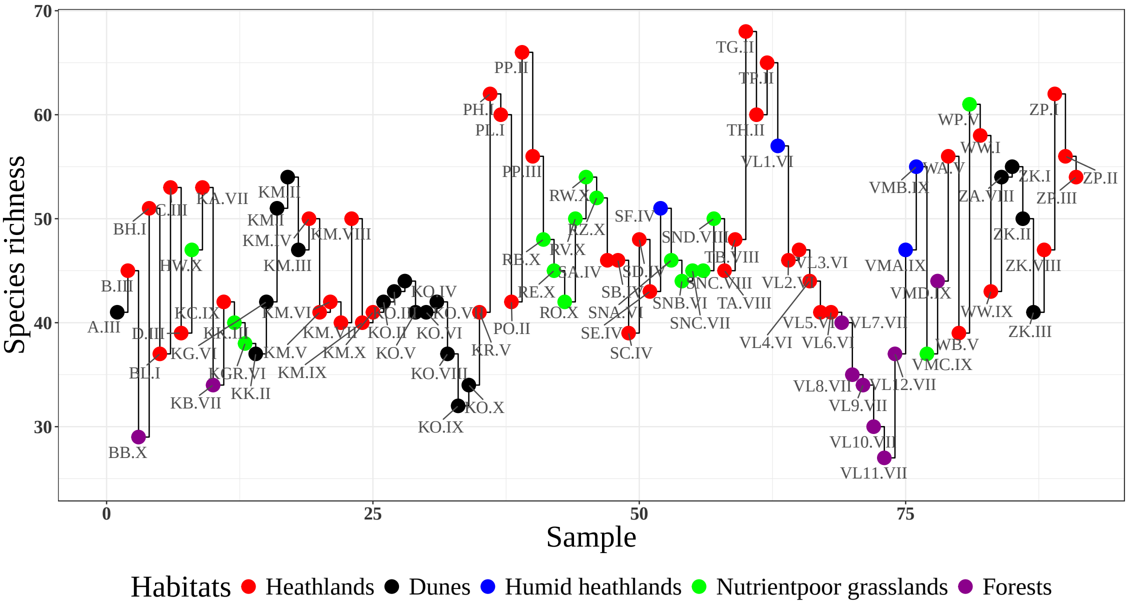


Figure 5.4: Species richness of samples taken from the different habitats. The samples have been arranged in alphabetical order.

The accumulation curves (Figure 5.5) were plotted according to habitat type. As a consequence of the unequal sampling effort across the different habitats, the curve for heathlands is considerably longer than the others. Humid heathlands accumulate the least great number of species and heathlands the most, but the two curves coincide. At its maximum sample size, the nutrientpoor grassland curve begins to diverge from the first two curves, while the dune/heathland and forest curves have already diverged.

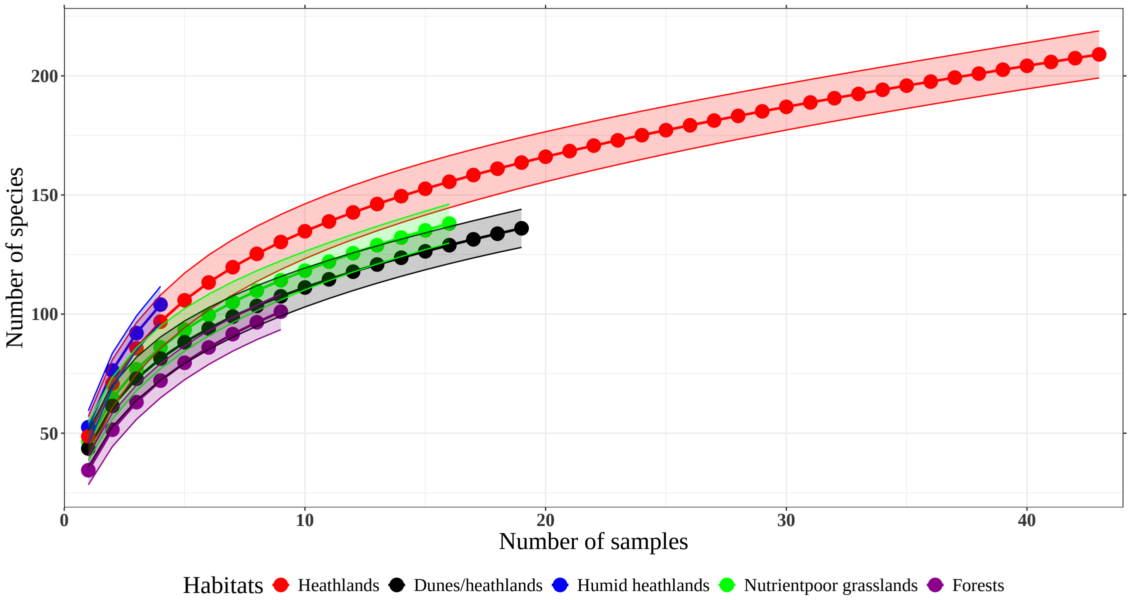


Figure 5.5: Species accumulation curve of spiders. A curve is plotted for each habitat based on the number of samples.

Estimates of species richness using the Chao index are shown in table 5.3. The estimated species richness is highest for heathland. Forests are the habitat with the lowest richness, although their estimates recover those of humid heathlands. The trend is slightly different for Fisher's alpha diversity (figure 5.6), "Heathland" is the habitat with the most important but also the most dispersed Fisher's alpha, followed by the other heathland types.

Table 5.3: Extrapolated species richness according to habitats. The Chao index was calculated for each habitat with a correction for small samples. (SE: standard error)

Habitat	Species	Chao	SE	Number of samples
Heathland	209	382.7102	65.34444	43
Nutrientpoor grassland	138	193.1042	22.08705	16
Dune/heathland	136	190.7401	22.82023	19
Humid heathland	104	143.2727	15.42428	4
Forest	101	138.4269	15.85021	9

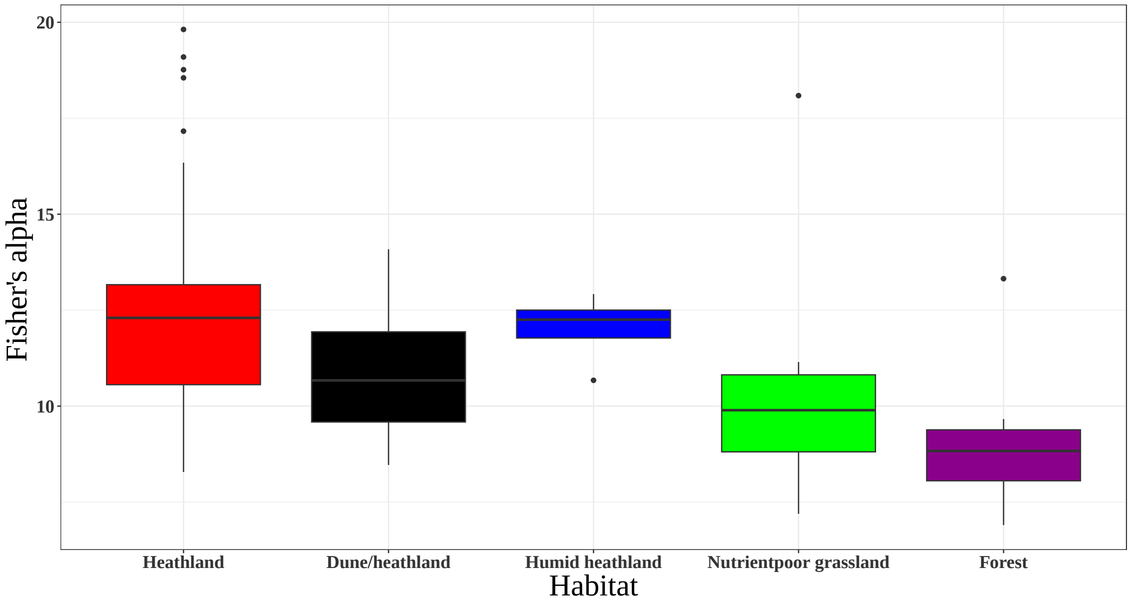


Figure 5.6: Fisher's alpha according to habitats. The dispersal of values of the index for each habitat category.

In consideration of the hill numbers based on sample coverage and illustrated in Figure 5.7, it can be observed that q=0 is analogous to the accumulation curve. For values of q=1 and 2, it can be discerned that heathlands are distinguished from the other habitats, which exhibit a considerable degree of overlap in their respective curves and confidence intervals. The line representing humid heathland is the only one that cross that representing heathland.

