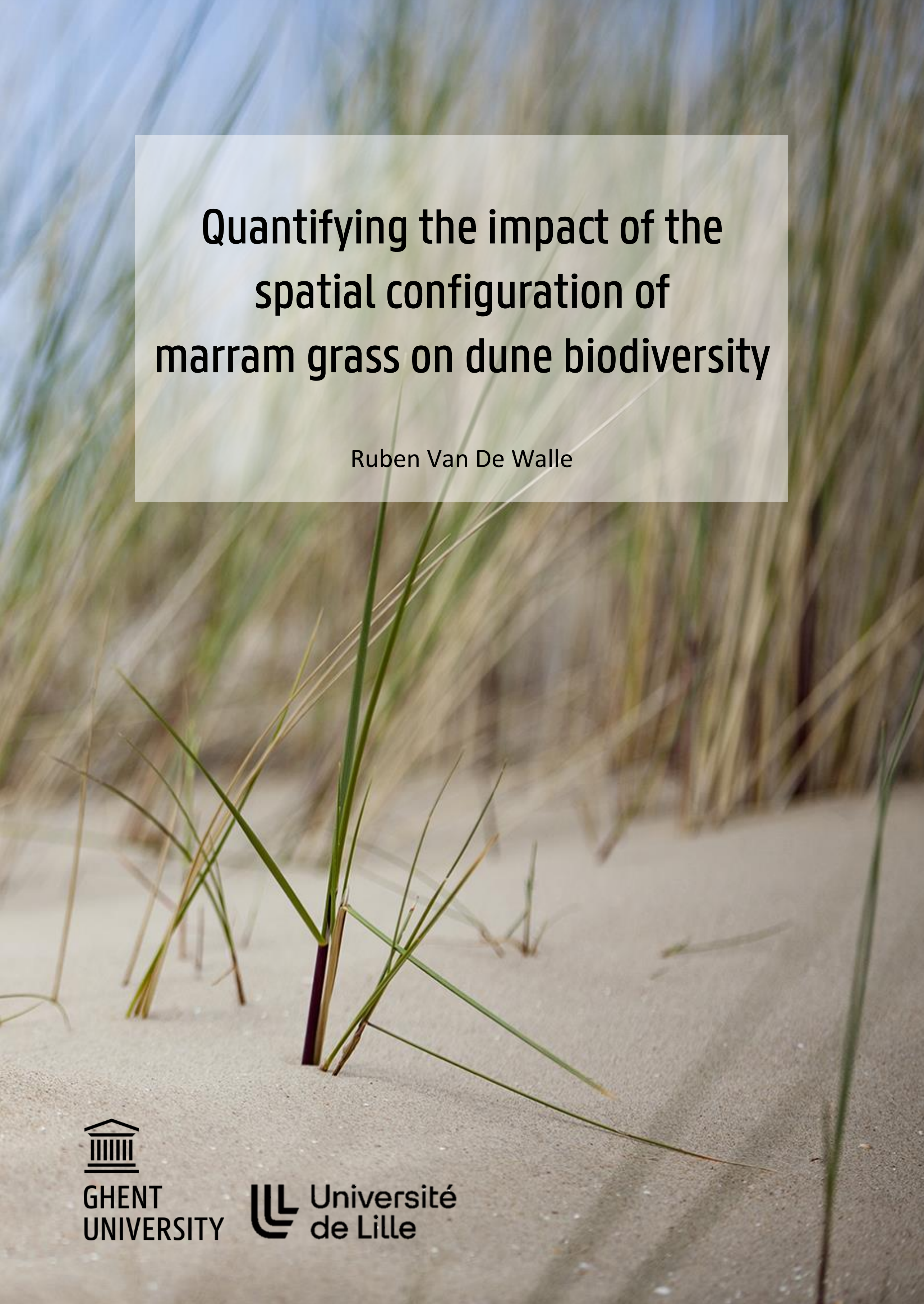

Quantifying the impact of the spatial configuration of marram grass on dune biodiversity

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Quantifying the impact of the spatial configuration of marram grass on dune biodiversity

Quantifier l'impact de la configuration spatiale de l'oyat sur la biodiversité des dunes

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Table of Contents

1. General introduction 5

1.1 Importance of vegetation for coastal protection 5

1.2 The Ammophila problem 8

1.3 Invasive coastal vegetation 9

1.4 Coastal dune ecosystems in Europe 12

1.5 Biodiversity theory in a coastal setting 14

1.6 Biotic interactions shape biodiversity 16

1.7 The ENDURE project 18

1.8 Objectives and outline of the thesis 21

2. The distribution and impact of an invasive plant species (*Senecio inaequidens*) on a dune building engineer (*Calamagrostis arenaria*) 23

2.1 Abstract 24

2.2 Introduction 25

2.3 Material & Methods 28

2.4 Results 34

2.5 Discussion 37

2.6 Supplementary material 42

3. The functional composition of dune nematode communities is structured by both biogeographic region and the local marram grass environment...... 49

3.1 Abstract 50

3.2 Introduction 51

3.3 Material & Methods 54

3.4 Results 57

3.5 Discussion 61

4. Plant-associated invertebrate communities in coastal dunes are more related to regional than to local environmental factors 66

4.1 Abstract 67

  4.2 Introduction ... 68
  4.3 Material & Methods ... 71
  4.4 Results ... 75
  4.5 Discussion ... 81
  4.6 Supplementary Materials ... 86
5. Arthropod food webs predicted from body size ratios are improved by incorporating prey defensive properties ... 94
  5.1 Abstract ... 95
  5.2 Introduction ... 96
  5.3 Material & Methods ... 99
  5.4 Results ... 104
  5.5 Discussion ... 109
  5.6 Supplementary material ... 113
6. General discussion ... 123
  6.1 Overview of main conclusions ... 123
  6.2 Plant-mediated interactions ... 124
  6.3 Implications for conservation ... 126
  6.4 Implications for coastal protection ... 129
  6.5 Perspectives and opportunities ... 131
  6.6 Conclusion ... 133
Summary ... 134
Samenvatting ... 137
Résumé ... 140
Acknowledgements ... 143
Curriculum Vitae ... 147
References ... 149

1. General introduction

1.1 Importance of vegetation for coastal protection

The consequences of climate change and global warming are ubiquitous and affect people all around the world. Regardless of the climate change scenario, more than half a billion people worldwide are expected to be affected by increased coastal risk due to rising sea level and increased frequency of extreme storm events by 2050 (Chaplin-Kramer et al. 2019). Building hard defence structures such as sea walls, dikes and groins is historically used to mitigate coastal flood risk. However, these have as drawbacks that they are costly to maintain and need be restored after sustaining damage. Costs will further increase in the future because hard infrastructures need to be heightened in order to keep up with the rising sea level, especially under a business as usual scenario (Sutherland and Gouldby 2003, Temmerman et al. 2013). A final drawback of using hard defence structures is the possibility for multiple adverse effects such as accelerated erosion or alteration of natural sediment transport (Gittman et al. 2015, Gracia et al. 2018). This could potentially exacerbate the erosion of sandy coastlines due to the rising sea level, consequently enhancing, rather than mitigating, flood risk (Hanley et al. 2014, Vousdoukas et al. 2018, 2020). Costly beach nourishments are frequently used as a countermeasure for coastal erosion. These have to be maintained as well every few years, depending on the local conditions and the amount of sand used during the nourishments (Hanley et al. 2014, Devriese et al. 2018, Singhvi et al. 2022).

Another way of protecting coastal regions from the sea, is by making use of the natural protection provided by the fauna and flora already present in coastal areas, such as wetlands or biogenic reefs (Barbier et al. 2011, Duarte et al. 2013, Gracia et al. 2018). For example, organic structures formed by coral reefs and mussel beds reduce wave energy and dampen the impact of the waves before they hit the shore. Coastal vegetation growing in mangroves, salt marshes or foredunes captures sediment transported by waves or wind, gradually building up the land at the sea-land interface to naturally protect the lower laying hinterland (Barbier et al. 2008, Borsje et al. 2011, Duarte et al. 2013, Gracia et al. 2018, Bonte et al. 2021). The potential integration of natural ecosystems into coastal protection for their protective capabilities can be considered a “Nature-based solution” (Borsje et al. 2011, European Commission 2015, Singhvi et al. 2022). Nature-based solutions are defined by the European Commission as “the use of features and complex system processes of nature, such as its ability to store carbon and regulate water flow, in order to achieve desired outcomes, such as reduced disaster risk, improved human well-being and socially inclusive green growth” (European Commission 2015). In general, nature-based solutions have received considerably increased attention from both researchers and policy makers during the last decade (Singhvi et al. 2022) because they offer many additional benefits and are multifunctional. For instance, additional to increasing flood protection, coastal dunes increase biodiversity, are beneficial for tourism, help with water regulation, are more resilient to erosion (compared to hard infrastructure) and consequently less costly in maintenance (Heslenfeld et al. 2004, European Commission 2015, Van der Biest et al. 2017, Gracia et al. 2018).

Coastal sand dunes, more specifically foredunes, represent the most important natural flood barriers along coastlines worldwide (Martínez and Psuty 2004, Bonte et al. 2021). These foredunes are only one habitat type within the collective term of "coastal dunes", which includes multiple habitat types that gradually succeed each other, driving the process of dune formation (Provoost and Bonte 2004, Maun 2009). On the Belgian coast, these transitional habitat types between land and sea follow each other in a succession away from the coastline, forming the coastal vegetation zonation (Fig. 1.1). From coast to inland, these vegetation types are shadow and embryonic dunes, blond dunes, grey dunes, dune grasslands and dune slacks, dune shrubs and dune forests. This elegant succession of vegetation types is mainly driven by salt stress, decalcification and the interplay between aeolian sand dynamics and the current vegetation (Kulmatiski et al. 2008, Brown et al. 2018). Shadow dunes are the first dunes formed on the bare beach, mainly consisting out of organic material, such as driftwood or ephemeral plants, which captures little sand (Maun 2009). These dunes do not survive long because they cease to exist when the organic material is broken down or completely covered by sand. Nevertheless, they facilitate the establishment of the next successional stage: embryo dunes. Embryo dunes form around perennial plant species such as sand couch grass (*Elytrigia juncea* subsp. *boreoatlantica*) that root within shadow dunes and make use of the locally elevated nutrients to grow (Provoost and Bonte 2004). Embryo dunes capture more sand as they grow until eventually salt stress is lowered by the formation of a fresh water lens. It is at this point that European marram grass (hereafter marram grass; *Calamagrostis arenaria* (L.) Roth, formerly known as *Ammophila arenaria* (L.) Link) is able to colonize the dune and from then onwards, dune growth is drastically increased (Huiskes 1979, Provoost and Bonte 2004). It is here, in these marram dunes, also known as blond dunes or foredunes, that my thesis work is situated.

***Figure 1.1** A schematic representation of the coastal vegetation succession. The illustrated species are chosen because they are characteristic for the vegetation type. From the coast to the land we see: Shadow dunes, represented by prickly saltwort (*Salsola kali*) and Sea Rocket (*Cakile maritima*). Embryo dunes represented by sand couch grass (*Elytrigia juncea subsp. Boreoatlantica*). Marram dunes represented by marram grass (*Calamagrostis arenaria*). Narrow-leaved ragwort (*Senecio inaequidens*) is found in both marram dunes and grey dunes, while the latter is represented by dune pansy (*Viola tricolor subsp. Curtisii*).*

My research focussed specifically on marram grass because it is considered an ecosystem engineer due to its capacity to stabilize sand. Marram grass owes this capacity to its capability to withstand burial rates of up to one meter per year (Huiskes 1979, Bonte et al. 2021), enabling dunes to grow like no other vegetation does. As a result of this high capacity for sand stabilization, marram grass was and still is frequently used for artificial dune building purposes (van der Putten and Kloosterman 1991, Weeda et al. 1991, HHNK 2020), although knowledge on several aspects of dune ecology and functioning is still missing. For instance, marram grass is still mainly planted in a regular, grid-like pattern, yet, little is known about dunes with regular spatial configurations, since marram grass mainly grows clustered under natural conditions (Bonte et al. 2021, Reijers et al. 2021). Furthermore, marram grass was shown to adapt its growth pattern to local sand conditions (Reijers et al. 2021) and sand-trapping efficiency seemed higher for patchy plant configurations (Reijers et al. 2019a). Due to these new insights and the increasing interest in nature-based solutions, pilot studies are recently being implemented to better understand the relationship between dune growth and the spatial configuration of vegetation (e.g. Derijckere et al. 2022). However, the effect of plant spatial configuration on dune biodiversity still remains understudied.

1.2 The Ammophila problem

The succession in foredune vegetation is associated with the gradient in sand dynamics from the sea to the hinterland, with, in general, less dynamic conditions found in more developed dune habitats, as explained in the previous section. Marram grass grows optimally under relatively high sand dynamics and is replaced by other plant species when sand dynamics decrease (van der Putten et al. 1993, Nolet et al. 2018). The decline in marram grass performance resulting from the cessation of sand dynamics is referred to as the ‘Ammophila problem’ (Marshall 1965). Added nutrients or the creation of an enemy-free space were the main two hypotheses for the observed phenomenon, with the latter receiving much more scientific attention than the former (Vandegehuchte 2010). So did the first growth experiments prove the soil community to negatively influence marram grass performance. This was done by contrasting the performance of marram grass grown on unsterilized sand originating from its rhizosphere with marram grass grown on sterilized rhizosphere sand or sand from the sea floor (van der Putten et al. 1988, van der Putten and Troelstra 1990). Enhanced plant growth after the use of selective nematicides pointed towards nematodes as the main cause of this detrimental effect (Van der Stoel et al. 2002), with species identity of the root-feeding nematodes and competition among them altering the decline in marram grass performance (Brinkman et al. 2005a). The need for exceptionally high nematode numbers under laboratory conditions (De Rooij-Van Der Goes 1995) and experiments in a more natural setting (Brinkman et al. 2005b) implied other soil biota, such as fungi, to be more involved in the whole process than previously thought. Interactions between root-feeding nematodes and other soil biota made everything even more complex. So were arbuscular mycorrhizal fungi shown to protect marram grass roots against nematodes (De La Peña et al. 2006) while bacteria and fungi attacked root-feeding nematodes and even deterred them from colonizing marram grass roots in the first place (Piśkiewicz et al. 2009a, 2009b).

Although already much is known about nematodes in the rhizosphere of marram grass, until now, research was done either via growth experiments with a limited amount of interacting soil species or by using point measurements from field surveys. These methods did not allow investigation of spatial effects, even though van der Putten et al. (1993) already mentioned that the spatial development of the soil-borne net negative effect needed further investigation. Understanding these spatial effects will be especially important in the nature-based solutions framework because it could enable the construction of foredunes that experience minimal negative effects of soil biota. The spatial structuring of nematode communities can further be of interest for pest control, to better predict population dynamics, or to other scientific areas such as invasion biology in order to understand the resulting influence on plant-plant interactions.

1.3 Invasive coastal vegetation

How and when species can be defined as "invasive" is a temporary debate that is still ongoing (e.g., Ricciardi and Cohen 2007, Cassini 2020, Mattingly et al. 2020). In this thesis, I follow the definitions *sensu* Richardson (2000), meaning that non-native species are labelled "invasive" when they are able to spread to other sites distant from the initial introduction after achieving viable population sizes (i.e., "naturalization"; Richardson et al. 2000). This definition decouples the invasiveness (i.e., establishment success) of non-native species and their impact on local biodiversity. This approach allows a more clear estimation of invasiveness, since the impact on local biodiversity can be estimated in a lot of different ways (Bartz and Kowarik 2019) and, additionally, because there is no clear link between them (Ricciardi and Cohen 2007). Nevertheless, invasive species can threaten biodiversity during their invasion process by affecting establishment or growth of native plant species or by changing local faunal communities (Vilà et al. 2011, Pyšek et al. 2012, Ricciardi et al. 2013, Litt et al. 2014). For instance, *Carpobrotus* sp., a well-documented invasive species in Mediterranean dunes, is known to influence soil parameters, consequently hindering local plant growth (de la Peña et al. 2010). It is additionally shown to alter invertebrate herbivore species composition (Rodríguez et al. 2021). Extensive changes in biodiversity induced by invasive species can resonate through ecosystems, drastically changing their provided services (e.g. Walsh et al. 2016). Therefore, it is important to try to predict where invasive species can establish and what the possible consequences can be, especially for ecosystems that provide critical services to society such as the coastal protection provided by dune areas (Duarte et al. 2013, Temmerman et al. 2013, Van der Biest et al. 2017).