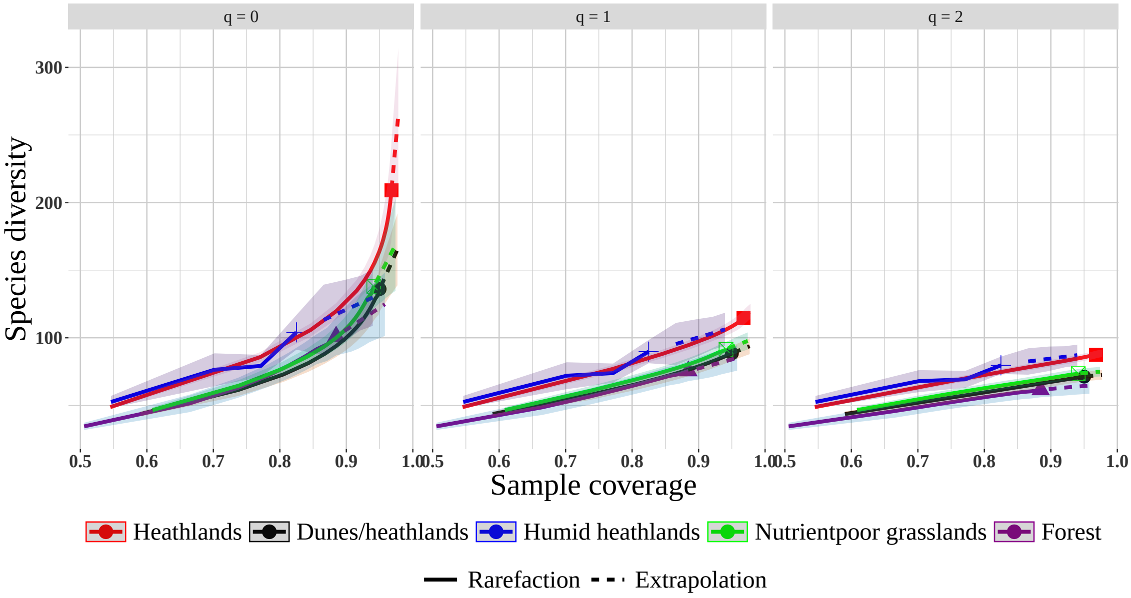
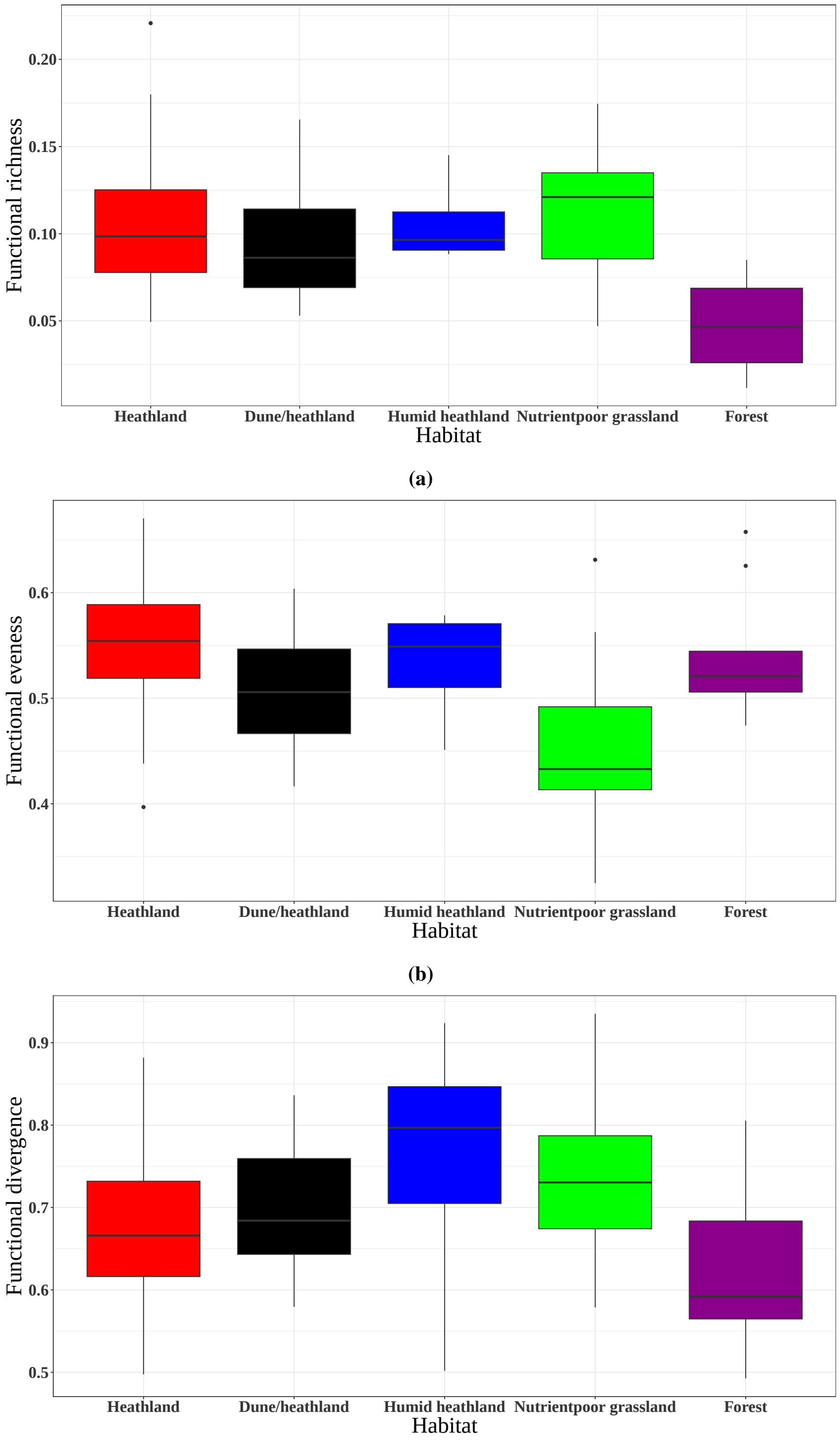


Figure 5.7: Curves of Hill numbers according to habitat. Species diversity is expressed in effective number of species (i.e. the corresponding number of equally abundant species that would yield the same index value). The Hill numbers q=0 (left panel), q=1 (middle panel) and q=2 (right panel) were calculated on species frequencies by habitat, both by rarefaction (solid line) and extrapolation (dashed line) in order to achieve a base coverage of 96.7%. The 95% confidence intervals were based on 100 bootstrap replications.

The dispersion of functional diversity indices is illustrated in Figure 5.8.



(a)

(b)

(c)

Figure 5.8: Boxplot of functional diversity indices according to habitat. Distribution of values for **(a)** functional richness, **(b)** functional regularity and **(c)** functional divergence between habitats. The indices were calculated on the Gower dissimilarity matrix weighted by species activity. The black dots represent outliers, while the black line indicates the median value of the index.

The ranking of species abundance by habitat is shown in Figure 5.9. For the IndVal analysis, no indicator species were isolated for heathland by the multipatt function, but species are found for combinations with other habitats (see Table 5.4). Red-listed species are highlighted in bold.

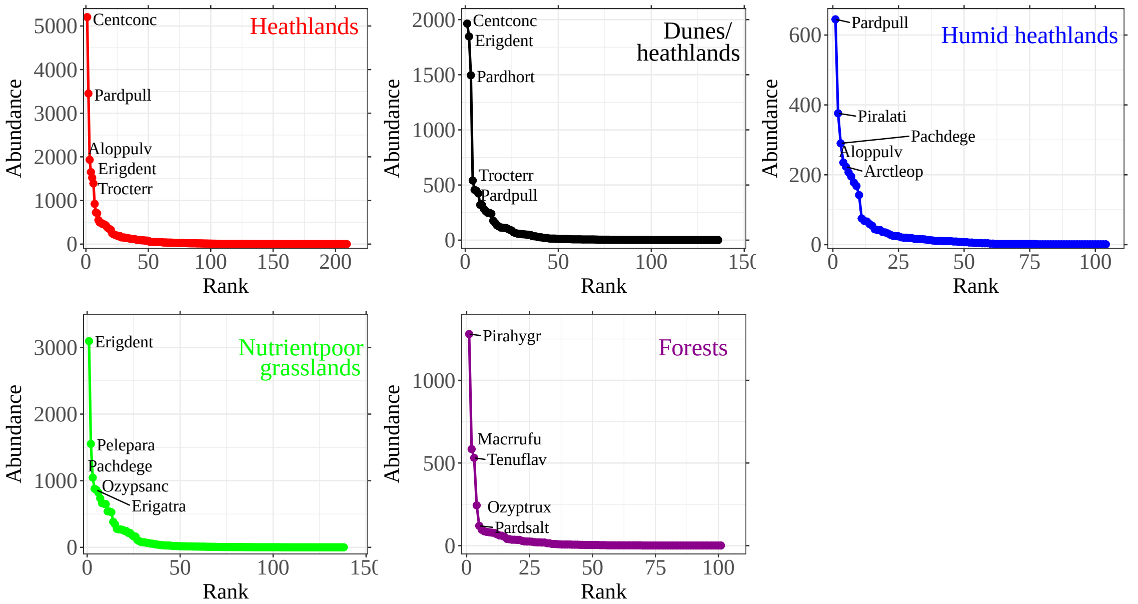


Figure 5.9: Rank abundance of species according to habitats. The five most prevalent species have been pinned. The species name was abbreviated in accordance with the CEP standard, comprising the first four letters of the genus and the first four letters of the specific epithet.

Table 5.4: Species isolated by Indval multipatt analysis. A represents the level of specificity, while B represents the level of fidelity. Species highlighted in bold are listed as threatened on the red list of Flemish spiders (Maelfait et al., 1998), regardless of category except that of geographical restriction, which has not been taken into account. (H : Heathlands, D/h : Dune/heathlands, Hh : Humid heathlands, Npoorg : Nutrientpoor grasslands, F : Forests).

List of species associated to each combination:				
Group D/h			species : 1	
	A	B	stat	p.value
Xerolycosa miniata	0.8388	0.6842	0.758	0.007 **
Group F			species : 22	
	A	B	stat	p.value
Tenuiphantes flavipes	0.9887	1.0000	0.994	0.001 ***
Macrargus rufus	0.9379	1.0000	0.968	0.001 ***
Ozyptila praticola	0.9877	0.8889	0.937	0.001 ***
Clubiona terrestris	0.9552	0.8889	0.921	0.001 ***
Diplocephalus picinus	0.9410	0.8889	0.915	0.001 ***
Haplodrassus silvestris	0.9571	0.7778	0.863	0.001 ***
Tenuiphantes zimmermanni	0.9975	0.6667	0.815	0.001 ***
Palliduphantes pallidus	0.7272	0.8889	0.804	0.001 ***
Microneta viaria	0.6723	0.8889	0.773	0.006 **
Saaristoa abnormis	0.8395	0.6667	0.748	0.005 **
Centromerus brevipalpus	0.9755	0.5556	0.736	0.004 **
Pardosa saltans	0.7872	0.6667	0.724	0.008 **
Gonatium rubellum	1.0000	0.4444	0.667	0.006 **
Euryopis flavomaculata	0.7759	0.5556	0.657	0.012 *
Neriene clathrata	0.7756	0.5556	0.656	0.012 *
Maso sundevalli	0.9598	0.4444	0.653	0.006 **
Gongylidium rufipes	0.9901	0.3333	0.574	0.011 *
Tegenaria silvestris	0.7005	0.4444	0.558	0.031 *
Clubiona comta	0.7066	0.3333	0.485	0.038 *
Clubiona brevipes	1.0000	0.2222	0.471	0.046 *
Porrhomma errans	0.9348	0.2222	0.456	0.041 *
Thyreosthenius parasiticus	0.9053	0.2222	0.449	0.049 *
Group Hh			species : 12	
	A	B	stat	p.value
Piratula latitans	0.9167	0.7500	0.829	0.001 ***
Arctosa leopardus	0.8023	0.7500	0.776	0.006 **
Pardosa amentata	0.5887	1.0000	0.767	0.005 **
Gongylidiellum vivum	0.7491	0.7500	0.750	0.004 **
Troxochrus scabriculus	0.8000	0.5000	0.632	0.007 **

Pardosa lugubris	0.7187	0.5000	0.599	0.021 *
Micrargus herbigradus	0.6199	0.5000	0.557	0.029 *
Walckenaeria nudipalpis	0.5460	0.5000	0.522	0.043 *
Araneus quadratus	1.0000	0.2500	0.500	0.043 *
Episinus truncatus	1.0000	0.2500	0.500	0.045 *
Oedothorax apicatus	0.9149	0.2500	0.478	0.050 *
Ozyptila westringi	0.7818	0.2500	0.442	0.037 *
Group Npoorg				species : 8
	A	B	stat	p.value
Pelecopsis parallela	0.9000	0.8125	0.855	0.002 **
Pardosa palustris	0.8167	0.7500	0.783	0.004 **
Centromerus prudens	0.9298	0.5000	0.682	0.008 **
Diplocephalus graecus	1.0000	0.3750	0.612	0.011 *
Zelotes electus	1.0000	0.3750	0.612	0.012 *
Asagena phalerata	0.9949	0.3750	0.611	0.009 **
Argenna subnigra	0.8247	0.3125	0.508	0.038 *
Porrhomma microphthalmum	0.9307	0.2500	0.482	0.026 *
Group D/h + H				species : 2
	A	B	stat	p.value
Agroeca proxima	0.8908	0.5645	0.709	0.015 *
Cheiracanthium virescens	1.0000	0.3387	0.582	0.043 *
Group D/h + Npoorg				species : 4
	A	B	stat	p.value
Alopecosa cuneata	0.8993	0.7714	0.833	0.001 ***
Typhochrestus digitatus	0.9277	0.6286	0.764	0.010 **
Arctosa perita	0.8849	0.5714	0.711	0.011 *
Palliduphantes insignis	0.8621	0.4571	0.628	0.025 *
Group F + Hh				species : 6
	A	B	stat	p.value
Ozyptila trux	0.9636	0.8462	0.903	0.002 **
Piratula hygrophila	0.9817	0.7692	0.869	0.003 **
Eratigena picta	0.7610	0.6154	0.684	0.011 *
Robertus lividus	0.8189	0.5385	0.664	0.012 *
Xysticus lanio	0.9364	0.3846	0.600	0.009 **
Hahnia pusilla	0.7604	0.3846	0.541	0.033 *
Group Hh + Npoorg				species : 8
	A	B	stat	p.value
Pachygnatha degeeri	0.9076	1.0000	0.953	0.001 ***
Pardosa tenuipes	0.8342	0.8500	0.842	0.002 **
Tiso vagans	0.8334	0.8500	0.842	0.018 *
Dicymbium nigrum	0.8784	0.6500	0.756	0.013 *
Stemonyphantes lineatus	0.8212	0.4500	0.608	0.019 *
Tapinocyba praecox	0.9200	0.4000	0.607	0.021 *
Drassodes pubescens	0.7984	0.4500	0.599	0.018 *
Tetragnatha extensa	0.9892	0.3000	0.545	0.013 *
Group D/h + H + Hh				species : 3
	A	B	stat	p.value
Pardosa hortensis	0.9115	0.9394	0.925	0.001 ***
Pardosa nigriceps	0.9736	0.7727	0.867	0.001 ***
Xerolycosa nemoralis	0.9983	0.6515	0.806	0.006 **
Group D/h + H + Npoorg				species : 1
	A	B	stat	p.value
Ozyptila sanctuaria	0.9771	0.9103	0.943	0.001 ***
Group D/h + Hh + Npoorg				species : 1
	A	B	stat	p.value
Oedothorax fuscus	0.9029	0.5385	0.697	0.041 *
Group H + Hh + Npoorg				species : 3
	A	B	stat	p.value
Xysticus cristatus	0.9400	0.8730	0.906	0.001 ***
Zelotes latreillei	0.9651	0.4444	0.655	0.035 *
Group D/h + F + H + Hh				species : 3
	A	B	stat	p.value
Walckenaeria acuminata	0.9754	0.8400	0.905	0.001 ***
Agroeca brunnea	1.0000	0.7600	0.872	0.001 ***
Zora spinimana	1.0000	0.4533	0.673	0.027 *
Group D/h + H + Hh + Npoorg				species : 16
	A	B	stat	p.value
Centromerita concinna	0.9965	1.0000	0.998	0.001 ***
Alopecosa pulverulenta	0.9984	0.9878	0.993	0.001 ***
Pardosa pullata	0.9996	0.9756	0.988	0.001 ***

Erigone dentipalpis	0.9958	0.9634	0.979	0.001 ***
Drassyllus pusillus	1.0000	0.9512	0.975	0.001 ***
Erigone atra	0.9947	0.9512	0.973	0.001 ***
Mermessus trilobatus	0.9821	0.9390	0.960	0.001 ***
Bathyphantes gracilis	0.9813	0.8780	0.928	0.001 ***
Xysticus kochi	1.0000	0.8415	0.917	0.001 ***
Agyneta rurestris	1.0000	0.8049	0.897	0.001 ***
Drassodes cupreus	0.9923	0.7683	0.873	0.002 **
Haplodrassus signifer	1.0000	0.7439	0.862	0.001 ***
Trochosa ruricola	1.0000	0.7439	0.862	0.004 **
Centromerita bicolor	1.0000	0.7317	0.855	0.003 **
Phlegra fasciata	1.0000	0.6829	0.826	0.004 **
Phrurolithus festivus	0.9887	0.5732	0.753	0.031 *
Group F + H + Hh + Npoorg				species : 1
	A	B	stat	p.value
Enoplognatha thoracica	0.9766	0.5278	0.718	0.035 *

5.2 Objective 2

The graph of the tbPCA including other parts of Flanders is presented in Figure 5.10. For the latter, colours similar to those used for Brugge are used.