As established previously, coastal dunes are characterized by water scarcity, salinity and sand burial. These harsh environmental conditions make dunes no benign environment for the establishment and growth of non-native plant species. Nonetheless, coastal dune habitats in general accommodate considerable amounts of invasive species and they are considered to be among the most invaded European terrestrial habitats (Chytrý et al. 2008, Giulio et al. 2020). In Western Europe, the high pressure of non-native species in coastal dunes is twofold: non-native species either escaped from ornamental gardens or were intentionally planted to lower aeolian sand dynamics for dune stabilization purposes (Weeda 2010, Campoy et al. 2018, Adriaens et al. 2019). Invasive species in coastal dunes are mainly generalist species occurring in a wide variety of habitats in their native range (Giulio et al. 2020). They rely on their good colonizing capacity to rapidly grow in suitable areas rather than developing mechanisms that enable them to cope with chronic environmental stress or biotic competition. Suitable areas can be open patches created by human-made or natural disturbances, or patches with locally lowered environmental stress. Again using *Carpobrotus* sp. as an example, it is shown to occur more frequently at intermediate distances from the shoreline where conditions are milder (Bazzichetto et al. 2018).

Another plant species recently invading coastal dune areas is narrow-leaved ragwort (*Senecio inaequidens* D.C., Asteraceae, also known as South African ragwort). It arrived in Europe from South Africa via wool transport and was first recorded in Hannover and Bremen (Germany) in 1889 and 1896 respectively, while it first occurred in Belgium in 1922 (Ernst 1998, Lachmuth et al. 2010). After naturalizing at multiple introduction sites, its expansion started from 1950 onwards and was facilitated in urban areas throughout Europe by man-made landscape elements, like harbours or railway lines (Ernst 1998, López-García and Maillet 2005, Lachmuth et al. 2010). In a more natural setting, *S. inaequidens* is able to migrate along river banks (e.g., its migration into the Netherlands along the Meuse; Ernst 1998). It was first found in dune areas in 1935 (López-García and Maillet, 2005), where its spread could potentially be facilitated by wind (Ernst 1998).

S. inaequidens occurs in its native range as both polyploid and diploid, while only the polyploid cytotype is found in Europe (Lafuma et al. 2003). The invasive polyploid was shown to produce more flower heads than its native diploid (Thébault et al. 2011), consequently increasing propagule pressure in the case of a single colonisation. A large plant was estimated to be able to produce up to 29 000 seeds when pollinated. Self-fertility was initially thought to further enhance propagule pressure (Ernst 1998), but the effect was only minimal since the species seemed to be geitonogamous rather than autogamous (i.e., pollen from the same plant from another flower, but not from the same flower, is able to fertilize the stamen; López-García and Maillet 2005). Propagule pressure is further exacerbated by the establishment of a new generation in the same year due to low dormancy of early summer achenes, while late summer achenes have higher dormancy to enhance winter survival (Ernst 1998). Nevertheless, herbivory by snails was found to decrease propagule production (Scherber et al. 2003).

Apart from snails, only a handful of other small invertebrates such as aphids or beetles are known to feed on *S. inaequidens* (Witte et al. 1990, Scherber et al. 2003). For livestock it is mainly unpalatable or even toxic (Dimande et al. 2007, Gottschalk et al. 2015). If it is eaten by larger animals (rabbits), then only young shoots get eaten and regrowth is left untouched, probably due to changes in plant chemistry (Scherber et al. 2003). More specifically, the low palatability of this and closely related species is mainly attributed to pyrrolizidine alkaloids (PAs; Caño et al., 2009; Macel et al., 2014; Scherber et al., 2003), chemical compounds characteristic for *Senecio* species (Witte et al. 1990, Joshi and Vrieling 2005). They are used as a defence mechanism against both above- and belowground herbivory (Joshi and Vrieling 2005; Caño et al. 2009; Thoden et al. 2009; Joosten and Van Veen 2011).

Out of Europe, marram grass itself is, ironically enough, considered an invasive species on a lot of sandy coasts in, among others, North America, South-Africa and New Zealand (Wiedemann and Pickart 1996, Beckstead and Parker 2003, Knevel et al. 2004, Hilton et al. 2005). It was initially planted in the introduced areas in the 19th and 20th century for sand stabilization purposes, but quickly spread along the coast, outcompeting and displacing native plant species (Hilton et al. 2005), although its invasiveness seemed to depend on the local species composition (Knevel et al. 2004). This provides the unique opportunity to study marram grass growth and performance outside its native range and try to pinpoint drivers of its enhanced competitive ability. Marram grass forms such a dominant threat to native species in its introduced range, that eradication programs have been installed (e.g., Wiedemann and Pickart 1996, Konlechner et al. 2014). The invasive success of this species is mainly driven by its capacity to withstand high sand burial compared to other species (Wiedemann and Pickart 1996, Hilton et al. 2005) in combination with a high dispersal capacity, facilitated through transportation of the rhizomes via sea water and consecutive sprouting of said rhizomes (Baye 1990, De la Peña et al. 2011, Hilton and Konlechner 2011). Additionally, it is thought to benefit from a reduction in (specialised) herbivores in its introduced compared to its native range (van der Putten et al. 2005), a phenomenon known in ecology as the Enemy Release Hypothesis (ERH; Keane and Crawley 2002). Indeed, Beckstead and Parker (2003) did not find pathogenic nematodes in sand gathered in California. Nevertheless, reduction in marram grass performance by the soil community as a whole remained almost identical, thus only partly confirming the ERH. Release of aboveground herbivore species was additionally proposed as a viable explanation (Vandegehuchte et al. 2012).

If marram grass is such a highly invasive species outside its native range, should we even be worried about other plants invading its native range? Assuming there is enough aeolian sand transport in order to enable marram grass to evade its pathogenic soil community while burying competitors, it should probably be able to outcompete most species. Nevertheless, some invasive plant species are known to decrease marram grass performance (de la Peña et al. 2010). Coastal sandy areas are being squeezed by the continuing need of urbanization of coastlines, especially in Europe (Bonte et al. 2021, IPCC 2022). Due to these shrinking sandy areas and increasing sand stabilization, sand supply could drop drastically, consequently facilitating invasive species establishment. Marram grass itself could possibly also facilitate invasion by locally lowering sand dynamics, as is shown for other ecosystem engineering species (Uyà et al. 2020). Where invasive species will establish in coastal dunes is a relevant question because is somewhat paradoxically. On the one hand, dynamic dunes with more open sand patches form an ideal situation with less competition from other plant species. On the other hand, environmental stress in the form of sand dynamics is higher in those dunes, while it is lowered in more stabilized dunes with more vegetation cover. Establishment of invasive plant species in foredunes will thus depend on their ability to either withstand high environmental stress or to outcompete native species.

1.4 Coastal dune ecosystems in Europe

Next to sea level rise, climate change has many other negative consequences. In combination with human-induced changes such as land-use change and facilitation of invasive species spread, it is thought to cause species extinction on a scale only observed a few times in history, prompting scientists to describe it as "the sixth mass extinction in the era of the Anthropocene" (e.g., Bellard et al. 2012, Ceballos et al. 2015, Wagner et al. 2021). Less notable species, such as nematodes or insects, seem to be going extinct faster than they can be described by science. Keeping in mind that a lot of those species are crucial for important ecosystem functions such as pollination, biological control and nutrient cycling (Wagner et al. 2021, Potapov et al. 2022), conservation of biodiversity should be at the top of our priority list. Since beneficial conservation measures for one species could be harmful for others, understanding the ecological mechanisms and complex process shaping biodiversity in a natural environment is crucial in order to conserve biodiversity in the most optimal way.

Even though the required climate conditions are buffered by the sea (see further), coastal habitats are still limited in their range relative to other terrestrial habitats because they can, by definition, only occur in close proximity to the sea. This inherent spatial limitation in combination with the substantial urbanization of coastal areas in Europe over the past 150 years (Provoost and Van Landuyt 2001, Heslenfeld et al. 2004) caused coastal habitats to be relatively rare in overall land cover. Specialist species relying solely upon these areas for their survival are, by extension, also quite rare (Provoost and Bonte 2004). Additional to specialist species, many generalist species can also be found in dune areas, making them biodiversity hot spots (Heslenfeld et al. 2004, Provoost et al. 2020). Because of this high ecological value, coastal dune nature reserves in Belgium and Europe are thoroughly monitored, managed and protected (e.g., Martínez and Psuty 2004, Provoost and Bonte 2004, Provoost et al. 2020).

Within Europe, coastal habitats are mainly protected via the Convention on the Conservation of European Wildlife and Natural Habitats, or the Bern convention, and the Habitat directive. In 1979, the Council of Europe adopted the Bern convention to protect the European biodiversity and to promote co-operation between countries. It is currently signed by more than 50 countries both inside and outside the EU (Council of Europe 2023). The EU implementation of the 'Bird Directive' (1979) and the 'Habitat Directive' (1992) resulted from this convention (and earlier ones such as the Bonn- and Ramsar convention). This way, several types of sand dunes are protected by EU policy under either the 'Habitat Directive' as natural habitat (e.g., Shifting dunes with *Ammophila arenaria*) or because of the presence of a priority species. If the priority species concerns an endangered European bird, the dune area is protected under the 'Bird Directive' (Heslenfeld et al. 2004, Decleer 2007). Both directives allow for the implementation of sanctions and are thus more enforceable than earlier signed conventions (Decleer 2007). The ecological Natura 2000 network originated from these two directives and protects special areas of conservation. It is the largest coordinated network of protected areas worldwide and spans several dune areas (Heslenfeld et al. 2004, Decleer 2007). Marram dunes are classified within the Natura 2000 framework as habitat 2120. Another frequently used classification of habitat types is CORINE ("Coordination of information on the environment"), where marram dunes are classified as biotope 16.21 (Decleer 2007). Additionally, national policies can further bolster the protection of coastal areas. For instance, In Belgium in 1993 "the Dune decree" (NL.: het Duinendecreet) was approved in an effort to stop and reverse the urbanization of the already fragmented coastal dunes ecosystems (Defoort 1995).

The different dune vegetation types introduced in section 1.1 harbour different species compositions (Provoost and Bonte 2004). Most studies linking coastal vegetation with faunal species richness investigated the effects of the vegetation zonation perpendicular to the shore on species richness (McLachlan 1991). The species community found within marram dunes specifically is relatively small because of the earlier highlighted environmental stress due to salt spray, temperature variability and wind and sand dynamics (McLachlan 1991, Kulmatiski et al. 2008, Brown et al. 2018). Consequently, most larger terrestrial vertebrate species are mainly observed passing through, breeding or foraging (McLachlan 1991, Provoost and Bonte 2004); with natterjack toads (*Epidalea calamita*) and European rabbits (*Oryctolagus cuniculus*) as two mentionable exceptions. Other residential species found in the foredunes are rather small and inconspicuous, and occur associated with marram grass because it mediates the physical stress and provides a sheltered habitat (McLachlan 1991, Bonte and Maelfait 2001, Maes et al. 2006). Common invertebrate species found in marram grass tussocks belong mainly to the phyla Arthropoda (mainly insects and spiders) and Mollusca (snails). Nonetheless, some dune specialist insect species are known to use open sand e.g. for hunting or egg-laying, leading to some species preferring habitat patches with more bare sand (Provoost and Bonte 2004, Maes et al. 2006). These examples stress the need for a heterogenous mix between open sand and vegetation in order to achieve a diverse arthropod community in coastal dunes.

Less notable species, such as nematodes or insects, seem to be going extinct faster than they can be described by science. Keeping in mind that many of those species are crucial for important ecosystem functions such as pollination, biological control and nutrient cycling (Wagner et al. 2021, Potapov et al. 2022), conservation of biodiversity should be at the top of our priority list. Since beneficial conservation measures for one species could be harmful for others, understanding the ecological mechanisms and complex process shaping biodiversity in a natural environment is crucial in order to conserve biodiversity in the most optimal way. In the light of the recent increasing interest in marram grass for sand stabilization projects, I wanted to investigate whether and how marram grass cover and spatial configuration affect the invertebrate dune biodiversity associated with it. I did this with the hope that dune-specific biodiversity could benefit from a potential increase in area covered by coastal dunes instead of, once again, becoming collateral damage.

1.5 Biodiversity theory in a coastal setting

In ecology, the complex processes shaping biodiversity have been studied extensively, leading to many different theories and approaches to analyse and understand community data. On the one hand, local community composition was believed to be stochastic (e.g., Gleason 1926), while on the other hand it was thought to be deterministic (e.g., Phillips 1931). One frequently used framework trying to integrate different approaches is the Community Assembly Rules framework. This framework comprises hierarchical rules shaping local species composition and restricting them to the prevailing conditions (Keddy 1992, Zobel 1997, Götzenberger et al. 2012). These rules are defined as “restrictions on the observed biodiversity patterns” (Wilson 1999) and are driven by different, not mutually exclusive, processes acting on different spatial scales. Large-scale restrictions in species composition because of historical patterns of speciation, extinction and migration are referred to as phylogeographic assembly rules. For instance, two species might co-occur infrequently because the physical barrier driving allopatric speciation also prevents the species to occupy the same habitat (Gotelli and McCabe 2002). These form the conceptual filter between the global and the regional species pool (Fig. 1.2). At smaller spatial scales, from the regional to the local species pool, filtering happens through ecological assembly processes, which can be further distinguished in dispersal, abiotic and biotic assembly rules (Götzenberger et al. 2012, Ovaskainen and Abrego 2020).

Large-scale differences between coastal dunes in Europe driving (phylo)geographic assembly rules are mainly related to geology, historical land use, human influence and management, sand accretion-erosion dynamics, ... The coastal dunes where the work for my thesis is situated (see section 1.7), can all be considered to be part of the North Sea region (Martínez and Psuty 2004). Nevertheless, differences in soil characteristics (see Bonte et al. 2003 and references therein), and to a lesser degree in their historical use and current management, are still present. The coastal dune areas situated in France and Belgium are characterized by lime-rich soil due to the proximity of lime formations situated around Calais (Ampe 1999, Bonte et al. 2003). More northwards, lime concentrations gradually decrease, probably due to river activity (e.g., the Scheldt and the Rhine), sea water currents and rain water (Eisma 1968, Ampe 1999, Bonte et al. 2003) washing away the soluble calcium. In the North of the Netherlands, the sand has lower nutrient concentrations, is completely decalcified and has a higher acidity due to the lack of the buffering capacity of the limestone (Eisma 1968, Ampe 1999, Bonte et al. 2003).

Climate conditions governing species assembly are an example of a driver of abiotic assembly rules. Plant species are heavily dependent on climate conditions in most regions. This dependency on the local climate is lowered for dune species compared to other plant species owing to the ameliorating effect of the sea (Wiedemann and Pickart 2004), resulting in broad distributions for a lot of embryo- and foredune plant species (Del Vecchio et al. 2018).