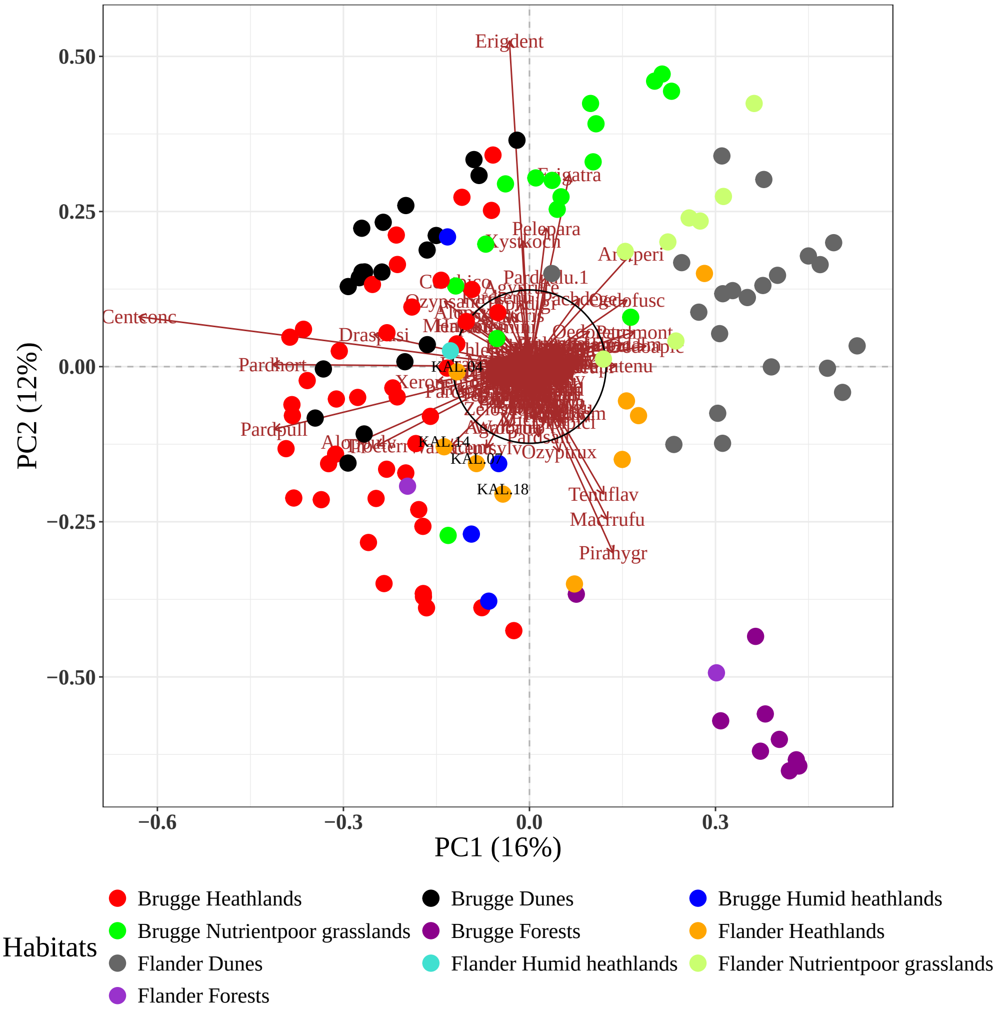
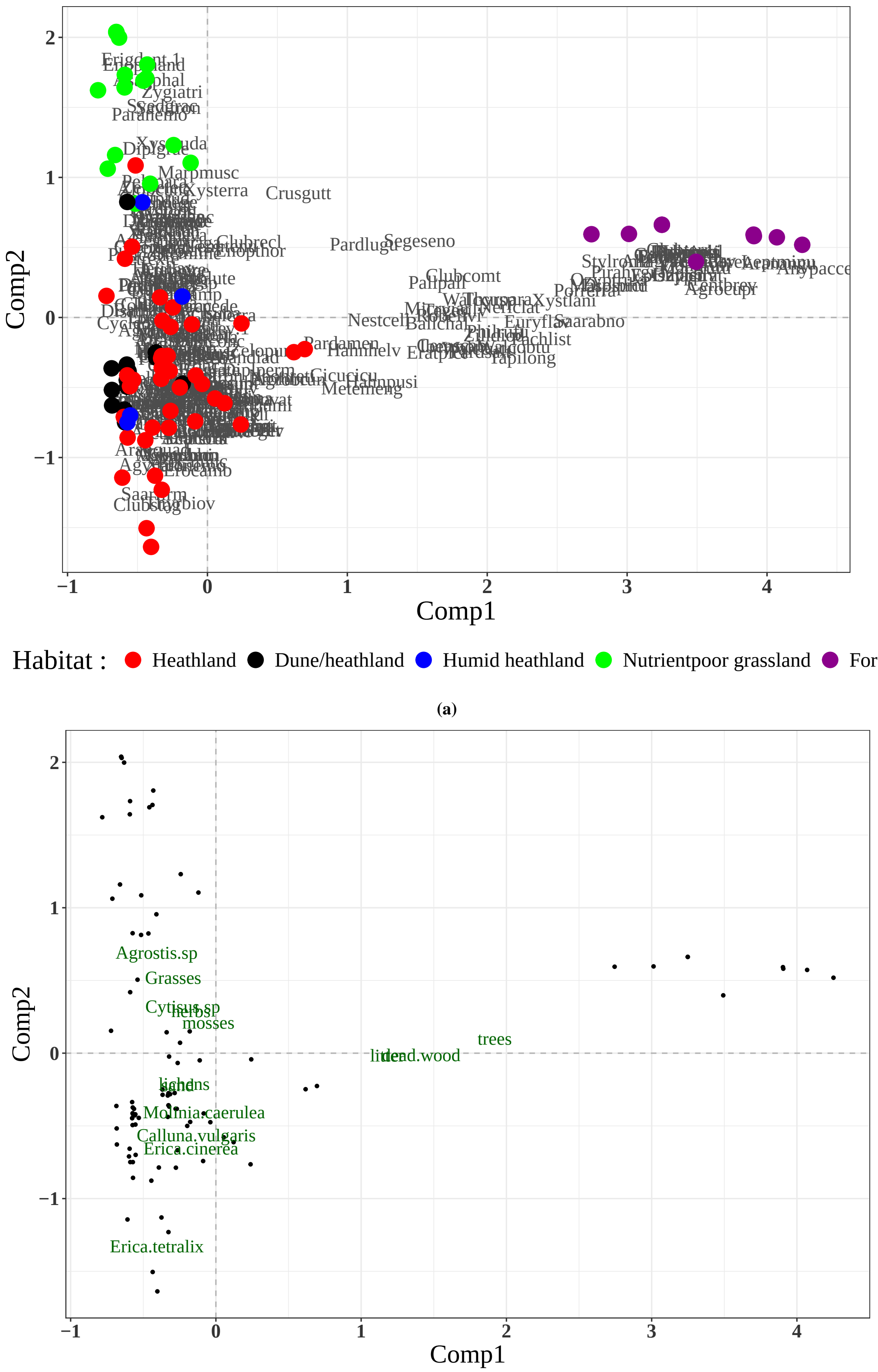


Figure 5.10: tbPCA ordination of the samples x species matrix including other parts of Flander. A principal component analysis (PCA) was conducted on species data that had been transformed using the Hellinger transformation. The figure is presented with the scaling 1 (i.e. the distances among sites are approximate representations of the Euclidean distance between them in multidimensional space). The first two axes account for 16% and 12% of the total variance respectively. The species name was abbreviated in accordance with the CEP standard, comprising the first four letters of the genus and the first four letters of the specific epithet. Labelled stations are heathlands from Kalmthout.

5.3 Objective 3

The CoCa graph is illustrated in Figure 5.11. The first two axes account for 19.76% of the variance in the spider data and 61.17% of the variance in the vegetation data. The four initial axes accumulate the highest cross-validated fit, with a value of 19.4%.



(a)

(b)

Figure 5.11: Asymmetric CoCA of spiders and vegetation structure. An asymmetric CoCA was performed on the data for spiders (a) and vegetation structure (b), with plants as predictors. The maximum fit peaked with four axes. The first two axes accounted for 19.76% of the variance in the spider data and 61.17% of the variance in the vegetation data.

The dbRDA plot is presented in Figure 5.12, while the significance of the model and the differences between the management modalities are detailed in Table 5.5. The proportion of variance explained by management is 22.92%. Of the total variance, the first axis accounts for 11.78%, while the second accounts for 5.12%.

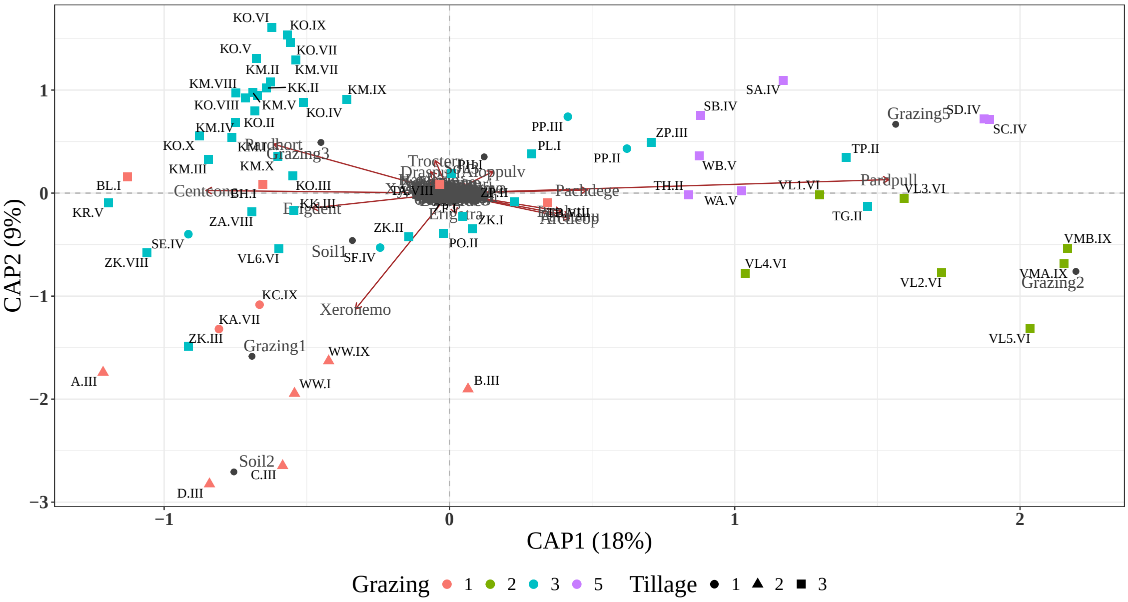


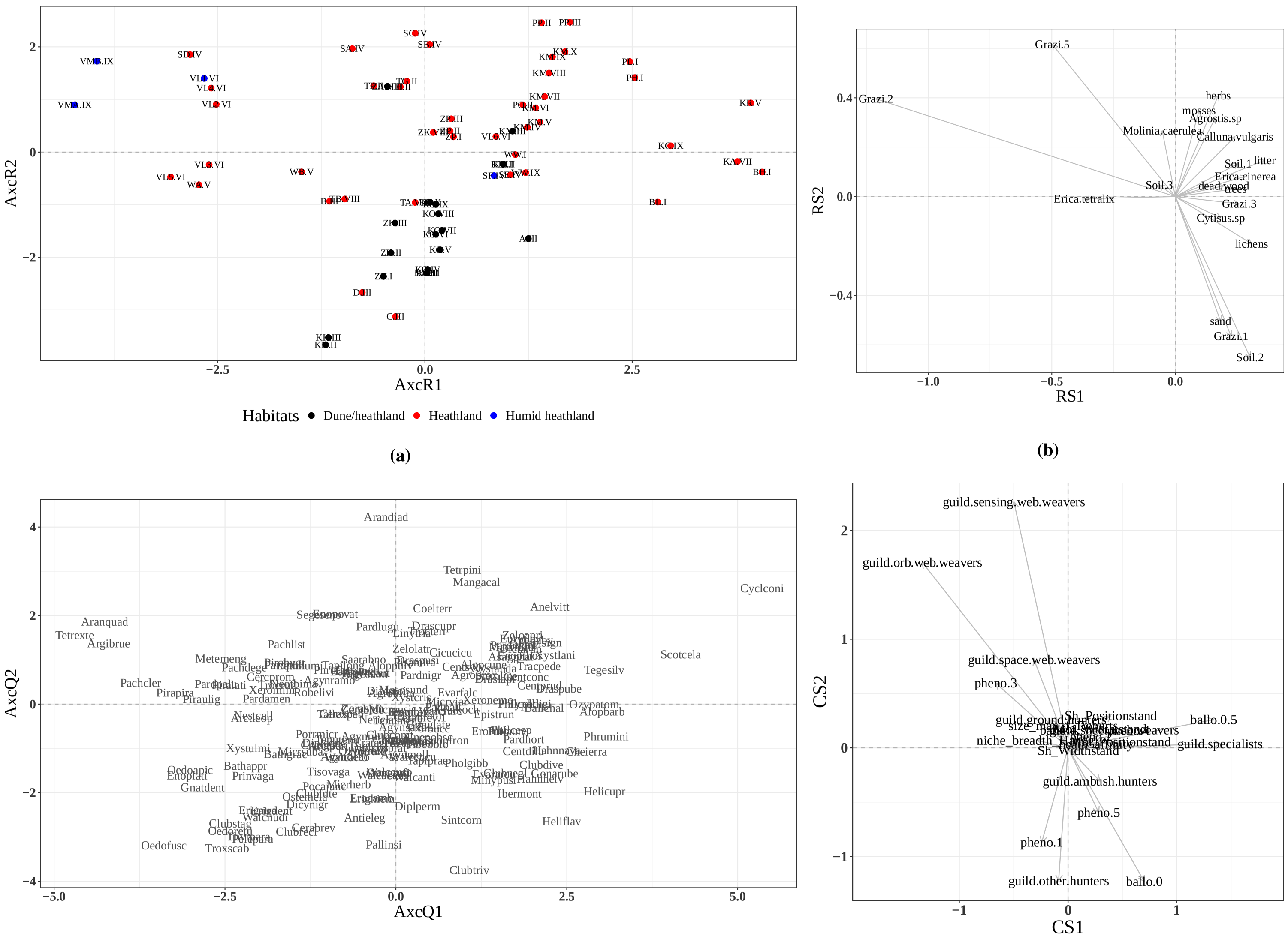
Figure 5.12: dbRDA of samples x species matrix constrained by management modalities. A redundancy analysis (RDA) was conducted on the Hellinger distance matrix of the species data. A Lingoes correction was implemented to prevent negative eigenvalues. Tillage methods: deforested but without topsoil removal (1), no topsoil removal (2), topsoil removal (3). Grazing : non-grazing (1), mowing (2), temporary grazing by sheep and permanent grazing by rabbits (3), Galloway grazing (4), permanent grazing by sheep and rabbits (5), temporary grazing by donkeys (6), grazing by donkeys and sheep (7)