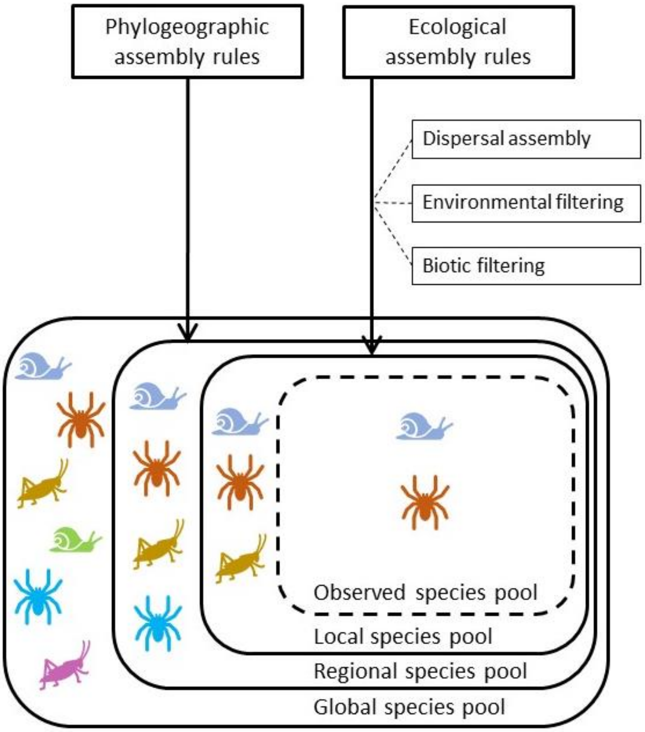

Figure 1.2 *Schematical representation of the Community Assembly Rules framework.*

1.6 Biotic interactions shape biodiversity

The variables affecting biodiversity discussed in previous paragraphs were all important on large to medium spatial scales. On the smallest spatial scale, species richness and community composition can be potentially driven by species-species interactions. Species interactions can be subdivided into facilitating (e.g., facultative mutualism and commensalism) and antagonistic (e.g., competition, predation and parasitism) species-species interactions. Interspecific competition is a clear example of a driver of biotic assembly rules. The scale on which this process has to be observed, depends on the studied species (e.g., metres when trees are considered vs. centimetres when nematodes are studied), but is small relative to the processes discussed before. Another subdivision that can be made between different kinds of interactions, is the distinction between direct (e.g., herbivory or predation) and indirect (e.g., apparent competition or plant-mediated) interactions.

Plant-associated species (e.g., invertebrate herbivores, fungi, bacteria, …) can influence each other’s fitness without interacting directly. The general mechanism for such interactions is an induction of chemical changes in the host plant (e.g., defensive secondary metabolites or nutritional condition) which spread from its leaves to its roots, consequently affecting all species associated with it (van Dam et al. 2003, Leimu and Koricheva 2006). This can cause a shift in the associated (herbivore) species composition if some species are better adapted to cope with or benefit from these changes in plant physiology. In fact, some specialist herbivore species are even able to sequester chemical compounds used by the plant for its own defence (Opitz and Müller 2009, Kos et al. 2015). Species can be separated on a host-plant either in space (i.e. below- vs. aboveground) or time (i.e. priority effects). Both cases will be discussed further in this section.

Plant-mediated interactions between the associated above- and belowground communities are very diverse. Leaf herbivory is shown to cause an increased transport of nutrients to the root system, which subsequently positively affects the belowground community (Johnson et al. 2009, Kaplan et al. 2009). On the other hand, aboveground herbivory is also shown to decrease plant productivity and consequently belowground herbivore abundances (Masters et al. 1993, Moran and Whitham 1993). Similarly, root-herbivory is known to both benefit (Johnson et al. 2009) and hinder (Wurst and van der Putten 2007) aboveground herbivores. Although the plant-mediated interactions are mainly important for the associated herbivory community, associated arbuscular mycorrhizal fungi might also affect plant growth, benefiting aboveground herbivores (Wardle et al. 2004). Since the soil community of marram grass was relatively well studied because of the research done on the Ammophila problem, it was regularly used as a study system for the interactions between the above- and belowground herbivore communities (e.g., Vandegehuchte 2010).

Communities inhabiting the same plant in the same environment, but separated in time, can look distinctly different. This biotic assembly rule can be driven by the assembly history of the local community, a phenomenon known as 'historical contingency' caused by priority effects (Chase 2003, Fukami 2015). Early arriving species can alter the species composition either via niche pre-emption or niche modification, but only if local dynamics are fast enough (Fukami 2015). It is not only observed in plant-associated communities, but also in other systems, for instance in freshwater pond communities (Chase 2003), plant communities (Gleason 1926) and microbial communities (Peay et al. 2012).

Trophic interactions, such as the interactions between predator and prey, are probably the best known and studied example of direct interactions. Predators usually feed on prey that are smaller than themselves, leading to the use of body size as a general proxy to identify potential trophic interactions (Gravel et al. 2013). This relationship seems less pronounced in terrestrial ecosystems (Potapov et al. 2019), however, data is still relatively scarce for some terrestrial faunal groups, for instance invertebrates (Traugott et al. 2013, Gongalsky 2021). This relationship between body size differences and likelihood of predator-prey interactions could be partly obscured by species identity. Both the predator and prey species could influence the outcome of predator-prey interactions either via the predator hunting strategy (Miller et al. 2014, Brose et al. 2019, Potapov et al. 2022) or via the prey defence strategy (Peschel et al. 2006, Jeschke et al. 2008). The invertebrate community inhabiting marram grass is perfectly fitted to help fill this research gap because arthropod species of all trophic levels, employing different strategies, are found in one single tussock. There are detritivores (e.g., isopods, millipedes and beetle species) feeding on the dead organic matter at the base of the tussock, while herbivores (e.g., aphids and true bugs) are feeding on the phloem of fresh marram grass leaves. In the meantime, most of the aforementioned species can be predated by spiders or predatory beetle species (Weeda et al. 1991). Trying to understand whether species interact in a predictable manner is important because species loss is thought to be decoupled from the loss of interactions, with the latter going more rapidly (Valiente-Banuet et al. 2015). This could mean that species loss might be even more damaging for ecosystem functions and services than initially thought (Griffiths et al. 2016, Keyes et al. 2021).

1.7 The ENDURE project

My PhD project was integrated for the first half within the Interreg 2-seas project ENDURE, which was short for “ENsuring DUne REsilience against climate change”. For this project, a field campaign sampling biodiversity in coastal foredunes in the 2-seas-area was carried out with help of the whole consortium (Fig. 1.3). This area determined my study area, which spans Belgium (sampled in 2017), France (2018), NL (2018-2019) and the United-Kingdom (2019). The areas to survey were determined based on aerial photographs and local information provided by the partners within the project. Within each area, a transect of about 1 km parallel to the sea was indicated and marram grass tussocks along these transects were sampled for biodiversity while also taking measures of the tussock itself. The sampled marram grass tussocks were located in the first 100 m from the seaward side of the foredune. We aimed at sampling marram grass tussock without much other surrounding vegetation (e.g., shrubs or other herbaceous species) in order to limit spill-over effects. We tried to sample tussocks at least 50 m apart, however, due to practical limitations (e.g., too much other vegetation along the transect or shorter transects) sampled marram grass tussocks were finally separated by at least 20 m.

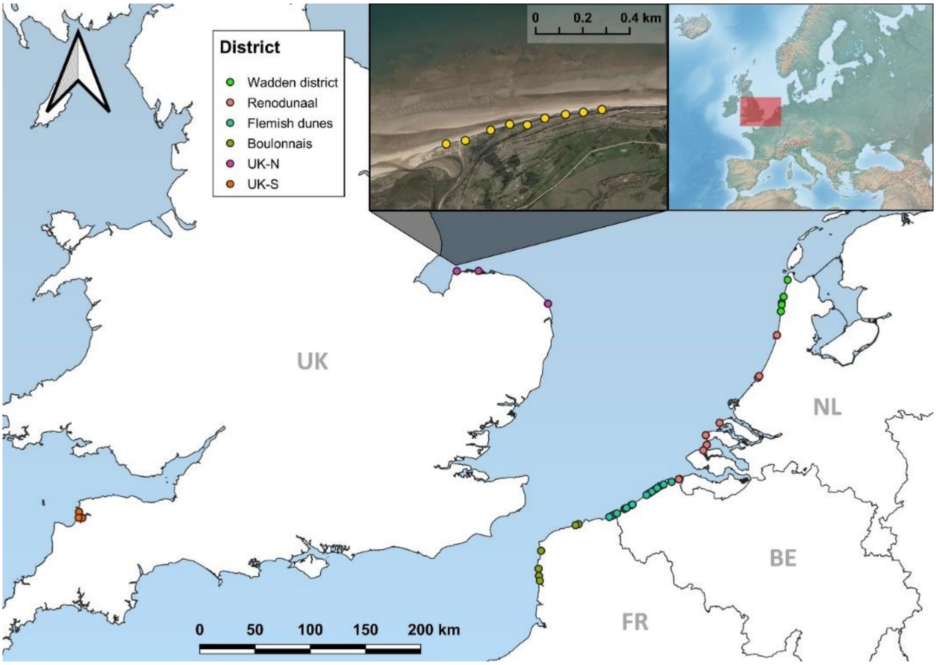

__Figure 1.3__ The geographical scope of the ENDURE-project. Transects are indicated by dots and coloured per biogeographical district. The left inset shows an example of the sampling unit locations (yellow dots) within the indicated transect (Holme, UK) (satellite image: © 2022 Google). Figure made with QGIS v3.2.3- Bonn (QGIS Development Team, 2018).

Different data were gathered from one marram grass tussock and combined to multiple data sets, which were subsequently analysed separately and used as the base of the chapters. In the field, first a photograph was taken from the tussock, which was the basis for the deduction of a vitality measure. Then, aboveground biodiversity was sampled by respectively sweep-netting for 15 seconds and manually searching the base of the marram grass tussock for 5 minutes. A root- and soil sample were taken next by searching (i.e., digging) for vital marram grass roots and harvesting them together with 500 mL surrounding rhizosphere sand. Finally, the occurrence of an invasive plant species (*Senecio inaequidens*) was registered in a 5 m circle. For chapters 2 and 5, additional lab experiments were conducted which will be described in the individual chapters.

Vegetation maps from the specific dune areas were also available via the ENDURE project. These vegetation maps were based on aerial photographs and LIDAR data as input and constructed via machine learning. For a detailed explanation of the construction of these vegetation maps, I refer to the Supplementary material S2 in Bonte et al. (2021). From these vegetation maps, measures for the spatial configuration of marram grass were calculated on different scales. This was done because of the large difference in dispersal capacity between above- and belowground fauna. Consequently, the 10 m scale was used in the analysis of the belowground biodiversity data, while the 50m scale was used in the analysis of the aboveground biodiversity data. Because we had no clear expectation for the relevant spatial scale for the invasive plant occurrence, model selection was used between models fit on different spatial scales.

A total of 638 samples were taken across three years, four countries and 46 transects. Due to different reasons, the number of included samples was different for the separate analyses. So were samples only included in the analysis of the occurrence of *S. inaequidens* if there was at least one Senecio plant found along the whole transect. This was done to exclude false zeros (i.e., samples along dune sites where *S. inaequidens* is not yet established). Due to time related issues, not all belowground samples could be counted, limiting the number of samples for this analysis. The aboveground biodiversity data set was limited because we had to make a subset due to convergence issues with the statistical model used.

Spatially explicit vegetation cover can be measured in a lot of different ways, e.g. as patch size, total patch area, area-perimeter ratio, connectivity, all stressing one part of the spatial complexity while neglecting another (Crotty et al. 2018). For this thesis, vegetation configuration was measured as the combination of two parameters calculated within circles around each sampled marram grass tussock, with the radius of the circles depending on the studied species (see above). The first parameter was the proportional cover of marram grass within this area. This parameter gives an idea about how much vegetation there is present within the surrounding area, without indicating how it is spatially structured. The second parameter was a measure for the spatial autocorrelation of the vegetation, independent from the covered area. The normalised join count statistics (JC; Cliff and Ord 1981) was used as the measure for spatial autocorrelation in the second chapter. This measure is positive when the vegetation is clustered together, close to zero when the vegetation is randomly distributed and negative when the vegetation is homogeneously distributed throughout the landscape. Theoretically, this measure is scale-independent (Cliff and Ord 1981), however, the actual calculated JC values increased with increasing spatial scale. Due to this apparent scale dependency, I switched from JC (in chapter 2) to Moran's I (chapters 3 & 4) as the measure for spatial clustering. This scale dependence was probably caused by a wrong implementation of the JC measure in the spded package in R. I personally think the results in chapter 2 to be robust, since the actual JC values increased with increasing spatial scale, whereas the values of the variable did change to negative when I tested the package with a fictive, homogeneous marram grass configuration. Additionally, marram grass occurs highly clustered under natural conditions, causing this parameter to vary from positive values to larger positive values. The decision to switch was mainly made because this would allow me to compare the results between chapters (3 and 4) without having to worry about potential scale dependencies.

As already mention before in section 1.5, all coastal dune areas visited for the fieldwork be considered to be part of the biogeographical North Sea region (Martínez and Psuty 2004). Nevertheless, because of differences related to soil characteristics, historical use and current management, I further subdivided them into five subregions. During the rest of my thesis, I will refer to these subregions as “biogeographical districts”. Since different countries were sampled during different years, and because the countries overlap for a large degree with these biogeographical districts, we cannot completely rule out that the effects we find are correlate with the weather conditions varying between years. I discuss this in more details were necessary in the discussion of the specific chapters (3 and 4).

1.8 Objectives and outline of the thesis

The aim of this thesis was to gain a better understanding of the processes shaping invertebrate biodiversity in marram dunes, with a specific focus on the effect of marram grass spatial configuration. A vast amount of data gathered during three consecutive field years was used for this purpose. Where necessary, field data was supplemented with lab experiments. A schematic overview of the data types gathered and how they were used for the different chapters can be found in Fig. 1.4.

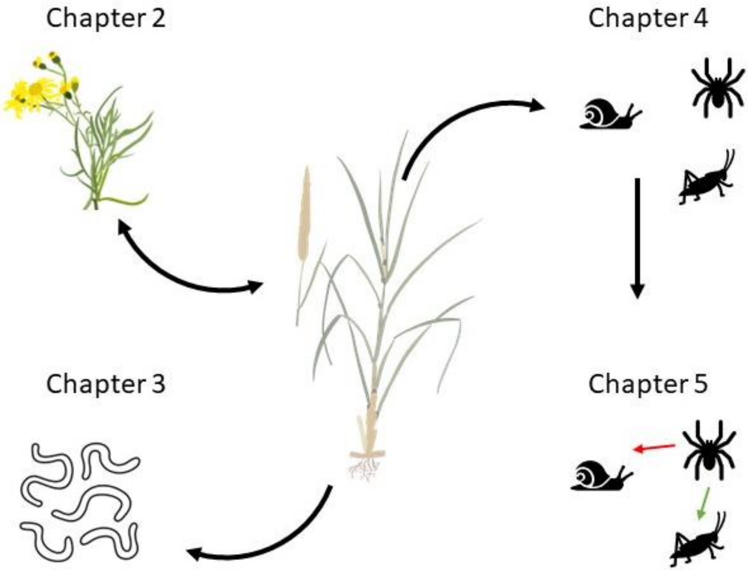

Figure 1.4 *Schematic overview of the different data types gathered from one marram grass tussock and how they are used in the different chapters. Chapter 2 uses occurrence data of Senecio inaequidens in the immediate proximity to the marram grass tussock. Chapter 3 analyses nematode community data extracted from the roots of the plant. In chapter 4, I study the invertebrate community found in the marram grass leaves and in chapter 5 I try to estimate trophic relationships between them. Chapter 1 and 6 are the general introduction and general discussion respectively.*

In chapter 2, I used occurrence data of an invasive plant species (*Senecio inaequidens*) to study its potential to establish in European coastal dunes where it was hitherto not found. This potential spread was correlated to marram grass configuration, which can be used as a reliable proxy for sediment supply. I hypothesised the highest probability of *S. inaequidens* establishment to be at intermediate marram grass cover because too low cover would increase sand burial, whereas too high cover would increase competition. Since marram grass plays a crucial role in natural dune formation, I further evaluated the possible effects *S. inaequidens* establishment could have on this process. To this end, a growth experiment was conducted to study whether *S. inaequidens* was able to alter marram grass performance. I expected a negative impact of *Senecio*-altered soils on marram grass growth mediated by an increase in soil biota.

For chapter 3, I analysed the nematode functional abundance data extracted from root and soil samples to study their spatial structure and its possible arise from marram grass' spatial configuration. The relative importance of factors structuring nematode abundances was further analysed using joint species distribution modelling (JSDM). I hypothesised that nematode abundance would by higher in lime-rich coastal dune regions because of the higher soil pH. At smaller spatial scales, nematodes found in the roots would positively correlate with marram grass cover and all nematode abundances would increase with clustering of the host plant as a consequence of the less efficient sand-capture of these configurations. Furthermore marram grass vitality would affect functional groups differently, while all nematode abundances would decline when *S. inaequidens* is present.