Table 5.5: Summary of results of significance tests for differences between management methods. A permutational multivariate analysis of variance (PERMANOVA) was initially conducted to ascertain the significance of the differences between modalities. The interaction between Tillage and Grazing was not significant but each factor was. The differences between the modalities were evaluated through a pairwise multilevel comparison. Modalities for tillage are 1: cleared but without soil removal, 2: no soil removal, 3: soil removal. Modalities for grazing are 1: No grazing, 2: mowing management, 3: temporary grazing by sheep and always by rabbits, 4: Galloway grazing, 5: year-round grazing by sheep and rabbits, 6: temporary grazing donkeys, 7: grazing donkeys and sheep

	Test	Factor	Adjusted p-value
PERMANOVA	/	Tillage	0.001 ***
		Grazing	0.001 ***
		Tillage:Grazing	0.092
Tillage	Multilevel pairwise comparison	2 vs 3	0.006 *
		2 vs 1	0.128
		3 vs 1	0.182
Grazing	Multilevel pairwise comparison	1 vs 3	0.006*
		1 vs 5	0.006*
		1 vs 2	0.006*
		3 vs 5	0.006*
		3 vs 2	0.006*
		5 vs 2	0.010*

5.4 Objective 4

The results of the RLQ analysis is presented in Figures 5.13. The four graphs of the RLQ analysis should be interpreted in conjunction with one another. The first two axes of the RLQ account for 57.60% and 21.17% of the total variation, respectively. The correlation with the first axis is 0.32, while that with the second is 0.28. The variance is preserved to the extent of 78.77%. The proportion of variation preserved on the first two axes was 85.37% for vegetation structure and management practices, 64.12% for ecological characteristics and 56.79% for species abundances. The combined randtest adjusted p-value is 0.2695, indicating that the null hypothesis of the overall model (i.e., traits and environmental variables are not related) is not rejected. However, the null hypothesis of model 2 (species composition is independent of environmental variables) was (adjusted p-value: 0.0001). Among the traits, only shade position exhibited a correlation with the environmental variables according to the fourth corner analysis. Specifically, it was positively correlated with the amount of litter, cover of *C. vulgaris* and *E. cinerea*.



(a)

(b)

(c)

(d)

Figure 5.13: RLQ analysis of the heathlands complex. A correspondence analysis was conducted on the sites x species matrix. A Hill-Smith analysis weighted by CA scores was performed on the sites x env matrix and the species x ecological features matrix. The three resulting ordinations were then combined by RLQ analysis. The first two axes of the RLQ account for 57.60% and 21.17% of the total variation, respectively. The correlation with the first axis is 0.32, while that with the second is 0.28. The variance is preserved to the extent of 78.77%. The proportion of variation preserved on the first two axes was 85.37% for vegetation structure and management practices, 64.12% for ecological characteristics and 56.79% for species abundances.

5.5 Objective 5

The Brugge data set encompasses all five phenological classes. Figure 5.14 illustrates the data for three species. The evolution of their activity during monitoring at station KO is depicted in Figure 5.15. The projection of the traps on the tbPCA is illustrated in Figure 5.16.

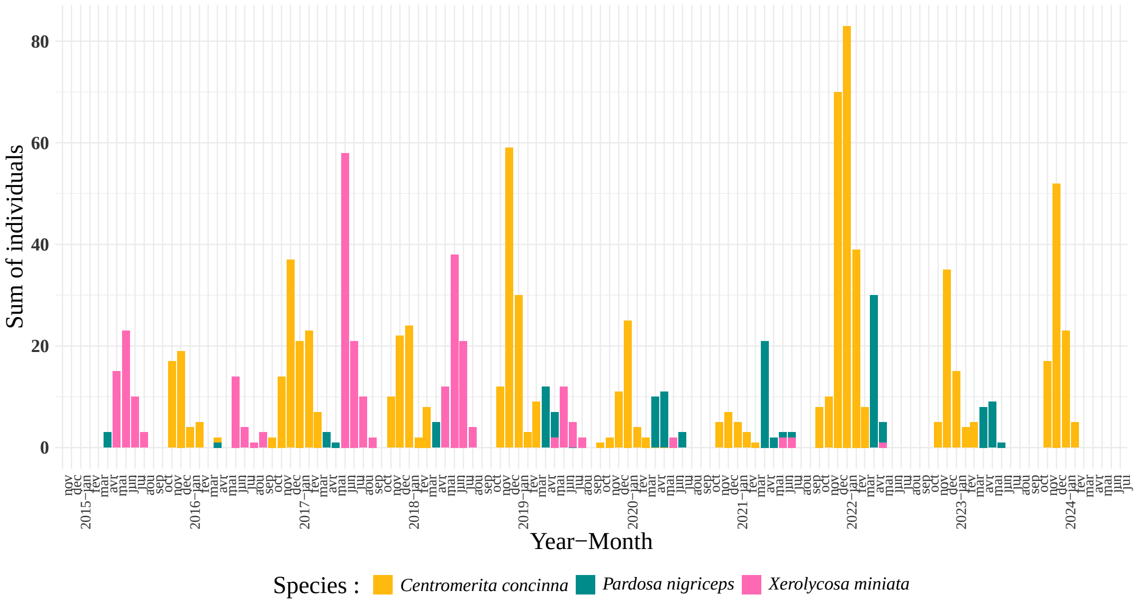
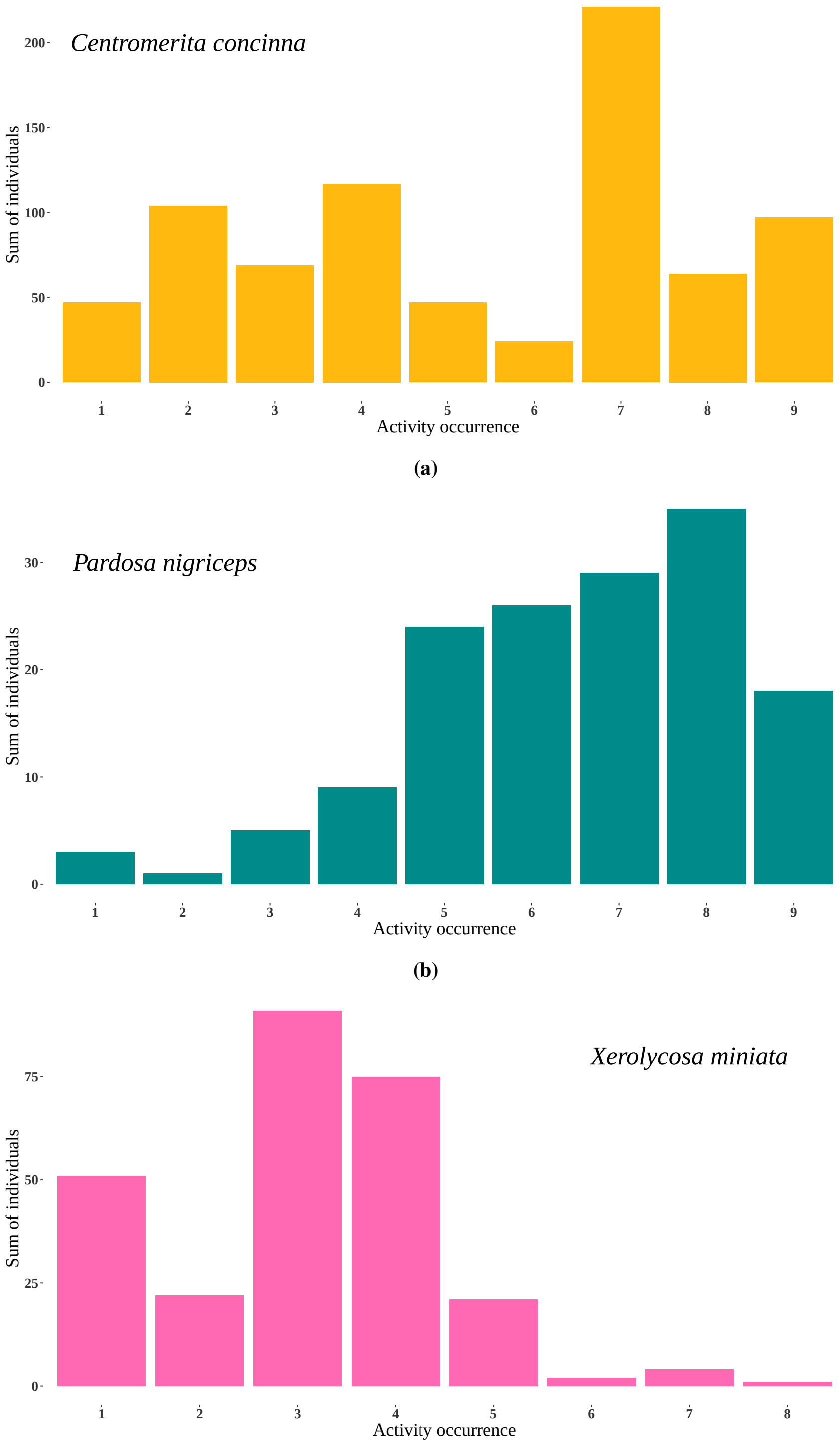


Figure 5.14: Evolution of month recordings for three species in the KO station. Monitoring began in 2015 and ended in 2024. The traps are left year-round, from April to April.



(a)

(b)

(c)

Figure 5.15: Evolution of activity of three species in KO station. Monitoring began in 2015 and ended in 2024. The traps are left year-round, from April to April. A period of activity corresponds to the number of consecutive months, or months separated by a maximum of two months, during which the species in question is caught. (a) *Centromerita concinna*, a primarily euryoecious, winter active species (last occurrence : 2023), (b) *Pardosa nigriceps*, a mainly euryoecious, early-summer active species with preference for high vegetation (last occurrence : 2024) and (c) *Xerolycosa miniata* a stenoecious, summer active species associated to open dry habitats with large patches of bare ground and coastal sand dunes (last occurrence : 2022).

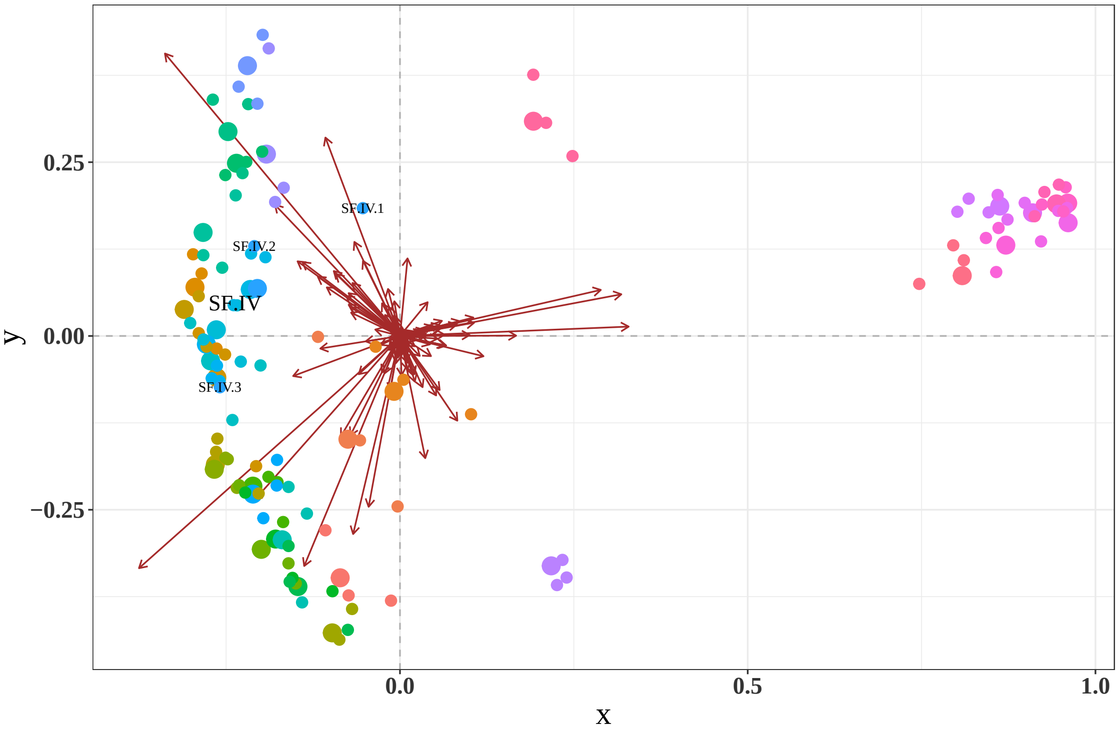


Figure 5.16: *Posthoc* projection of trap data onto tbPCA. The larger dots correspond to the pooled sample data, while the smaller dots of the same colour represent the corresponding trap data.

6. Discussion and perspectives

6.1 Limitations

Prior to an in-depth examination of the results, it is essential to highlight some limitations. The database is both large and of good quality, which can contribute to the robustness of the results. However, the sampling was not conducted with a pre-established design. The data set is imbalanced with regard to habitat types (e.g. 43 samples for Heathland and only 9 for Forest) and management practices. In a similar vein, the samples are not independent at several levels. Firstly, some sites were monitored for several consecutive years, while others were not. Additionally, there is a spatial correlation between the sampling sites. Although this does not preclude the execution of diversity analyses and ordinations, it does complicate the evaluation of statistical significance, as the majority of the conditions to apply common methods such as ANOVA are not met (independence, homoscedasticity, balance, etc.) and makes the formulation of models challenging. Therefore, it was decided to use permutation tests and linear mixed models. These methods have their own limitations and require particular care in the choice of parameters (character to be permuted, number of permutations, factor to be randomised, interactions between factors, etc.) (Bakker, 2024). Other techniques, such as non-linear mixed models or resampling, could have been considered. For the sake of clarity and ease of use, the formulation has been kept simple, however, this may not fully reflect the structure of the data and may have introduced bias.

Secondly, the ecological characteristics of the species are derived from various sources and describe the species in general. The values for the populations in the Brugge region may be slightly different. As previously pointed out by Duffey, 2005, the majority of species covered by Hänggi et al., 1995 appear to occupy a wide range of habitats. This may be due to regional variation in tolerance, which artificially broadens the extent of the niche. However, Bonte et al., 2003 demonstrated that the values derived from Hänggi et al., 1995 correlated with those obtained through the IndVal analysis in the case of Flemish coastal dunes. For the purposes of this work, the Hänggi values are deemed sufficient. For the other characteristics, care was taken to select data as close as possible to the context of Brugge. It is also important to stress that the exclusion of species with missing values, 45 in total, for the ecological characteristics is one choice among others. This represents almost 20% of the species of the heaths group, which is a significant proportion. Furthermore, some of the deleted species are rare and stenoecious, which would have provided valuable insight. Other options exist, such as imputation, i.e. calculating the missing values based on the values of the other objects. However, as well as introducing potential biases into the interpretation, in the case of ecological traits, imputation is tricky because it should ideally take phylogeny into account, although this is no guarantee of accuracy (de Bello et al., 2021).

In light of the aforementioned considerations, the results can be properly discussed. As a reminder, this work was divided into four objectives. The first was to isolate a spider community that is characteristic of the heath in the context of the Brugge region. The second was to situate the spider assemblages of Brugge within the broader context of the Flemish landscape. The third objective was to determine whether there is a correlation between vegetation structure and/or management practices and the composition of spider assemblages. The last two objectives were to identify the most effective management practices for the heathland spider community and to evaluate the monitoring.

6.2 Objective 1

In consideration of the PERMANOVA, the alpha and beta diversity analysis, it can be posited that, at least with regard to the subjective habitat categories, the sites classified as heathland are distinct from forests and nutrient-poor grasslands. For example, on the tbPCA plot (Figure 5.2) a clear and pronounced distinction is observed along the first axis, with forest samples positioned to the right and open habitats to the left. This can be interpreted as a shading gradient. The only sample that occupies an intermediate position between the forest and the heathland categories is KB.VII. This is the sole forest sample in which grazing is practiced (see infra), which allows for a more open structure of the vegetation in this case. Heneberg et al., 2023 demonstrated that grazing can facilitate the establishment of an epigeic spider community that is typical of open habitats and early succession stages within forests. On the second axis (whose interpretation is less clear), nutrientpoor grasslands can be distinguished from the complex formed by heathlands, humid heathlands and dunes/heathlands. Despite both being poor, open habitats, the composition of these categories differs. This finding is consistent with Lyons et al., 2018. There is greater overlap between heathlands and dunes/heathlands, but less when the forests are removed (and thus the main gradient). This overlap on the ordination plane (also evident on the third axis) may be attributed to the subjectivity and difficulty of distinguishing these categories in the field, primarily based on the presence and proportion of sand. However it seems more probable that the dunes/heathland are an initial stage of heath rather than a clearly delineated heath type or habitat. This is well illustrated by the KM and KO samples, the two principal time series. The early KM samples (I, II and III) are designated as dunes/heathlands, whereas the subsequent ones are classified as heathland. In contrast, the KO samples have consistently been in the dunes/heathlands. Nevertheless, both stations exhibit a similar pattern and are close on the ordination plane. Furthermore, on the tbPCA including samples from other regions of Flander, dunes are distinctly separated from the ‘Heathland + Dunes/heathland’ group. This finding is in accordance with Gajdoš et al., 2000b who found that dunes have a distinct community from that of grey dunes and heaths. In contrast, grey dunes, heaths and limestone grasslands have a comparable vegetation structure, as mentioned by Bonte et al., 2003. The category of dune/heathland requires thus redefinition. The following discussion will consider it as an initial stage of the heathland category. The case of humid heathlands is more complex, although in this instance it appears to be a distinct entity from heathland. The number of samples is relatively limited (n=4) with one sample, SF.IV, exhibiting notable heterogeneity (see infra).