The aboveground invertebrate data were analysed in chapter 4. Here, I studied the effect of the cover and vitality of marram grass on the invertebrate community in different biogeographical regions. Using JSDMs, I could additionally take into account species traits and phylogenetic relationships. From these models, residual species-associations could be extracted to gain further insights into the community assembly rules structuring dune biodiversity. I hypothesised species richness to be mainly affected by local marram grass parameters, while species composition would be mainly influenced by the biogeographic districts.

Chapter 5 was a joint effort between me and a colleague, where we wanted to validate the predicted trophic interactions based on body size ratios between predator and prey. This is particularly interesting because we would be able to test a well-established rule within ecology. Additionally, this chapter enabled me to gain some more experience in the setup of experimental work. Furthermore, we also tested whether predator hunting strategy and general taxonomy (as a proxy for prey defensive properties) could explain possible deviations from this size-based rule. We expected the general rule to hold up, but expected predator hunting strategy and prey taxonomy to explain additional variation.

In chapter 6, the results presented in the previous chapters are discussed in a broader context. The implications of the results for conservation of biodiversity are explored, while the possible impact of invasive species for coastal protection are discussed as well as the potential increase in coastal habitat for invertebrates due to coastal protection. The chapter ends with a few concrete suggestions for future experimentation.

Chapter 2

The distribution and impact of an invasive plant species (*Senecio inaequidens*) on a dune building engineer (*Calamagrostis arenaria*)

**Ruben Van De Walle, François Massol, Martijn L. Vandegehuchte &
Dries Bonte**

Senecio inaequidens growing in between *Calamagrostis arenaria*.

Adapted from: Van De Walle R, Massol F, Vandegehuchte ML, Bonte D (2022) The distribution and impact of an invasive plant species (Senecio inaequidens) on a dune building engineer (Calamagrostis arenaria). NeoBiota 72: 1–23.

2.1 Abstract

Disturbance is thought to enhance the probability of invasive species establishment, a prerequisite for naturalisation. Coastal dunes are characterised by disturbance in the form of sand dynamics. We studied the effect of this disturbance on the establishment and spread of an invasive plant species (*Senecio inaequidens*) in European coastal dunes. Local sand dynamics dictate the spatial configuration of marram grass (*Calamagrostis arenaria*). Therefore, marram grass configuration was used as a reliable proxy for disturbance. Since marram grass plays a crucial role in natural dune formation, we evaluated the possible effects *S. inaequidens* could have on this process, when it is able to colonize European coastal dunes.

We expected the highest probability of *S. inaequidens* establishment at intermediate marram grass cover because too low cover would increase sand burial, whereas high cover would increase competition. However, results from our field survey indicated that *S. inaequidens* is quite capable of handling higher levels of sand burial. Thus, the probability of *S. inaequidens* establishment was high under low marram cover but slightly lowered when marram cover was high, hinting at the importance of competition.

We expected a negative impact of *Senecio*-altered soils on marram grass growth mediated by soil biota. However, marram grass grew better in sand gathered underneath *Senecio* plants due to abiotic soil modifications. This enhanced growth may be caused by *Senecio* leaf litter elevating nutrient concentrations in an otherwise nutrient-poor substrate. If such increased plant growth is a general phenomenon, further expansion of *S. inaequidens* could accelerate natural succession in European coastal dunes.

2.2 Introduction

Due to human activity the number of invasive species worldwide is ever-increasing. In Europe alone, the number was estimated to be well over 12 000 in 2019 (Roy et al. 2019). The causes of introduction of non-native species range from intentional introduction, e.g., for pest control, horticulture, coastal defence and restoration purposes (Cox 1992, Beckstead and Parker 2003, Richardson and Rejmánek 2011, Camacho-Cervantes et al. 2017, Buerdsell et al. 2021) to unintentional introduction such as escape from planting sites and introduction via tourism (Davenport and Davenport 2006).

After reaching a new habitat, the non-native species needs to establish and naturalize in order to become invasive (Richardson et al. 2000). It is generally thought that disturbance benefits establishment of non-native species and that it could even facilitate the spread of invasive species. Several mechanisms, such as reduced competition, increased resource input and increased habitat availability, are proposed to be behind this phenomenon (Mack et al. 2000, Pyšek and Richardson 2006, Jauni et al. 2015, Lear et al. 2020).

Several hypotheses have been proposed to explain the long-term success of invasive species (Mack et al. 2000, Chabrerie et al. 2019). Among these, the enemy release hypothesis (ERH) and the Evolution of Increased Competitive Ability hypothesis (EICA) are particularly important in the context of harsh, temporally variable environments in which biotic interactions can be hampered. The ERH states that the success of invasive species can be attributed to the release from natural enemies such as (specialized) herbivores or pathogens (Keane and Crawley 2002). The EICA adds to this that, due to the release from natural enemies, invasive plant species can reallocate resources otherwise used for protection towards growth and other performance traits (Blossey and Notzold 1995).

Invasion can also be promoted via both intra- and interspecific facilitation (Jordan et al. 2008, Proença et al. 2019, Uyà et al. 2020), especially in harsh environments, or by decreasing fitness of native species (Jordan et al. 2008, Vilà et al. 2011). One underlying mechanism in plant communities is modification of the soil (Aldorfová et al. 2020). The effect of such modifications can be very useful because invasive species can provoke generic effects against the whole native community, which enables them to invade if they suffer less from their created disaster. Contrastingly, it is hard for the native community to specifically target a newly arrived, invasive species (David et al. 2017). The term ‘plant-soil feedback’ (PSF) refers to the process of plants altering the soil with effects on the performance of other plants subsequently growing in this soil (Bever et al. 1997, van de Voorde et al. 2011, Buerdsell et al. 2021). The soil characteristics altered can be biological, chemical or structural (Ehrenfeld et al. 2005, Kulmatiski et al. 2008). Biological modification of the soil occurs via changes in the soil community, including soil microbes and soil fauna. Depending on the affected species, these effects can be negative, e.g., when root-feeding nematodes or pathogens accumulate (Van der Stoel et al. 2002, Bever et al. 2015) or mutualistic interactions are disrupted by the non-native plant (Callaway et al. 2008, Brouwer et al. 2015), or positive, e.g., by accumulation of mycorrhizal fungi or nitrogen-fixing bacteria in low-nutrient soils (Rodríguez-Echeverría et al. 2009, in ’t Zandt et al. 2019). Root exudates, litter decomposition and root-supported microbial activity can alter different components of the soil chemistry such as soil acidity and nutrient availability (e.g., Lazzaro et al. 2014). Structural modification occurs via changes in soil temperature, water content or the overall soil structure and soil aggregates (Ehrenfeld et al. 2005). Again, these effects can be either negative or positive, depending on the species (Bezemer et al. 2006).

Plant-soil interactions can affect the process of species invasion at different scales. Plant-soil interactions are local and thus mainly affect the plant itself or other plants in the near vicinity, both conspecifics and heterospecifics. Invasive tree species can, however, have more wide-ranging effects using their fallen leaves as agents of soil change (e.g. Gómez-Aparicio & Canham 2008). At larger spatial scales, different local plant-soil interactions give rise to a heterogeneous, spatially structured landscape (Bever et al. 1997, Mack and Bever 2014) which influences biodiversity, population dynamics and ecosystem functioning (Levine et al. 2003, Vilà et al. 2011, Mack and Bever 2014). This heterogeneity can, in turn, influence the processes facilitating species invasions, such as enemy release or fitness decrease in native competitors.

European marram grass (*Calamagrostis arenaria* (L.) Roth, formerly *Ammophila arenaria*) is one of the most extensively studied systems regarding PSF, with studies investigating abiotic and biotic PSFs going back to the 60s (Marshall 1965) and 80s (van der Putten et al. 1988) respectively. This study focuses on marram dunes (Natura 2000 habitat 2120, CORINE biotope 16.21), a coastal habitat type dominated by marram grass, which occurs relatively early in the dune succession, characterised by high levels of stress (Kulmatiski et al. 2008) due to e.g. sea spray and aeolian sand burial (Brown et al. 2018). Marram grass is perfectly adapted to grow in these conditions. Several studies have shown that marram grass even needs sand burial to grow optimally (i.e. Ievinsh & Andersone-Ozola 2021, Nolet et al. 2018) because the biological soil community accumulating around the roots of marram grass has a negative impact on its performance and growth (van der Putten et al. 1988, Van der Stoel et al. 2002). Deposits of sand blown in from the beach are relatively free of root pathogens and parasites and thus enable marram grass to develop new roots in this temporarily enemy-free soil. Additionally, marram grass also interacts with the aeolian sand dynamics by locally lowering the wind speed and thus promoting sand capture (Zarnetske et al. 2012, Reijers et al. 2021), resulting in a positive feedback between marram growth and sand capture. This interplay between marram grass and sand dynamics leads to a range of possible spatial configurations of marram grass, which depend on the local sand dynamics. Reijers et al. (2021) found that marram grass grows highly clustered together under sediment-poor conditions. When there is enough sediment supply, it grows more randomly, albeit still clustered (Reijers et al. 2021). This allows marram grass cover to be used as a proxy for the intensity of sand dynamics. Marram grass can reach a high density when enough fresh sand is provided by strong sand dynamics. Under moderate sand dynamics, an optimal spatial configuration is expected to occur with a heterogeneous mosaic of bare sand and marram grass. Since this species grows via lateral vegetative growth, natural configurations show variable degrees of clustering, but rarely occur in truly random, let alone regular configurations.

The bare sand patches between marram grass tussocks may provide an opportunity for invasive species to establish. On the other hand, too dynamic conditions will probably hinder settlement due to too high levels of sand burial (Maun 1998, Kent et al. 2005). These conflicting pressures could determine where invasive species are able to establish in marram-dominated dunes. If these sand patches become overgrown, sand dynamics can further decrease (Gao et al. 2020) and in turn this can negatively affect the vitality of marram grass. This could lead to the invasive species becoming competitively stronger and outcompeting marram grass (i.e., a form of positive density dependence). Such changes in competition could have extensive consequences for coastal dunes and their ecosystem services (Klironomos 2002), especially coastal defence, as they could trigger feedbacks that change system dynamics (Bonte et al. 2021).

One species invading coastal dunes around the North Sea is narrow-leaved ragwort (*Senecio inaequidens* D.C., Asteraceae, also known as South African ragwort). It is originally a South African species, but with a long history of invasion in Europe (Ernst 1998), where it arrived via wool transport (Lachmuth et al. 2010). Although much is known about the invasion of *S. inaequidens* in other habitats in Europe (Ernst 1998), far less is known about its colonisation of sandy dune areas. It was first found in dune areas in 1935, more specifically in the dunes of Calais, France (López-García and Maillet 2005).

Senecio species contain pyrrolizidine alkaloids (PA) as a defence mechanism against both above- and belowground herbivory (Joshi and Vrieling 2005, Caño et al. 2009, Thoden et al. 2009, Joosten and Van Veen 2011). Several studies have shown these allelopathic defences can influence entire soil communities (Kowalchuk et al. 2006, Thébault et al. 2010, Harkes et al. 2017) and therefore *Senecio* species are able to affect their own spread (Engelkes et al. 2008). However, the exact mechanisms are, to our knowledge, still unknown. Passive release from roots (and leaf litter) is the most probable pathway, although it is speculated that direct secretion from the roots is possible as well (Kowalchuk et al. 2006, Joosten and van Veen 2012, Selmar et al. 2019). Not many studies have tried to investigate the direct effect of PAs on plant growth (but see Ahmed & Wardle 1994). Recently, even uptake of PAs by other plant species was demonstrated (Nowak et al. 2016, Selmar et al. 2019), although the general consequences of this horizontal transfer for the receiving plants are unknown at the moment.

We suspect that PAs in sandy soil will have little effect on marram grass growth directly. The sign of the total effect of *S. inaequidens* will depend on the response of the soil community. It will be negative if marram pathogens can accumulate or if PAs prevent symbionts from associating with marram roots. However, it can be positive if PAs prevent accumulation of marram pathogens and thus create an enemy-free space for marram roots, as aeolian sand does.

Here, we investigate the relation between marram grass spatial configuration and the probability of establishment of *Senecio inaequidens* in marram dunes, together with the potential effects of this invasion on marram dunes. We hypothesize that (1) due to the potentially positive effect of disturbance on invasive species (Scherber et al. 2003, Jauni et al. 2015), *S. inaequidens* will likely get established in more disturbed areas, i.e. areas with stronger sand dynamics. However, since too high sand burial is probably detrimental for the growth of *S. inaequidens*, we expect to find an optimum at intermediate sand burial which is also associated with intermediate vegetation cover. We further postulate that (2) the biotic compartments of *Senecio*-altered soils will negatively affect marram grass growth, except if PAs prevent marram pathogens from accumulating.

2.3 Material & Methods

Study Area

This study was carried out in coastal dune areas along the Channel and the North Sea, covering the North of France, Belgium, the United Kingdom and the Netherlands (Fig. 2.1). Within this area, we focussed on sandy coasts with marram-dominated, yellow dunes. This area included the location of *S. inaequidens* settlement and the northernmost location within its distribution in coastal dunes, thus enabling us to study the front of the ongoing invasion.

For a recent biodiversity study, 46 dune transects spread along the study area were selected. The transects had a mean length of 1212 m (shortest: 230 m, longest: 3348 m) and were located within the first 100 m from the front of the foredunes. Within each transect a number of sampling locations was chosen based on the length of the dune transect with an average of 14 samples (min 5; max 37). Each sampling location was characterized by a central marram grass tussock. Individual sampling locations were separated by at least 20 m and chosen with the aim to maximise the variety of surrounding marram grass configurations. For the total number of samples and transects per country, see table 2.1.

Table 2.1 *The number of samples taken in each country within the study region.*

Country	Samples	Transects	Mean length of transects
BE	206	18	822
FR	184	9	2232
NL	188	13	800
UK	60	6	720

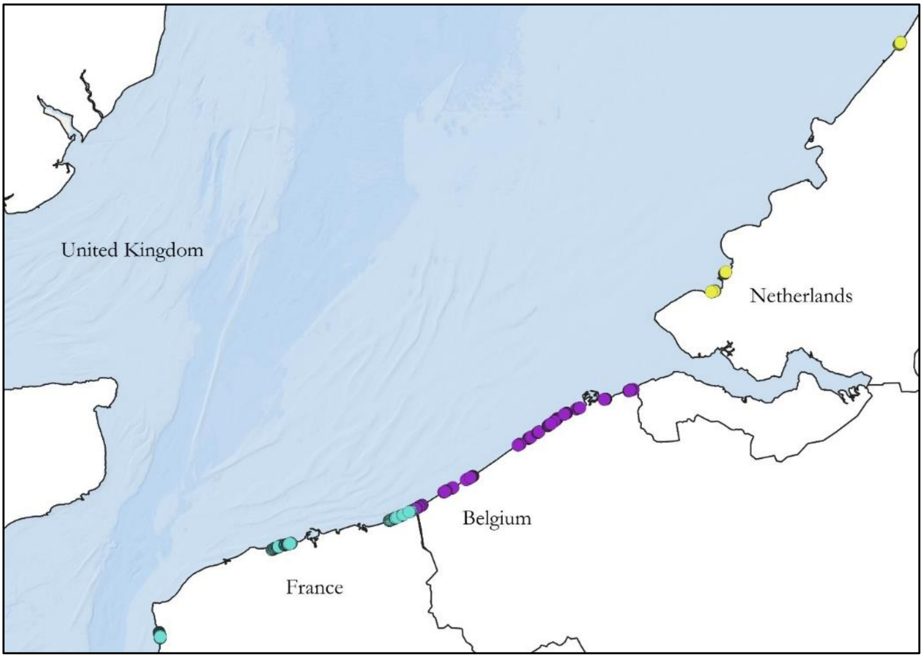

Figure 2.1 *The samples included in the analysis. Colours indicate the different countries.* Senecio inaequidens *was not found in the UK. Map made with QGIS v3.6* (QGIS Development Team 2021).