Heathlands stand out in other aspects. A greater diversity of species is typically observed in this category, as seen on the accumulation curve (Figure 5.5, and extrapolated richness (Table 5.3 and Figure 5.6). In terms of regularity and dominance (Hill number

q=1 and q=2, Figure 5.7) of specific diversity, heathlands are again the richest, whether all species are considered equally or whether the emphasis is placed on the most abundant or dominant species. However, the differences are less pronounced in the latter case.
However, this finding needs to be nuanced, as it is not persistent over time, some older heathland communities are less rich (Figure 5.4). To illustrate, in the KM and KO time series, species richness initially increases over two years followed by a decline toward forest values, although year-on-year variation must be considered (decrease in year III and increase in year VIII). The shorter time series, such as ZP, also demonstrate a decrease in richness. In contrast, the oldest heaths (restored prior to KM and KO), such as TH, PL and PH are among the richest samples. The response of spider species richness to restoration is not uniform. Various patterns have been observed in the literature, depending on the context, the time step studied, etc. (for example, stability in Hacala et al., 2020 or an increase in Cristofoli et al., 2010). In general, species richness tends to increase with heterogeneity (Uetz, 1979). In the case of Brugge, the ageing and forest colonisation can reduce the variability of heathlands, which are characterised in their early stages by heterogeneity of cover. They feature large stretches of bare, sandy ground, which give the habitat a more complex structure with more niches likely to host different species. It should be remembered that spiders are more affected by vegetation structure than by plant species *per se* (Duffey, 1993), although the two can be interrelated (for instance, the clump structure of *Molinia caerulea* or the cushion structure of mosses). It is important to note, however, that even the oldest heaths, with more trees and a denser structure than the younger stages, have a species composition that differs not only from the younger stages but also from that of the forests. This may mean that the spider communities evolve as the heath ages, but that the tree cover needs to be more developed to shift to a ‘forest’ community. The absence of indicator species may be either attributed to the fact that communities evolve through the different stages. The labelling of samples in the dataset, irrespective of stage, introduces a bias in the IndVal analysis. Indeed, spider assemblages may vary according to subtle changes in succession in heaths (Platen, 2003; Haase et al., 2015). Moreover, when the tbPCA is conducted solely on the KM and KO time series, a clear demarcation is visible on the first axes, with the first samples on the left and the last ones on the right. Further investigation into this topic would be beneficial.
On the other hand, with regard to functional diversity (i.e. the composition, differences and repartition of traits across a community), heathland does not exhibit any particularly distinctive characteristics. The most notable differences are observed between forests and open habitats. However, in the case of heathlands, these indications of a diverse community must be contextualised, given that several stages are included, thus creating more niches. Functional diversity is not constant over time. The FRic of the KM station decreases while the FEve and FDiv increase, revealing a loss and homogenisation of characteristics over time. This may be due to the disappearance of the heterogeneity, observed in the early stages.

In terms of specific composition of the samples, the *Linyphiidae* family is the most prevalent, with particularly two species, *Centromerita concinna* (Thorell, 1875) and *Erigone dentipalpis* (Wider, 1834). Both exhibit a preference for open environments, with a slight inclination towards wet habitats in the case of *E. dentipalpis* (Entling et al., 2007). The other most abundant families are those typically captured in pitfall traps, such as the cursorial hunters *Gnaphosidae* and *Lycosidae*. (Duffey, 1972). The five most abundant species across the different categories are primarily wide-niche species (Figure: 5.9). Conversely, the presence of indicator species in the red list, which are mainly steneoecious, is a good conservation indicator. Their absence and the over-representation of euryèces and aeronaut species are a sign of poor habitat quality with a weak structure and faunal impoverishment whatever the habitat (Bonte et al., 2003; Buchholz, 2009; Toft et al., 2024).

6.3 Objective 2

As previously stated, the coastal dunes constitute a clearly distinct group. The shadow gradient persists, though its influence on the first axis is less pronounced. A series of ecological transitions can be observed. However, the intermediate habitats between heathland and forest and wetlands are absent. The dry heaths of Kalmthout are similar to those of Brugge. This can be explained by the analogous contexts, characterised by sandy terrain and under marine influence.

6.4 Objective 3

With respect to the third objective, it appears that species assemblages are influenced by vegetation structure, in accordance with the literature. The habitat categories align well with the expected structure. Forests are characterised by high tree cover, dead wood and a high level of litter, while grasses are more closely associated with meadows, *Calluna* and *Erica* with heaths. *E. tetralix*, a species associated with meso-hygrophilic heaths, is less prevalent in the dunes/heathlands. Concerning spiders, the indicator species are mainly concentrated around the stations corresponding to the respective habitat, although the indicator species for humid heathlands are more dispersed. There is a slight differentiation in the KM time series, much less in KO, but to a lesser extent than if only spiders were taken into account. This provides some support for the hypothesis that the change in spider assemblage for these series is due to changes in vegetation structure, but other factors are also at work. For example, annual weather conditions may also play a role, as spider activity is influenced by temperature (Entling et al., 2010).

The influence of management is also significant when only the heathland, dune/heathland and humid heathland complex is taken into account. The practice of temporary grazing by sheep is distinguished from that of permanent grazing and mowing, which can be conceptualised as an intensity gradient. The sites that have not been subject to grazing are mainly situated on axis 3 of the dbRDA.

6.5 Objective 4

The absence of indicator species isolated for heathland makes it challenging to define best management practices that favour them. However, both vegetation structure and management influence the species composition of heathlands complex. Notwithstanding that only the shading position is significantly related to vegetation structure (see fourth corner analysis), RLQ analysis is useful for identifying the mutual influences of ecological characteristics, vegetation structure and management practices. Moreover, the conditions associated with the presence of dune/heathland indicator species can be considered as characteristic of the initial heathland stages, whereas woodland indicator species are associated with the later stages of the succession. Similarly, the dbRDA provides additional information on the species favoured by management. In this perspective, a number of points can be raised.

Management is essential to prevent excessive overgrowth and to deplete nitrogen, as deposition is believed to be relatively high in the region (De Pue, 2019; European Environment Agency, 2021). The unmanaged stations are those located on the far right in the RLQ (Figure 5.13a). They display a high proportion of *Calluna* and *Erica* but also a greater tree cover and litter, a sign of advanced succession (see Figure 5.13b). Spiders in this area exhibit a higher shading preference. On the contrary, station with mowing have species characterised by a more expansive niche breadth and a heightened propensity for ballooning (Figure 5.13d), traits considered as more eurycoecious and whose increase is indicative of faunal impoverishment in heathlands (Toft et al., 2024; Bonte et al., 2003). It has been demonstrated that intensive mowing can reduce the growth of *Calluna* and promote those of graminoids in heaths, particularly when nitrogen deposition is high, (Barker et al., 2004; Kaae et al., 2024). Low-intensity mowing still represents a cost-effective alternative when grazing is not a viable option (Barker et al., 2004; Blindow et al., 2017). However, the maintenance of refuges and the implementation of rotation and various mowed areas are essential to minimise the impact on spiders (Cattin et al., 2003).

Conversely, heaths with grazing modality 3 (temporary by sheep and permanent by rabbits) are similar to unmanaged sites (see Figure 5.13a), but with a higher cover of herbs, mosses and *Agrostis sp.* It appears that the grazing pressure is insufficient to impede the growth of bushes and trees, while allowing the proliferation of grasses. In contrast, stations with the modality 5 (yearly by sheep and rabbits), which is slightly more intense in terms of temporal frequency than modality 3, are comparable to those with mowing. Intensive grazing can have similar detrimental effects as intensive mowing (Bell et al., 2001; Damgaard et al., 2013; Freiberg et al., 2019), although heathers may be more resilient to intensive grazing in the short term (Gallet et al., 2001). It is also important to consider the time of grazing, as summer grazing can favour certain brushes, with humid heathlands being more susceptible (Gallet et al., 2001). The reasonable intensity of grazing is commonly considered to be the removal of 40% of the year's growth, although this could be smaller, around 20% (Pakeman et al., 2009). In terms of grazing density for continuous management, the optimal range of units per hectare should be of 0.8 to 1.5 for sheep and for cattle <0.5 (Zerbe, 2023).

In literature, the best management strategy is a combination of low-intensity practices over the short term and high-intensity intervention over a longer time frame (Niemeyer et al., 2005; Krause et al., 2016; Blindow et al., 2017; Delescaille et al., 2022). Furthermore, as is frequently asserted in the field of conservation ecology (e.g. Stieperaere et al., 1983; Bonte et al., 2004; Pétillon et al., 2008; Schirmel et al., 2011; Diemont et al., 2013; Delescaille et al., 2022), a diverse landscape comprising a mosaic of habitats at different stages is important for preserving biodiversity and notably spiders. In addition, heathlands appear to harbour rare and very rare species, particularly during the early stages. The case of *Xerolycosa miniata* is illustrative. This xerophilous species, which is characteristic dry and bare habitats such as dune systems, seems to find a suitable habitat in young heathlands, but disappears as the cover closes in (see Figure 5.15c). In order to achieve the desired target of management (removal of grasses, rejuvenation of Calluna, productivity, etc.) it is essential to select species and race of grazers with care (Jáuregui et al., 2009; Osoro et al., 2015;

Blindow et al., 2017). The association of grazing species can increase heterogeneity (Rosa García et al., 2013). Additionally, material should be taken into account. In the context of Brugge, caution should be exercised when undertaking operations with machinery, given the sandy terrain and the potential for significant disruption to the relief (Blindow et al., 2017). Overall, in order to refine the study of the impact of management on the spider community, further details on management are required. However, a general methodology for using this taxonomic group as an indicator can be draw up (Figure 6.1).

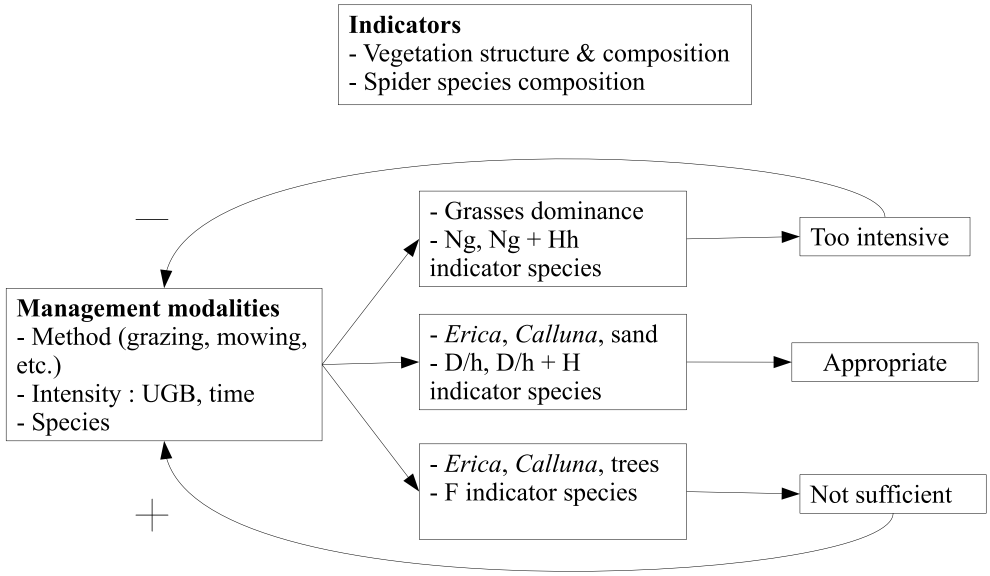


Figure 6.1: General management assessment procedure. The indicator spider species for the different categories can be used in conjunction with the vegetation structure to assess whether management is in line with the heather heathland conservation objective. An assemblage close to that found in grassland is indicative of over-intensive management, whereas a woodland assemblage reflects advanced succession. The presence of xerophilous species in conjunction with heathland vegetation is an indicator of heterogeneity and early stages of succession.

6.6 Objective 5

In regard to monitoring, the pooled data are largely consistent with the data obtained from individual traps. Of the 30 samples tested, some however, such as SF.IV, displays notable differences between the individual traps and the pooled data. In this station, the line of traps was placed perpendicular to the shoreline of a pond, resulting in each trap being subjected to different humidity conditions. In such a station, it is preferable to place the traps perpendicular to the gradient to avoid excessive heterogeneity.

With regard to year-round monitoring, all five phenological classes are represented in the samples. It is therefore difficult to isolate a single optimal sampling period, as reducing its duration would result in a loss of information. Diplochronous species in particular pose a problem for defining a shorter sampling period. Moreover, as (Duffey, 1972) points out, it is preferable to extend the sampling period rather than augment the number of traps. It is also crucial to consider phenology in the temporal analyses, as the graphical representation does not yield the same trends according to year, sampling period or activity period. For example, data on winter-active spiders are split between two sampling periods. To accurately estimate the evolution of species, it is preferable to group data by period of activity.

6.7 Perspectives

The three objectives were achieved, however, the analyses should be further refined. The primary limitation of the study is the unbalanced sampling of habitat categories. A more formal block design could be implemented. Differentiation between the different types of heathland is not easy and may be influenced by seasonal variation in the case of humid heathlands. It would be beneficial to define it more precisely. The different heathland stages should also be better characterised. Classification could be a useful approach to achieve this.

Further investigation could be conducted into additional factors that may contribute to the observed patterns of assemblages. For instance, weather conditions may play a role in explaining the observed changes, including the high diminution in year III and the increase in year VIII. The potential influence of distance to well-preserved heathland and landscape connectivity have not been explored due to a lack of data and time. However, given the importance of dispersal in ecological restoration, these factors warrant further investigation. From this perspective, the presence of the E40 motorway may exert an influence on the distribution of species. The impact of this type of infrastructure on habitat connectivity for spiders has been little studied but could prove to be significant (e.g. Knapp et al., 2013). Secondly, the measurement of functional traits *stricto sensu* should be ideal for carrying out functional diversity analyses and the RLQ-fourth corner method. However, this process is time-consuming, requiring the measurement of individual specimens or samples. Moreover, the ecological characteristics in question appear to provide sufficient information in and of themselves.

The present work focuses exclusively on pitfalls data. While this method of monitoring is straightforward and effective, it is not without certain limitations, as outlined in the literature review (subsection 2.2.3). Data from other methods could provide supplementary information, particularly for assessing management impact. For example, immobile Linyphiidae, which are favoured by intensive practices, are underestimated using pitfalls (Gibson et al., 1992). Furthermore, spiders represent only one component of the biocenosis and the interaction with other taxonomic groups have to be taken into account. While certain management practices may favour spiders, they may also have a detrimental impact on other taxonomic groups. An illustrative example is the Carabidae, which some species appear to be more mobile, with forest species moving to open habitats at night. This emphasises the importance of maintaining a mosaic of habitats. In this context, the reforestation projects around the city of Brugge raise a number of questions. While some, such as *Sint-Anne street*, are documented and their design appears to be consistent with the heterogeneity of the habitat, the situation is less clear for others due to a lack of available documentation. It is also noteworthy that the communities seem to undergo rapid evolution along the succession, with the early stages serving as refuges for some specialised and endangered species. But anthroposition is just as rapid, if not at a faster rate. It would be beneficial to update the red list of spiders in Flanders (and potentially create one for the entire Belgium?) as it can serve as a valuable resource, particularly when it incorporates ecological information.

7. Personal contribution

This work was conducted in collaboration with the entomological department of the RBINS. The subject was proposed by my co-supervisor, Wouter Dekoninck. The data concerning Brugge and Flander was provided to me by the RBINS. I identified the objectives and established the methodology with the advice of Wouter Dekoninck and Grégoire Noël. I searched the data for ecological features. I ran the analyses and interpreted the results. Additionally, I participated in the sampling campaign in Brugge this year, between April and July.

8. Conclusions

From a conservation perspective, the spider community of heathlands in the Brugge region are distinct from other habitats, such as forests and grasslands. It is even more diverse in some respects. Furthermore, they are comparable to the large heathland complex of Kalmthout. However, differentiation according to the stage is necessary, as the composition evolves along the succession. The primary determinant of the assemblages is vegetation structure. The management, by altering this, has the potential to influence the evolution or the maintenance of the community. The intensity, in terms of utilisation, space and time must be adapted accordingly. In addition, indicator species can serve as both a descriptor of habitat and a marker for management. The monitoring programme is robust, but annual monitoring is still required to ensure comprehensive coverage of the full diversity of assemblages. Care must be taken when setting traps in very heterogeneous environments. Overall, If the objective of conservation is to maximise diversity, it is of great interest and importance to preserve a mosaic of different habitats at various stages of succession. Nevertheless, further investigation of numerous aspects are needed to enhance the analyses.

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R packages used in this work

Package	Version	Citation
ade4	1.7.22	Chessel, Dufour, & Thioulouse (2004); Dray & Dufour (2007); Dray, Dufour, & Chessel (2007); Bougeard & Dray (2018); Thioulouse et al. (2018b)
adegraphics	1.0.21	Siberchicot et al. (2017); Thioulouse et al. (2018a)
adespatial	0.3.23	Guénard & Legendre (2022); Dray et al. (2023)
afex	1.3.0	Singmann et al. (2023)
aomisc	0.652	Onofri (2023)
ape	5.8	Paradis & Schliep (2019)
base	4.2.0	R Core Team (2022)
BiodiversityR	2.16.1	Kindt & Coe (2005)
cluster	2.1.6	Maechler et al. (2023)
cocorresp	0.4.4	Simpson (2024)
doBy	4.6.22	Højsgaard & Halekoh (2024)
FactoMineR	2.8	Lê, Josse, & Husson (2008)
fundiversity	1.1.1	Grenié & Gruson (2024a); Grenié & Gruson (2024b)
ggforce	0.4.2	Pedersen (2024)
ggpubr	0.6.0	Kassambara (2023)
ggrepel	0.9.5	Slowikowski (2024)
ggsci	3.0.3	Xiao (2024)
gplots	3.1.3	Warnes et al. (2022)
gridExtra	2.3	Auguie (2017)
gtools	3.9.5	Warnes et al. (2023)
htmlwidgets	1.6.1	Vaidyanathan et al. (2023)
indicspecies	1.7.12	De Caceres & Legendre (2009)
iNEXT	3.0.1	Chao et al. (2014); Hsieh, Ma, & Chao (2024)
labdsv	2.0.1	Roberts (2019)
lme4	1.1.35.5	Bates et al. (2015)
mFD	1.0.7	Magneville et al. (2022)
mgcv	1.8.40	S. N. Wood (2003); S. N. Wood (2004); S. N. Wood (2011); S. N. Wood et al. (2016); S. N. Wood (2017)
multcomp	1.4.25	Hothorn, Bretz, & Westfall (2008)
pairwiseAdonis	0.4.1	Martinez Arbizu (2017)
readODS	1.8.0	Schutten et al. (2023)
rgl	1.2.1	Murdoch & Adler (2023)
Rmisc	1.5.1	Hope (2022)
SoDA	1.0.6.1	Chambers (2020)
sp	2.1.4	E. J. Pebesma & Bivand (2005); R. S. Bivand, Pebesma, & Gomez-Rubio (2013)
spdep	1.2.8	R. S. Bivand, Pebesma, & Gómez-Rubio (2013); R. Bivand & Wong (2018); Roger Bivand (2022); E. Pebesma & Bivand (2023)
tidyverse	1.3.2	Wickham et al. (2019)
vegan	2.6.6.1	Oksanen et al. (2024)
vegan3d	1.3.0	Oksanen, Kindt, & Simpson (2024)

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