Data collection

The occurrence of narrow-leaved ragwort (*Senecio inaequidens*) was mapped at each sampling location. The number of *S. inaequidens* plants was counted within a radius of 5 m around the central marram grass tussock for those sampled in France, the UK and the Netherlands. Due to a change in the protocol of the biodiversity study, in Belgium the occurrence was scored into four categories: “not present”, “sparse”, “moderate” and “abundant”. Data on the occurrence of *S. inaequidens* were collected during three consecutive summers: in July 2017 data were collected along the Belgian coast; in July, August and September 2018 along the French coast; in August and September 2018 and June 2019 along the Dutch coast; and in July and August 2019 along the coast of the UK (Norfolk and Devon).

From available vegetation maps of the foredunes (Bonte et al. 2021), the proportional cover by marram grass in the vicinity of the central marram grass tussock (P), together with a measure of spatial autocorrelation of marram grass occurrence (normalised join count statistics, JC; Cliff & Ord 1981), were calculated. These two parameters were used to express the spatial configuration of the surrounding marram grass. The proportion of marram grass cover is straightforward and ranges from 0 (no marram grass present) to 1 (the whole area is covered with marram). The measure of spatial autocorrelation is negative when the marram grass is regularly distributed in the landscape. If the marram grass is randomly distributed, the parameter is close to 0 and it is positive when the marram grass occurs clustered together. As pointed out by Bonte et al. (2021), marram grass distribution is almost always clustered (i.e., high JC values) and rarely random. These two parameters (P and JC) were calculated within four circles with different radii (5 m, 10 m, 20 m, 50 m) around the central marram grass tussock to represent different spatial scales. See supplementary material of Bonte et al. (2021) for a more in-depth explanation of construction of the vegetation maps and calculations of the spatial parameters.

Lab experiment

To study the effect of *S. inaequidens* on marram grass growth, we performed a growth experiment with a split-plot design: sand affected by *S. inaequidens* was gathered at the Belgian coast together with bare sand for the control group. Half of the volume of sand gathered was sterilised (by autoclaving at 121°C/1 bar for 30 minutes) in both groups to determine whether any observed effect could be biotic or abiotic.

Sand was gathered from three different sites situated on the western, central and eastern Belgian coast: in the foredunes in Oostduinkerke (Ter Yde) for the west coast, for the mid coast in Oostende (Fort Napoleon) and for the east coast between Wenduine and Zeebrugge (two locations were used due to low occurrence of *S. inaequidens*). Ten plots were sampled at each site (for a total of 30 plots). Each plot yielded two samples: 2L rhizospheric sand from underneath *S. inaequidens* plants and 2L of bare sand taken 5-10m away. This way, changes in soil between two paired samples, other than due to the influence of *S. inaequidens*, were minimised. The sand was stored in the fridge (max 3 days) to assure the survival of the soil biota until the sand was used. The 2L samples were divided into two 1L sub-samples from which one was sterilised and the other was not. Thus, we had four treatments: *Senecio*-influenced vs. bare sand at the plot level combined with sterile vs. non-sterile soil at the subplot level (Fig. 2.2). In other words, influence of *Senecio* was the whole-plot factor and soil sterilisation the subplot factor, with whole plots organized in pairs, which act as statistical blocks.

Marram grass seedlings were used for the experiment because seedlings are more susceptible to environmental influences than fully grown plants (Huiskes 1979). The seedlings were grown from seeds gathered at the Belgian coast (Oostduinkerke, ter Yde) from the same population in order to minimize genetic effects. The seeds were collected during the summer of 2019 and stored at room temperature in the lab. All seeds were surface-sterilised as in de la Peña et al. (2010) before they were left to germinate under standardized conditions (on commercially available sand saturated with demineralized water; photoperiod: 16/8 h light/dark; temperature: 22 ± 1°C) for 2 weeks prior to dune sand collection. As a baseline, the whole seedlings were weighed and the length of roots and leaves was measured before planting.

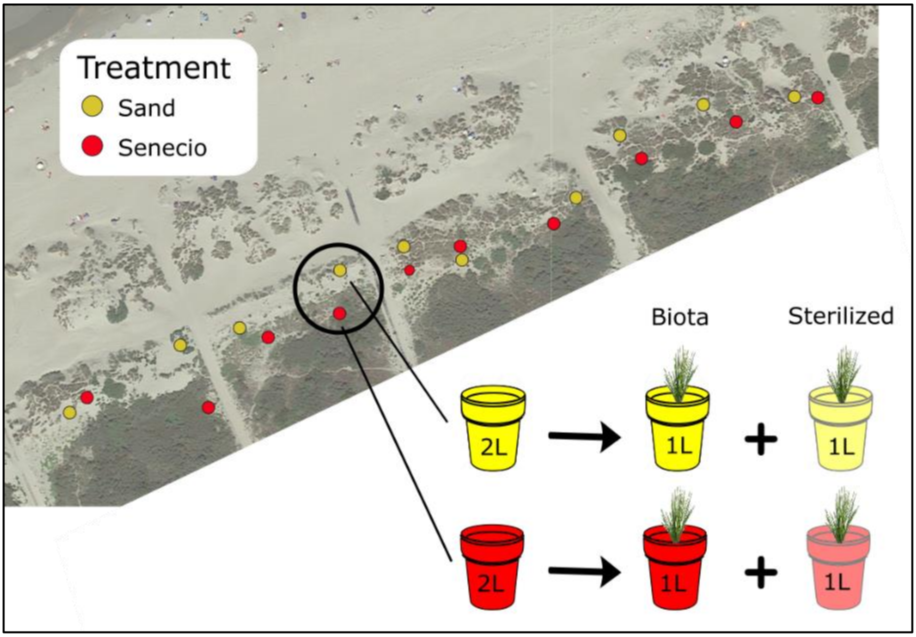

Figure 2.2 *Split-plot design of the marram grass growth experiment for the site at Oostduinkerke (Western Belgian coast). 2L samples of sand, (1) sand from unvegetated locations or (2) sand from underneath Senecio, were split into two 1L subsamples, one of which was sterilized. This enabled us to investigate whether the effect of Senecio on marram grass growth was achieved via the biotic or abiotic portion of the soil. Map made with QGIS v3.6 (QGIS Development Team 2021). Aerial photograph (summer 2018) source: Agency for Information Flanders (geopunt.be).*

All 120 pots (3 sites x 4 treatment combinations x 10 plots) were filled with 1L of sand in which three seedlings were planted. The pots were placed in a growing chamber under the same conditions as mentioned before for the germination of the seeds. All pots were watered twice a week, on the same day, with demineralised water until near-saturation. Each pot was labelled with a unique ID in order to prevent observer bias.

After 2 weeks of growing, the largest seedling was selected to grow for another 10 weeks. The other two seedlings were removed. This was done to ensure that all remaining seedlings had rooted properly in order to minimise die-off and resulted in only three plants dying during the whole experiment (one from each treatment, except for the sterilized bare sand treatment). At the end of the growing period the whole plants were collected, all leaves were counted and the length of the longest leaf and root was measured. Further, all leaves and roots were weighed separately, both before and after drying in an oven at 70°C for 48h.

Statistical analyses

Occurrence of *Senecio*

Due to two different methods of assessment of the occurrence of *Senecio inaequidens* (i.e. ordinal categories for the Belgian samples and count data for all other samples), all *S. inaequidens* data were converted to presence/absence. To exclude false zeros (i.e., samples along dune sites where *S. inaequidens* is not yet established) from the analysis, only dune transects where *S. inaequidens* occurred in at least one sample were included. This resulted in a final dataset comprising 26 out of the 46 original sites, which included 408 of the original 638 samples. The sites were located in three countries since *S. inaequidens* was not observed in the United Kingdom.

The marram grass spatial data were used as independent variables. As explained above, the spatial data consisted of two continuous variables: the proportion of marram grass (P) and its normalized join count statistic (JC) for each spatial scale (5m, 10m, 20m and 50m) per sample. The JC values were rescaled to the maximum value to alleviate convergence issues of linear models. This resulted in both parameters ranging between 0 and 1. Generalised linear mixed models were used with a logit link function and binomial distribution to analyse the occurrence data. A combination of first and second order terms of P and JC, together with interactions between them, were fitted to allow the relationship between the occurrence of *S. inaequidens* and the spatial parameters to be unimodal. The maximal (full) generalised linear mixed models were of the form:

$$\text{occurrence} \sim P + JC + (P \times JC) + JC^2 + P^2 + (P^2 \times JC) + (JC^2 \times P)$$

To determine which combination of P and JC best explained the occurrence data, different combinations of the spatial predictors were fitted (including interactions terms, see table S.1 in Supplementary material for all models) at all four scales (i.e. using P and JC computed at 5m or 10m or 20m, etc.), after which model selection based on the corrected Akaike Information criterion (AICc) was used to select the model and scale that optimised goodness-of-fit. Dependency is present within the data for samples along the same transect. Therefore, ‘transect’ nested within ‘country’ was included in the models as a random variable. ‘Country’ itself was excluded because it contained almost no variation (Chen and Dunson 2003). This way we also accounted for differences in weather, dune management and time (different countries were sampled in different years).

Growth experiment

We analysed the effect of the provenance of the sand (from beneath *S. inaequidens* vs. bare sand), of its sterilisation and of their interaction using linear mixed models. F-tests with Satterthwaite’s approximation of denominator degrees of freedom were used to determine the significance level of the fixed effects. All measured traits (number of leaves, length of longest leaf and root, weight of fresh and dry roots and leaves) where highly correlated (see supplementary material, S.2), so we used the first principal component (PC1) from a principal component analysis run on the trait data as response variable for the analysis. Sample site and plot were integrated in the mixed model as random effects to account for data dependency within block and whole-plots. Sample was initially also included to correct for dependency of the subsamples within each sample, but this random effect was removed because of a negligible variance component.

All data analyses were performed using R Statistical Software (R Core Team 2021). The calculation and normalisation of JC values was done with the ‘spdep’ package (Bivand and Wong 2018). The packages ‘lme4’ (Bates et al. 2015) and ‘lmerTest’ (Kuznetsova et al. 2017) were used for the Generalized linear mixed models. Package ‘MuMIn’ (Barton 2020) was used for automated model construction and comparison.

2.4 Results

Occurrence

Senecio inaequidens was observed at 176 of the 408 sites included in the analysis. The most northern and southern transect where *S. inaequidens* was observed are respectively at Wassenaar (52.1565°N; 4.3404°E; the Netherlands) and Wimereux (50.7931°N; 1.6074°E; France). *S. inaequidens* was most frequently present in Belgian samples, followed by France and the Netherlands (Fig. 2.3). In the United Kingdom, no *S. inaequidens* was observed.

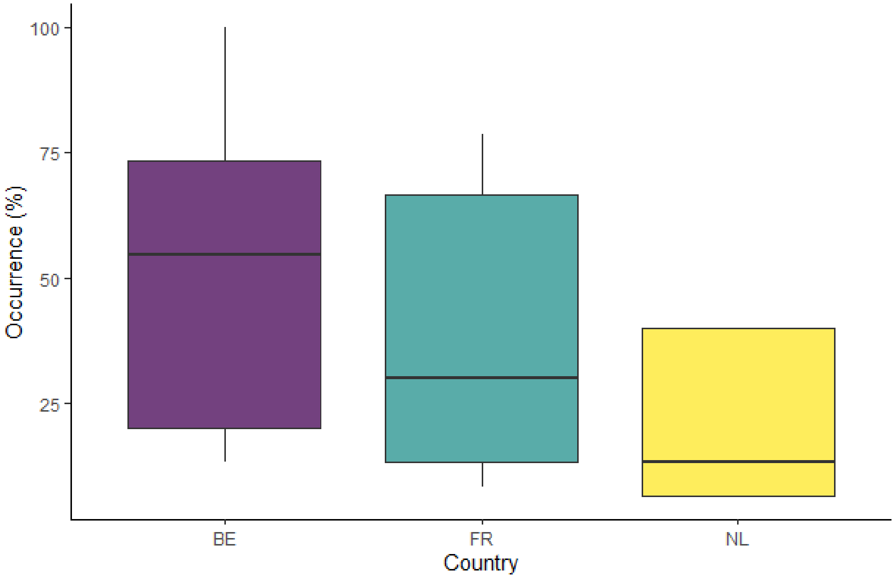

Figure 2.3 *The average occurrence of* S. inaequidens*, calculated as the proportion of samples within each transect where* S. inaequidens *was found. BE = Belgium; FR = France, NL = the Netherlands.*

The four models selected were all at the 5m scale (using an AICc delta value of 2; see table 2.2 for the selected models; see Supp. Mat. S2.1 for all models), implying that *S. inaequidens* reacts to marram grass spatial configuration at small distances. The predicted occurrence is depicted in Fig. 2.4a. When the vegetation is highly clustered together (high JC values), the occurrence of *S. inaequidens* is negatively correlated with marram grass cover. Further, we see a clear minimum probability of occurrence of *S. inaequidens* at more random distributions of marram grass (low JC values) with intermediate vegetation cover. Since no random configurations were found at intermediate P, the minimum is probably due to a small number of samples with a low JC (see Fig. 2.4b), thus caution is advised when interpreting this result. Although we actively tried to sample in a wide range of different spatial configurations of marram grass, there is still a low number of data points with low marram grass cover and less clustered configurations due to the nature of the system. To ascertain that the outcome of the analysis was not greatly influenced by those few samples, the analysis was redone after excluding those samples. The results did not differ greatly (see Supp. Mat. S2.3).

Table 2.2 *The coefficients, number of model parameters (df), AICc values, relative AICc (ΔAICc; i.e., difference between each model's AICc and the minimum AICc) and Akaike weights for all selected models.*

Spat. scale	**Intrcpt**	**JC**	**JC²**	**P**	**P²**	**JC*P**	**JC*P²**	**df**	**logLik**	**AICc**	**Δ AICc**	**weight**
5	-1.4	6.13		-8.84	15.75		-13.71	6	-182.35	376.96	0	0.13
5	-2.53	15.39	-11.49	-24.36	28.00	23.84	-32.06	8	-180.9	378.24	1.285	0.068
5	-3.14	12.46	-5.35	-8.92	14.82		-12.19	7	-181.99	378.32	1.367	0.065
5	-0.12	3.94		-16	22.28	11.32	-23.80	7	-182	378.34	1.379	0.065
Avg.	**-1.73**	**8.88**	**-3.45**	**-13.50**	**19.40**	**7.20**	**-19.21**					

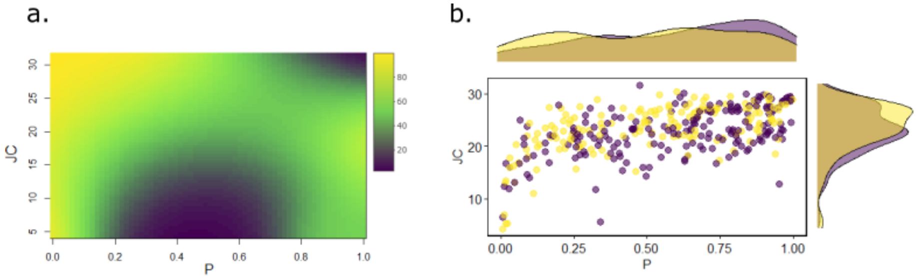

Figure 2.4 (a) *The overall relation between the probability of occurrence of* S. inaequidens *and the spatial configuration of marram grass. The colours indicate the probability of occurrence as %.* ***(b)*** *Density distribution plots of the observed cover (P) and spatial autocorrelation (JC) of marram grass within a 5m radius of the central marram grass tussock. This plot only contains the data of the transects where S. inaequidens was found. Colours indicate whether* S. inaequidens *was present (yellow) or absent (purple).*

Growth experiment

The first PC of the PCA of all measured plant traits explained 73.9% of the variation, while the second PC explained 14.7%. Scores along PC1 were significantly correlated with all plant traits (see Supp. Mat. S2.2), therefore, we used PC1 as a reliable indicator of overall plant growth. Marram grass growth was affected by both the abiotic and biotic components of the soil (Fig. 2.5). However, no significant interaction was found ($F_{1,82.7}$ = 1.10, p = 0.298). Soil sterilisation had a positive effect on marram growth ($F_{1,83.4}$ = 106, $p < 0.001$), which means that the soil biota had a negative effect on marram biomass. The plants grown on sand from underneath *S. inaequidens* grew better than plants grown on bare sand ($F_{1,82.7}$ = 59.2, $p < 0.001$).

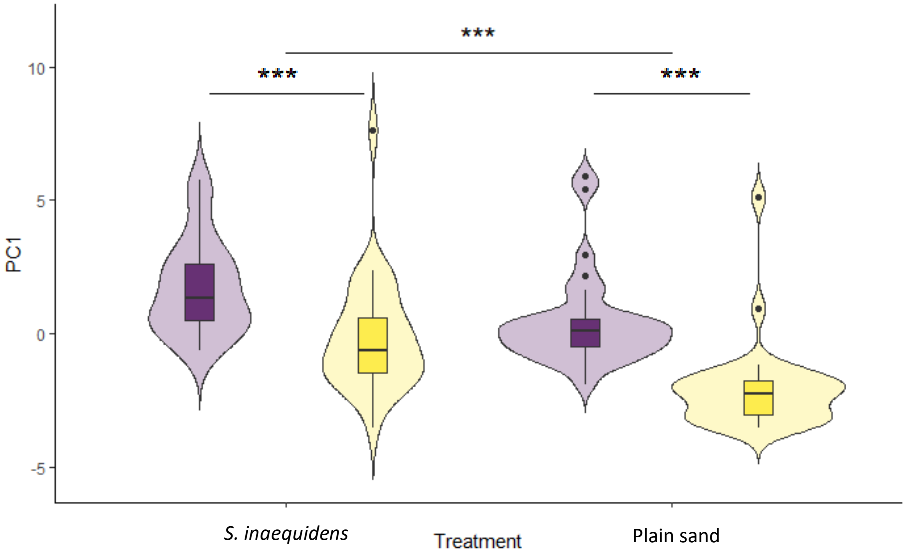

Figure 2.5 *Box- and violin plots represent distribution of PC1 values for marram grass growth. Horizontal lines above the boxplots indicate comparisons between treatments, *** indicate significant difference of p < 0.001. Colours indicate whether biota were present (yellow) or absent (purple). Number of samples per treatment is 29, except for sterilized sand from unvegetated locations, where it is 30.*

2.5 Discussion

Field data

No evidence was found for the hypothesized optimum probability of establishment of *S. inaequidens* at intermediate marram grass densities. In fact, our results indicated that *S. inaequidens* has no problem growing in sandy conditions, as we observed a negative correlation between vegetation cover and probability of establishment. This indicates that *S. inaequidens* is more susceptible to competition than to sand burial. Indeed, some studies found that this species is a good coloniser rather than a good competitor (Scherber et al. 2003, Caño et al. 2007, Thébault et al. 2011). Furthermore, the available area to root in – in this case open sand – also decreases as vegetation cover increases. This is especially important since *S. inaequidens* is an annual plant which relies on high propagule pressure to spread (Thébault et al., 2011).

Due to the nature of the system, higher proportions of marram grass occur mainly towards later stages of succession. In these later stages, marram starts to decay and the spatial configuration starts to return to a more random distribution (i.e. lower JC values and slightly lower P values) because marram grass is slowly being replaced by other plant species. This leads to a rise of the probability of *Senecio* establishing which may indicate that it is becoming a stronger competitor.

Overall, the probability of establishment of *S. inaequidens* displays high values across the whole range of sampled natural marram grass configurations. Since we aimed to maximise the variety of natural marram grass configurations surrounding the sample, configurations that were not sampled probably do not, or not often, occur in nature. In fact, such configurations arise probably mainly when marram grass is planted (i.e., for coastal protection) and afterwards when the planted dune is ‘maturing’. This makes it hard to extrapolate our findings to these specific situations.

Growth experiment

We hypothesised that the effect of *S. inaequidens* on marram grass growth would be negative, mainly because of interactions with the soil community. However, we concluded that the overall effect is positive. This effect is purely abiotic, since there is no significant interaction between sand sterilisation treatment and the provenance of the sand (underneath/away from *Senecio*). Similarly, intraspecific plant-soil feedbacks from *Senecio jacobaea* are also known to be (partly) abiotic (Wang et al. 2019), although the effect was negative in the cited study. Dassonville *et al.* (2008) showed that invasive species (*S. inaequidens* being one of the species included in their review) can have a positive effect on nutrient concentrations in plots with initially low concentrations. Since sand indeed has low nutrient concentrations (Reijers et al. 2020), this explanation is applicable here. Currently, we cannot verify this explanation since nutrient concentrations were not measured in the experiment.

Because marram grass growth was promoted in sand influenced by *S. inaequidens*, we can conclude that pyrrolizidine alkaloid concentrations had no, or a negligible, negative effect on marram grass. This is not surprising, since the most probable mechanism of PA enrichment of the soil is via passive release from roots and leaf litter (Joosten and van Veen 2012, Nowak et al. 2016, Selmar et al. 2019) and because some plants are even known to take up PAs without experiencing adverse effects (Nowak et al. 2016, Selmar et al. 2019). In contrast, Ahmed & Wardle (1994) found a negative effect of PA on plant growth. In our study, such a negative effect of PAs may have been counteracted by the simultaneous nutrient enrichment caused by *S. inaequidens*. This is in line with the observations by Reijers et al. (2020) that marram grass is more capable of coping with stressful conditions when nutrient availability is higher.

We observed a significant negative effect of soil biota on marram growth, with sterilisation of the soil having a positive effect on the biomass of marram, independent of the sand origin. This indicates that soil biota in the *Senecio* rhizosphere have approximately the same (negative) effect as the community within unvegetated sand. Thoden et al. (2009) found that PAs suppress the development of juvenile *Meloidogyne hapla* nematodes. Other species from this genus also colonise marram grass. However, it was suggested before that nematodes from this genus do not develop to adults on marram grass anyway (Van der Stoel et al. 2002). On the other hand, *Pratylenchus* nematodes are able to colonise both *Senecio* (Zasada et al. 2017) and marram grass roots (Van der Stoel et al. 2002), which would enable infection of marram roots by *Pratylenchus* spp. present on *Senecio* roots. However, arbuscular mycorrhizal (AM) fungi have low levels of endemism and host specificity (Davison et al. 2015, Aldorfová et al. 2020) and are known to colonise roots of *Senecio* spp. (van de Voorde et al. 2010, Alguacil et al. 2012, Reidinger et al. 2012). Since both European and American marram grass (*Calamagrostis arenaria* and *C. breviligulata* resp.) benefit from AM fungi when faced with nematode infection (Little and Maun 1996, De La Peña et al. 2006), it is possible that the negative effect of the nematodes is counteracted by the AM fungi also accrued on the *Senecio* roots. Furthermore, some studies have shown that *Senecio* species effectively reduce density or diversity, depending on the study, of whole soil communities (Kowalchuk et al. 2006, Thébault et al. 2010, Harkes et al. 2017). However, since these studies focussed on the effect on whole soil communities, it is difficult to make predictions for marram grass specifically. We conclude that PA concentrations in the field did not reduce the overall negative effect of the soil community, either because the community as a whole was affected and thus both negative and positive elements therein were reduced or because PA concentrations are too low to affect the soil community in general.

Our results indicate that the biotic soil community surrounding *Senecio* roots has approximately the same (negative) effect as the community within sand without plants growing in it (i.e., no significant interaction effect). Since endoparasites are known to be more damaging to marram grass (van der Putten and Van Der Stoel 1998), it could be that we excluded their effect because we did not use an inoculum from *Senecio* to infest the soil and consequently marram roots with endoparasites. On the other hand, the biota accumulating on the senecio roots could not be compatible with marram grass roots at all. Consequently, sand from unvegetated patches, which is thought to function as a temporary ‘enemy-free’ space for marram grass to root in (Van der Stoel et al. 2002), has the same biological effect on marram growth as *Senecio*-influenced sand.

The observed positive effect of sterilisation in the unvegetated sand is caused by soil biota, such as nematodes, who have survival stages that can disperse in the dunes (e.g., *Heterodera* cysts) and subsequently colonise the marram grass roots in the lab (e.g., De Rooij-Van Der Goes 1995, Van der Stoel et al. 2002). Indeed, studies investigating marram grass PSFs frequently used sand from the beach or even the sea floor for their control treatment (van der Putten et al. 1988, van der Putten and Troelstra 1990). However, we decided to take sand from the foredunes in order to maximise similarity of soil characteristics between *Senecio*-affected and unvegetated paired samples.

Since we only studied correlations, it could be that *S. inaequidens* established only on the more nutrient-rich sand in the dunes, which would in turn explain why marram grass grows better in this sand. However, this is very unlikely since dunes are extremely dynamic and hence the top layers of sand are thoroughly mixed, creating a homogenously resource-poor environment (Reijers et al. 2020). Furthermore, marram grass was growing in the dunes long before *Senecio*, thus, if there would be patches with more nutrients, those patches would likely already have been occupied by marram grass. When sand is fixated by plant roots, the mixing is halted and nutrient heterogeneity can start to occur. Since we took sand from the rhizosphere of *S. inaequidens*, higher nutrient availability caused by *S. inaequidens* is still a viable explanation for our findings.

Integration of field data and experiment

Sandy habitats, such as coastal dunes, are characterised by unstable substrate with many open patches of bare sand in between the vegetation. These patches are ideal opportunities for the establishment of new species (Axmanová et al. 2021). From our field survey, we can conclude that *S. inaequidens* is indeed capable of colonising these open patches. The results from our lab experiment further indicate that establishment of *S. inaequidens* can enhance marram growth in particular, but probably also plant growth in general, after it dies off and nutrients become homogenised. Analogous positive effects on growth of co-occurring plants have been found for other *Senecio* species (van de Voorde et al. 2011). This enhanced plant growth can lead to an overall shift towards more vegetated dunes, thus further intensifying the worldwide trend towards dune stabilisation (Gao et al. 2020). Dune stabilisation directly implies lower sediment transport to dune parts further inland, which may enable establishment of other species and hence accelerate natural succession.

For marram grass specifically, reduced sediment supply due to dune stabilisation leads to a shift towards a more clustered vegetation configuration (Reijers et al. 2021) which optimises sand capture at small spatial scales (Reijers et al. 2019a). In contrast, the potential for dune formation at larger spatial scales will be reduced, affecting dune geomorphology as a whole, ultimately resulting in lower dunes (Reijers et al. 2021). If lowered sediment supply indeed also accelerates dune succession, marram grass will be replaced more rapidly by other plant species less capable of forming dunes.

In conclusion, invasion of dune ecosystems by S. inaequidens could lead to a shift in sand dynamics by colonising bare sand patches, in turn accelerating the natural succession of dune vegetation. This could hamper dune growth and further reduce dune height. A reduction in dune height could in turn compromise coastal protection, since higher dunes are known to better protect the hinterland (Zarnetske et al. 2012, Seabloom et al. 2013).

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Author contributions

RVDW, MLV and DB designed the lab experiment. RVDW conducted the practical work, analysed the data and wrote the first draft of the manuscript. All authors contributed substantially to interpretation of the results and revision of the manuscript.

Competing interests

The authors have declared that no competing interests exist.

Data availability

The raw data are available via Zenodo at https://doi.org/10.5281/zenodo.6138540. (Van De Walle et al. 2022b)

2.6 Supplementary material

S2.1 Occurrence data Senecio inaequidens

Table S.1. *The spatial scale, coefficients, degrees of freedom (df), AICc values and weights for all models.*

Intrcpt	Scale	JC	JC^2	P	P^2	JC:P	JC:P^2	JC^2:P	df	logLik	AICc	delta	weight
-1.4	5	6.13		-8.84	15.75		-13.71		6	-182.35	376.96	0	0.13
-2.53	5	15.39	-11.49	-24.36	28	23.84	-32.06		8	-180.9	378.24	1.285	0.068
-3.14	5	12.46	-5.35	-8.92	14.82		-12.19		7	-181.99	378.32	1.367	0.065
-0.12	5	3.94		-16	22.28	11.32	-23.8		7	-182	378.34	1.379	0.065
-5.31	5	24.88	-19.21	-16.62	27.74		-32.03	18.12	8	-181.29	379.01	2.05	0.046
16.91	20	-48.58	35.72	-76		198.98		-131.09	7	-182.46	379.26	2.3	0.041
-0.37	5		6.74	-3.7	6.31			-10.87	6	-183.51	379.26	2.305	0.041
11.49	10	-27.49	18.04	-54.55		136.12		-86.61	7	-182.49	379.31	2.353	0.04
-0.82	10	18.97	-20.81	-47.71	43.24	58.18	-54.32		8	-181.54	379.5	2.547	0.036
-2.52	5	7.68		0.15	5.69	-12.43			6	-183.75	379.76	2.803	0.032
-2.52	5	8.23	-0.69	-4.38	5.96			-8.63	7	-182.99	380.32	3.366	0.024
-3	5	17.37	-13.38	-24.11	29.02	21.19	-33.63	3.41	9	-180.89	380.33	3.373	0.024
6.91	10	-6.81		-39.14	41.09	45.13	-50.06		7	-183.06	380.46	3.505	0.022
16.67	20	-47.91	37	-78.42	4.08	198.8		-134.01	8	-182.08	380.6	3.643	0.021
-4.05	5	15.33	-10.6	-2.21					5	-185.42	381.01	4.054	0.017
-5.24	20	30.89	-28.88	-64.04	61.77	79.24	-78.29		8	-182.31	381.05	4.097	0.017
11.52	10	-27.67	18.98	-54.22	1.77	132.73		-86.03	8	-182.36	381.14	4.188	0.016
4.68	10	0.37	-6.05	-55.4	32.6	93.58	-40.41	-32.76	9	-181.31	381.17	4.212	0.016
-3.84	5	13.13	-5.19	-1.11	5.4	-10.03			7	-183.45	381.24	4.281	0.015
7.44	20	-13.2	7.14	-79.03	34.83	157.72	-41.36	-78.02	9	-181.51	381.56	4.605	0.013
-0.09	5	0.3	5.41	-12.48	5.84	24.52		-26.25	8	-182.59	381.62	4.664	0.013
1.35	10			-2.41					3	-187.78	381.64	4.679	0.012
-8.17	10	41.23	-36.78	-29.24	50.07		-62.5	42.61	8	-182.71	381.86	4.906	0.011

-1.75	5	4.63		2.07		-6.34			5	-185.85	381.89	4.931	0.011
-4.66	5	18.76	-13.12	-4.83	2.44				6	-184.84	381.93	4.971	0.011
9.03	50	-35.64	31.29	-44.32		140.61		-105.75	7	-183.88	382.09	5.137	0.01
-0.44	5		3.78	0.46				-5.46	5	-185.99	382.15	5.194	0.01
5.43	20	-5.15		-44.85	48.86	53.27	-61.27		7	-184.01	382.36	5.406	0.009
-3.12	5	10.44	-5.47	-0.79				-2.88	6	-185.07	382.4	5.441	0.009
-3.62	5	12.47	-7.35	-0.07		-3.09			6	-185.21	382.67	5.714	0.007
1.03	50	8.55	-19.74	-57	58.37	97.43	-97.47		8	-183.19	382.81	5.85	0.007
1.08	5			-1.9					3	-188.49	383.06	6.102	0.006
-0.02	5	1.92		-2.39					4	-187.52	383.16	6.199	0.006
0.77	10				-2.08				3	-188.57	383.22	6.262	0.006
4.44	50	-9.05	0.47	-58.04	42.14	124.61	-66.43	-45.99	9	-182.37	383.28	6.322	0.005
-0.35	5	1.51	1.38	-10.89		29.82		-24.14	7	-184.54	383.42	6.461	0.005
1.64	10			-3.77	1.26				4	-187.66	383.44	6.48	0.005
-4.4	10	15.89	-10.62	-2.42					5	-186.7	383.57	6.613	0.005
-3.68	5	13.04	-9.26		-1.77				5	-186.7	383.58	6.622	0.005
0.97	10	0.55		-2.51					4	-187.74	383.6	6.643	0.005
1.34	10		0.03	-2.42					4	-187.78	383.68	6.726	0.004
-1.2	5	2.92			2.67		-6.24		5	-186.84	383.86	6.906	0.004
0.03	10	3.44		-7.69	12.9		-10.39		6	-185.88	384.01	7.049	0.004
1.48	20			-2.74					3	-189.05	384.16	7.205	0.004
8.93	50	-35.27	31.49	-44.69	1.17	139.69		-105.99	8	-183.87	384.17	7.21	0.004
0.67	5				-1.67				3	-189.07	384.21	7.257	0.003
0.75	5		0.95	-2.22					4	-188.11	384.34	7.383	0.003
0.85	20				-2.58				3	-189.32	384.71	7.755	0.003
-5.03	10	19.29	-12.94	-5.11	2.52				6	-186.25	384.75	7.798	0.003
-3.01	5	9.76	-5.97		1.1		-3.93		6	-186.3	384.86	7.9	0.002

-0.43	20	2.66		-3.18					4	-188.42	384.95	7.994	0.002
-0.29	5	1.53			-2.01				4	-188.42	384.95	7.995	0.002
1.19	5			-2.48	0.54				4	-188.46	385.04	8.079	0.002
0.1	5	1.96		-3.17	0.73				5	-187.46	385.09	8.133	0.002
-5.44	10	20.87	-15.4	-5.61		4.24			6	-186.45	385.14	8.187	0.002
4.59	50	-9.8		-36.48	38.72	64.82	-68.4		7	-185.41	385.15	8.192	0.002
-12.58	20	52.35	-43.63	-35.16	63.06		-79.96	52.32	8	-184.41	385.25	8.291	0.002
0.61	10	0.22			-2.11				4	-188.57	385.25	8.296	0.002
0.85	10		-0.15		-2.04				4	-188.57	385.25	8.298	0.002
0.76	10		1.13	-1.24				-2.03	5	-187.56	385.29	8.338	0.002
0.67	20		1.52	-3.12					4	-188.59	385.3	8.34	0.002
1.27	10	0.54		-3.85	1.25				5	-187.62	385.42	8.462	0.002
0.35	10	1.41		-1.12		-1.84			5	-187.65	385.49	8.532	0.002
1.65	10		-0.01	-3.76	1.27				5	-187.66	385.5	8.54	0.002
-5.08	10	18.75	-13.19	-3.14				1.24	6	-186.65	385.54	8.585	0.002
-2.93	10	12.49	-6.78	-7.34	10.49		-7.64		7	-185.63	385.59	8.632	0.002
-3.94	10	13.36	-9.18		-1.98				5	-187.78	385.73	8.773	0.002
-0.85	20	2.25			-2.92				4	-188.84	385.81	8.85	0.002
0.37	5		0.72		-1.88				4	-188.84	385.81	8.851	0.002
0.84	10		2.71	-3.75	4.07			-5.19	6	-186.82	385.89	8.929	0.001
0.05	20		1.37		-2.9				4	-188.94	385.99	9.033	0.001
-1.94	20	6.56		-9.01	14.77		-12.03		6	-186.89	386.04	9.083	0.001
1.43	20			-2.52	-0.22				4	-189.04	386.2	9.248	0.001
-4.9	20	15.1	-8.36	-3.17					5	-188.02	386.21	9.258	0.001
0.86	5		0.96	-2.81	0.56				5	-188.07	386.33	9.369	0.001
-0.22	20		3.26	-1.36				-3.18	5	-188.14	386.45	9.495	0.001
-0.17	10	3.21		-1.79	3.37	-5.7			6	-187.15	386.55	9.597	0.001

-1.35	20	3.99		-1.17		-2.73			5	-188.25	386.69	9.731	0.001
-4.21	10	16.14	-9.9	-4.88	3.27			-1.77	7	-186.19	386.72	9.76	0.001
0.05	10	0.98			0.42		-3.16		5	-188.32	386.81	9.858	0.001
-5.23	10	20.16	-13.88	-5.59	2.22	1.07			7	-186.24	386.82	9.864	0.001
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0.61	20		1.52	-2.83	-0.28				5	-188.59	387.35	10.392	0.001
-1.42	20	3.03			-0.5		-3.06		5	-188.66	387.5	10.54	0.001
-3.32	20	9.2	-4.73		-2.86				5	-188.71	387.61	10.652	0.001
-0.21	20		5.14	-4.07	4.49			-6.56	6	-187.71	387.66	10.708	0.001
-4.05	10	13.76	-9.51		-2.25		0.34		6	-187.77	387.8	10.841	0.001
-3.65	20	11.66	-3.62	-9.11	14.15		-11.07		7	-186.84	388.02	11.067	0.001
-5.79	20	18.44	-10.52	-4.83	1.61				6	-187.92	388.09	11.136	0
-3.78	20	10.86	-4.72	-2.26				-1.61	6	-187.95	388.14	11.187	0
-4.93	20	15.23	-8.48	-3.24		0.09			6	-188.02	388.29	11.33	0
-1.93	20	5.74		-1.84	3	-5.99			6	-188.06	388.38	11.42	0
-3.73	20	10.7	-2.72	-4.91	4.43			-5	7	-187.53	389.39	12.434	0
-2.5	20	6.27	-2.32		-1.01		-2.38		6	-188.64	389.52	12.568	0
-5.28	20	16.25	-8.01	-3.73	2.77	-3.1			7	-187.85	390.05	13.089	0
-4.01	5	15.09	-12.74						4	-191.44	390.99	14.033	0
-4.08	10	15.37	-12.64						4	-192.26	392.64	15.685	0
1.45	10		-2.32						3	-193.33	392.74	15.783	0
-0.23	50		2.39	-2.43					4	-192.41	392.93	15.974	0
-1.02	50	2.93		-2.39					4	-192.68	393.47	16.513	0
-0.64	50		2.23		-2.53				4	-192.68	393.49	16.532	0
2.31	10	-2.96							3	-193.83	393.73	16.778	0
-1.27	50	2.56			-2.36				4	-193.07	394.26	17.305	0
0.78	50			-1.57					3	-194.21	394.49	17.532	0

0.47	50				-1.68				3	-194.32	394.71	17.753	0
0.68	5		-1.3						3	-194.35	394.78	17.819	0
0.53	50	-2.53	4.26	-2.39					5	-192.34	394.85	17.898	0
-0.41	50		2.94	-2.02				-1.06	5	-192.36	394.9	17.939	0
-0.03	Int.								2	-195.45	394.94	17.979	0
-0.21	50		2.39	-2.52	0.1				5	-192.41	394.99	18.033	0
0.88	50	-4.99	6		-2.6				5	-192.41	395.01	18.049	0
-0.43	50	1.82		-3.92		2.53			5	-192.48	395.15	18.189	0
-0.92	50	2.99		-3.19	0.93				5	-192.65	395.47	18.513	0
-0.74	50		1.17						3	-194.87	395.8	18.847	0
0.74	5	-1.07							3	-194.99	396.05	19.096	0
-1.03	50	1.33							3	-195.02	396.11	19.154	0
-1.21	50	2.46			-2.72		0.5		5	-193.07	396.31	19.355	0
0.72	20		-1.12						3	-195.14	396.35	19.39	0
-1.45	50	5.22		-7.47	10.68		-7.6		6	-192.12	396.49	19.531	0
0.78	50			-1.57	0				4	-194.21	396.54	19.58	0
1.08	20	-1.38							3	-195.24	396.54	19.588	0
0.8	50	-4.73	7.07	-1.48				-2.26	6	-192.17	396.6	19.642	0
-0.38	50		4.56	-4.19	3.92			-4.11	6	-192.2	396.65	19.697	0
0.91	50	-5.7	6.96		-1.03		-2.29		6	-192.32	396.89	19.934	0
0.64	50	-3.28	4.81	-1.69	-0.81				6	-192.32	396.89	19.936	0
0.5	50	-2.15	3.71	-2.81		0.71			6	-192.33	396.91	19.951	0
0.02	50	-0.09		-2.72	-4.09	6.38			6	-192.33	396.91	19.957	0
0.38	50	-3.71	3.95						4	-194.7	397.52	20.566	0
-3.35	20	11.02	-8.37						4	-194.81	397.73	20.776	0
0.16	50	-1.31	5.1	-6.01	9.09		-7.8		7	-191.73	397.8	20.845	0
-1.78	50	12.01	-13.55	-13.92	26.24		-43.1	31.37	8	-190.86	398.16	21.205	0

0.63	50	-3.96	7.69	-3.34	3.14		-4.47	7	-192.07	398.48	21.526	0
0.81	50	-3.51	3.43	-1.78	-3.57	4.14		7	-192.21	398.75	21.796	0

S2.2 PCA growth experiment

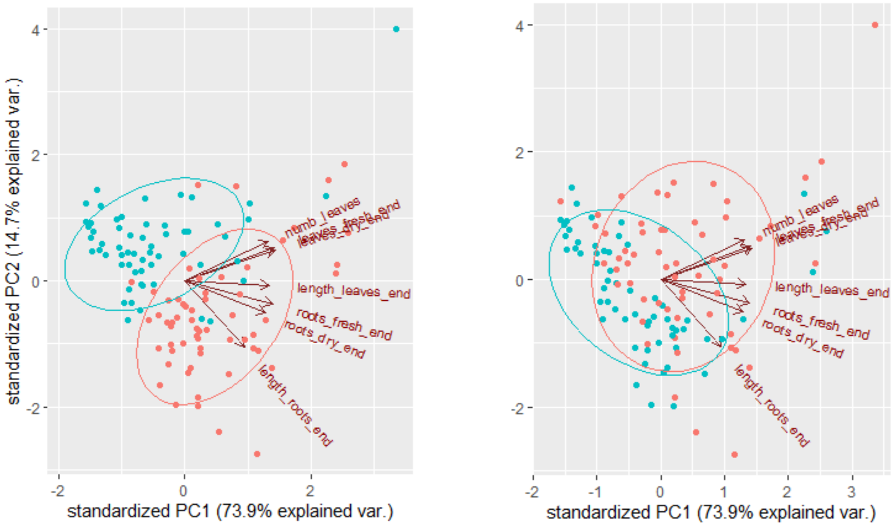


Figure S2.2 *PCA plots for growth experiment. Groups: (left) biota-treatment: red = sterilized, blue = unsterilized; or (right) Senecio-treatment: red =* S. inaequidens*, blue = unvegetated sand.*

Table S2.2 *Correlation of all measured traits with PC1*

Measured trait	**Correlation with PC1**
Number of leaves	0.86
Length of leaves	0.88
Length of roots	0.62
Weight of leaves (fresh)	0.93
Weight of roots (fresh)	0.91
Weight of leaves (dry)	0.94
Weight of roots (dry)	0.84

S2.3 Sensitivity analysis of results

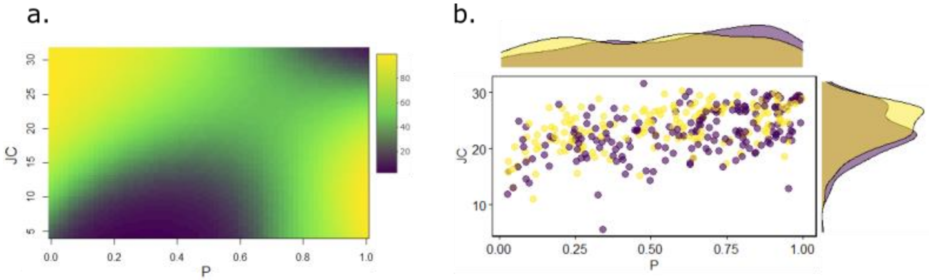
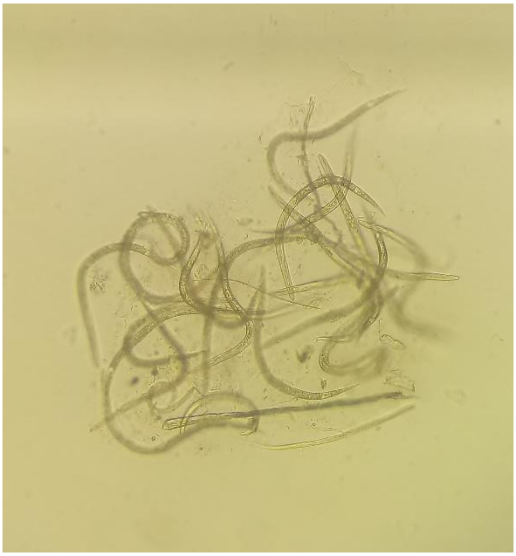


Figure S2.3 *The analysis of the occurrence data, rerun without samples with very low P and JC values.* ***(a)*** *The overall relation between the probability of occurrence of* S. inaequidens *and the spatial configuration of marram grass. The colours indicate the probability of occurrence as %.* ***(b)*** *Density distribution plots of the observed cover (P) and spatial autocorrelation (JC) of marram grass within a 5m radius of the central marram grass tussock. This plot only contains the data of the transects where S. inaequidens was found. Colours indicate whether* S. inaequidens *was present (yellow) or absent (purple).*

Chapter 3

The functional composition of dune nematode communities is structured by both biogeographic region and the local marram grass environment

Ruben Van De Walle, François Massol, Martijn L. Vandegehuchte & Dries Bonte



Nematodes extracted from the roots of *C. arenaria.*

Under review at European Journal of Soil Biology

3.1 Abstract

Nematodes are involved in many important ecosystem functions such as nutrient cycling and plant growth. Nematode communities are thought to be structured at regional scales mainly by abiotic soil characteristics and climatic drivers and at local scales by habitat heterogeneity and biotic interactions. In blond dunes, nematode food webs are associated with marram grass (*Calamagrostis arenaria*), the key dune-forming plant species in Western Europe.

We investigated the relative importance of regional biogeographic factors and local biotic drivers, such as the vegetation’s spatial structure and the occurrence of an invasive plant species, in determining the functional diversity of belowground nematode communities inhabiting the roots of marram grass and surrounding soil in coastal dune areas.

We found that nematode functional group abundances mainly differed among biogeographic regions, but that abundances could not be linked to plant-associated parameters. Additionally, the abundances of different functional groups seemed to be positively associated within both rhizosphere and bulk soil, an effect that could be the result of ecological filtering or facilitative interactions.

Nematode pressure has been assumed to be an important driver of marram grass degeneration under ceasing sand dynamics. We here show that variation in nematode functional group composition is only weakly related to these local changes in plant vigour, but that large-scale patterns in nematode communities may explain regional variation in marram dynamics in coastal dunes.

3.2 Introduction

Nematodes are the most abundant animals on the planet, occurring in all ecosystems. They are involved in many important ecosystem functions such as nutrient cycling and plant growth, coupling basal resources to higher trophic consumers and even killing larger animals such as insect larvae (Lacey and Georgis 2012, Bardgett and van der Putten 2014, van den Hoogen et al. 2019, Potapov et al. 2022). The distribution of feeding guilds or functional roles of nematodes within a soil food web is a well-established, useful indicator of soil food web functioning, as the different nematode feeding guilds represent links to the other major groups of soil organisms such as plants, bacteria and fungi (van den Hoogen et al. 2019, Potapov et al. 2022).

Nematode numbers and functional group composition are affected by abiotic factors at different spatial scales. Global analyses indicate total nematode and functional group abundances of soil nematodes to be mainly affected by regional soil characteristics such as soil organic carbon content or soil acidity (Song et al. 2017, van den Hoogen et al. 2019). Climatic drivers, such as precipitation and mean annual temperature, also affect nematode abundances, albeit not as pronounced as soil characteristics (Song et al. 2017, van den Hoogen et al. 2019).

Local processes are all the more important when trying to understand soil nematode community structure since nematodes are often thought to be poor dispersers. Complete taxonomic family lineages, for instance, have been reported to have restricted distributions (Nielsen et al. 2014), while nematodes in general only disperse up to one meter per year (Bardgett and van der Putten 2014). Nevertheless, passive dispersal seems to enable nematodes to disperse over longer distances (De la Peña et al. 2011, Fontaneto 2019). Soil disturbance and environmental heterogeneity are examples of small-scale phenomena commonly linked to nematode abundances (Gingold et al. 2010, Mateille et al. 2011, Orgiazzi et al. 2016, Song et al. 2017). Disturbed soils mainly host opportunistic bacterivorous nematodes, and are poor in predatory and omnivorous species (Bongers and Ferris 1999, Nielsen et al. 2014, Orgiazzi et al. 2016). An increase in potential niches due to environmental heterogeneity also increases nematode species diversity (Tews et al. 2004, Rahman et al. 2009, Gingold et al. 2010). Finally, the abundance and functional diversity of soil biota is not only driven by abiotic factors. Biotic interactions among nematodes and between nematodes and other taxa, especially host plants, can furthermore influence nematode abundances. The characteristics of the vegetation (plants species composition) will affect the nature and amount of resources available to the food web via root exudates, root turnover, leaf litter return, and water use (Rajaniemi and Allison 2009, Orgiazzi et al. 2016). Moreover, plants can defend themselves against herbivory either directly, e.g., via production of chemical compounds (Caño et al. 2009), or indirectly, e.g., by attracting natural predators of their pests (Sabelis et al. 2001, Hazir et al. 2016). Apart from host plants, invasive plant species can also drastically alter nematode abundances (Čerevková et al. 2020, Renčo et al. 2021), for instance, via altering the native plant community (Renčo et al. 2021) or by acidification of the soil (Lazzaro et al. 2018).

One host plant species from which the soil nematode community is already well described is marram grass (*Calamagrostis arenaria* (L.) Roth*,* formerly *Ammophila arenaria*). This plant received much attention due to its key role in the process of dune formation in Western Europe (Huiskes 1979), which is driven by the interaction between vegetation development and aeolian dynamics, the movement of sand by wind. Marram grass not only tolerates high levels of sand burial, it even needs sand burial to survive and it thrives best at intermediate burial rates of about 30 cm of sand per growing season (Nolet et al. 2018). If sand dynamics cease, marram grass slowly decays and is outcompeted by later successional plant species (van der Putten et al. 1993). This phenomenon was already observed more than fifty years ago and coined 'the *Ammophila* problem' (Marshall 1965). Marram grass is able to overcome this problem by capturing sand, which in turn positively affects its growth and sand accumulation capacity, causing a positive feedback loop. The reduction in marram grass performance is thought to be caused by the biological component of the soil, in particular the root-feeding nematodes (van der Putten et al. 1988, 1993, Brinkman et al. 2005b, Piśkiewicz et al. 2009a; see Bonte et al. (2021) for a review).

At the regional scale, dune soil characteristics depend strongly on the biogeographic history of the area, which is tightly linked with large-scale differences in soil pH, nutrient concentrations and climate variables. At this regional spatial scale, differences in nematode community patterns could be explained by the sediment origin of the foredune when comparing Southern and Western European samples (Mateille et al. 2011). Variation in soil characteristics in dune areas within Western Europe is mainly linked with acidity and nutrient concentrations. For example, the Belgian coast consists of lime-rich sand (Ampe 1999), while others are completely decalcified and thus more acidic, such as the Northern part of the Dutch coast (Eisma 1968). More acidic soils are known to harbour lower nematode numbers (Wu et al. 2011). In marram dunes, the constant sand burial can be seen as a form of (natural) soil disturbance varying locally, which is possibly linked to nematode abundances based on studies of nematodes in other ecosystems (Mateille et al. 2011, Song et al. 2017). If marram grass occurs in a patchy distribution, its sand-trapping efficiency is optimal (Reijers et al. 2019b, 2021, Bonte et al. 2021), and therefore the associated nematode abundances (especially those of predatory and omnivorous nematodes) are expected to be lower.

While marram grass is the dominant plant species in many European coastal dunes, the invasive herb *Senecio inaequidens* D.C. is expanding its range into European coastal dunes (Van De Walle et al. 2022a). Plants of the *Senecio* family are well-known for their production of pyrrolizidine alkaloids as defence mechanism against herbivory (Joshi and Vrieling 2005, Caño et al. 2009), with *S. jacobaea* even shown to protect surrounding plants via associational resistance (Liu et al. 2022). What the long-term effects of the colonization of coastal dunes by *S. inaequidens* will be is largely unknown

(Van De Walle et al. 2022a). However, giving its potent chemical defenses, effects of *S. inaequidens* invasion on dune soil food webs are plausible.

As marram grass seems to mainly rely on a combination of sand overtopping and associations with microorganisms to escape root-feeding nematodes (De La Peña et al. 2006, Piśkiewicz et al. 2009a), local biotic interactions are omnipresent in marram dunes. Interspecific competition among nematodes has been shown to alleviate average declines in marram grass fitness under lab conditions (Brinkman et al. 2005a). However, addition of the same species did not influence plant performance in a more natural environment (Brinkman et al. 2005b). Facilitating interactions between nematodes received far less attention; nevertheless it has been established in some lab experiments (Brinkman et al. 2008, Nieminen 2009, Blanco-Pérez et al. 2017, Gansfort et al. 2018).

We investigated the relative importance of regional biogeographic factors, associated with soil characteristics and climate, and two local biotic drivers: marram grass spatial structure and *Senecio inaequidens* occurrence, in determining the functional structure of belowground nematode communities inhabiting the roots of marram grass and the surrounding soil in coastal dune areas in Western Europe. We hypothesised that 1) at regional spatial scales, nematode functional abundance would be lower in the coastal dunes of the Wadden district and the UK than in the Boulonnais and Flemish dune regions as the former have a more acidic soil. 2) An increasing cover of marram grass would positively influence abundances of nematodes found in the roots, while 3) nematode abundances would increase with clustering of the host plant as a consequence of the less efficient sand-capture of these configurations. 4) The fungivorous and bacterivorous nematodes are expected to be more abundant in soil from underneath less vital marram grass tussocks due to the presence of decomposing organic matter and fungus growth, while root-feeding nematodes are expected to increase in abundance with marram grass vitality. 5) Since *Senecio* species are known to produce chemical compounds, we expect a decline in all, but especially root-feeding, nematode functional group abundances when *S. inaequidens* is present in the vicinity.

3.3 Material & Methods

Study area

Our study was conducted in the North of France, Belgium, the Netherlands and the United Kingdom. Respectively, 124, 39, 19, 30 samples were taken along 19 different transects parallel to the coast line in these countries. The transects were located within the first 100 m from the seaward side of marram-dominated, yellow dunes (Natura 2000 habitat 2120, CORINE biotope 16.21). The number of samples per transect depended on the length of the dune transect, with an average of 11 samples per transect (min 4; max 31). Individual sampling locations were separated by at least 20 m.

We subdivided our study area into five distinct biogeographical districts, which differ all in their soil characteristics because of their geological history (Bonte et al. 2003). These differences in soil covary with climatic variables, but also nutrient conditions, aeolian dynamics and overall vegetation characteristics. Because these parameters vary at regional scales, rather than at local scales in the blond dunes, any detailed analysis of putative abiotic and biotic drivers beyond the biogeographical effects, is therefore impossible. The first biogeographical district situated within the study area is the Southern UK, which is different from all other regions because it is not situated on the mainland. The Boulonnais region in Northern France stretches from Camiers to Dunkerque. The sand in this region is lime-rich due to the proximity of rocky lime formations. The Flemish dune region is situated from Dunkerque to Knokke. The sand in this region is again rich in lime, but it is situated on marine clay. The Renodunal region runs from Cadzand to Bergen-aan-Zee. These dunes are more influenced by the Scheldt and the Rhine and are still lime-rich, albeit a little less than the two previous regions. They are consequently a little more acidic. Finally, the Wadden district in the Netherlands continues northwards from Bergen-aan-Zee to Texel and is characterized by completely decalcified sand with low nutrient concentrations and a higher acidity (Eisma 1968, Ampe 1999, Bonte et al. 2003).

Data collection

Each sampling location had a central marram grass (*Calamagrostis arenaria* (L.) Roth) tussock from which soil and root samples were taken at the minimum depth at which live marram grass roots were found during the summer of 2018 or 2019. Samples were stored in the field in a box containing cooling elements to slow down nematode metabolism, consequently lowering mortality. In the lab, samples were stored in the fridge until processing for the same reason. Nematodes were extracted from roots and sand separately, using 2 +/- 0.5 and 20 +/- 1 g fresh material respectively, via the Baermann Funnel extraction method (Hooper 1990). This method ensures that only the active fraction of the nematode soil community is quantified. Roots and soil were sieved (2.0 mm mesh) and roots were gently washed before the extractions. 15 mL water was collected every 24 h for three consecutive days. Finding fresh roots was difficult for some sampling locations, resulting in a relatively large difference in the amount of roots used for the extraction. To account for this discrepancy, the number of nematodes per gram dry sand/roots was determined by drying separate portions of substrates in an oven at 70°C for 24 h to obtain relative moisture content, which was consecutively used to calculate dry weights of the portion of the sample used for the extraction. Nematodes were fixed and stored in 5% hot formalin (60-70°C). The vials were sealed with parafilm until they were counted. While counting, nematodes were classified into functional groups, using an inverse stereo microscope, based on characteristics of their mouth apparatus, pharynx, and cuticle. These functional groups differ in their feeding habits: plant feeders, bacterial feeders, fungal feeders, omnivores and carnivores (Potapov et al. 2022). A sixth "Unknown" class was used for nematodes too damaged to classify. When nematodes were very abundant, classification was done until 200 nematodes were counted and numbers were then extrapolated based on the area of the counting dish.

The following variables were used as explanatory variables in the analysis: The proportion of marram grass and its spatial configuration, the vitality of the tussock, the biogeographical district (as described above), and the presence-absence of *Senecio inaequidens*.

Within a 10 m radius around each central marram grass tussock, marram grass cover (P, expressed as proportion) and spatial auto-correlation (Moran's I; Moran 1950, Bivand and Wong 2018) were calculated from vegetation maps of the coastal dune areas (Bonte et al. 2021). Moran's I is negative when the marram grass is regularly distributed in the landscape. If marram grass is randomly distributed, the parameter is close to 0, and it is positive when the marram grass occurs in clusters. As pointed out by Bonte et al. (2021), marram grass distribution is almost always clustered and rarely random. The sample locations were chosen so that they maximised the variety of surrounding marram grass configurations within one dune transect.

Furthermore, local environmental heterogeneity is mainly linked with marram grass vitality in our study: vital tussocks provide mainly fresh plant material while less vital tussocks provide a mixture of both alive and dead plant material. To include this parameter in our analysis, each marram grass tussock was given a vitality score (integer value ranging from 0 to 4) based on the estimated % of green leaves visible in the tussock on a photograph. Finally, occurrence (presence/absence) of *Senecio inaequidens* was mapped within a 5 m radius around the central marram grass tussock.

Statistics

The nematode data were simultaneously analysed using Joint Species Distribution Modelling (JSDM). More specifically, we used the Hierarchical Modelling of Species Communities (HMSC) framework according to the methods described by Ovaskainen & Abrego (2020). For this multivariate analysis, the functional group data (abundance per g of dry root or soil) for both the soil and root sample for each marram grass tussock were (log + 1)-transformed. The proportion of marram grass and its spatial configuration, the vitality of the tussock, the biogeographical district and the presence-absence of *S. inaequidens* were used as explanatory variables. To test for a quadratic effect of the proportion of marram grass (P) and the vitality (V) of tussocks, four JSDMs were fitted with either P and/or V as a quadratic term or not. Among those, the 'best' model was selected using the Widely-Applicable Information Criterion (WAIC; Watanabe 2010, Ovaskainen and Abrego 2020). The random effect structure was implemented to account for the spatial context of our study. A large-scale random effect was modelled on the transect level to correct for possible dependency of data within transects. A local random effect was modelled on the marram grass tussock level. This enables us to infer residual associations between feeding guilds after accounting for the effects of the explanatory variables (Ovaskainen and Abrego 2020). Partitioning of the explained variance between all fixed and random effects was used to discern the importance of the different parameters for functional group abundances. The F-statistic of the fixed effects was manually calculated in order to account for the varying degrees of freedom when comparing relative importance of the effects.

For all models described above, the posterior distribution was sampled with three Markov chain Monte Carlo (MCMC) chains. HMSC specifically uses blocked Gibbs sampling (Tikhonov et al. 2020a). Each chain ran 150 000 iterations, with a burn-in period of 50 000 samples and thinning factor of 100. Each chain ran for 1000 posterior samples per chain for a total of 3000 posterior samples.

R Statistical Software version 4.0.4 (R Core Team 2021) was used for all data analyses. Moran's I of marram grass surrounding the central tussock was calculated using the "moran.test" function from the "spdep" package (Bivand and Wong 2018). The HMSC was performed using the R package "Hmsc" (Tikhonov et al. 2021). Trace plots, autocorrelation plots and posterior densities were made and calculated using the 'mcmcplots' package (Curtis 2018).

3.4 Results

Total nematode counts varied from 29 to 6800 individuals per gram of dry roots or 0.1 to 92 per gram of dry bulk soil, with means (median) of 1236 (890) and 6 (4.4) respectively. Root-feeding nematodes were most abundant in root samples, while bacterivores were most abundant in soil samples (see Fig. 3.1a and 3.1b). Total nematode abundances were lowest in the Renodunal district, followed by the UK, for both the root and soil portions of the samples (see Fig. 3.1c and 3.1d).

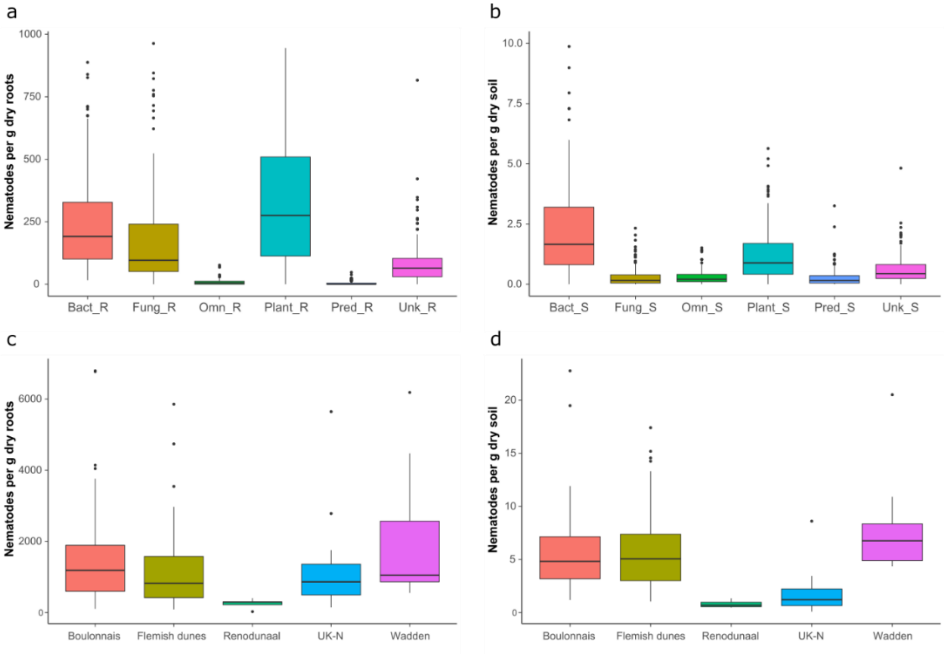


Figure 3.1 *The number of nematodes found per functional group in **(a)** the roots and **(b)** the soil. Bact: bacterivore nematodes, Fung: fungivore nematodes, Omn: omnivore nematodes, Plant: root-feeding nematodes, Pred: predatory nematodes, Unk: Unknown class., the last letter of the code indicates the substrate used for the extraction (R = roots, S = soil). The total number of nematodes found in **(c)** the roots and **(d)** the soil per biogeographical district. For c & d, boxplots are based on 74 samples for the Boulonnais, 89 samples for the Flemish dunes, 10 for the Renodunal district, 30 for the UK and 9 for the Wadden district.*

MCMC convergence and model selection

The potential scale reduction factors were all below the 1.1 threshold for all models and the trace plots of the iterations showed an irregular pattern with similar running means for all chains. Thus, convergence of the HMSC models was good for all four models. Based on WAIC, no clear best model could be discriminated, thus the least complex model was chosen for further analysis (also lowest WAIC, see table 3.1).

__Table 3.1__ Summary measures of model fit and model selection. For R2 and RMSE the mean is given over all species with the interquartile range between parenthesis. CV stands for cross-validation.

Model	Str.	R	R (CV)	RMSE	RMSE (CV)	WAIC
1	P + Vit	0.545 (0.244)	0.109 (0.131)	0.494 (0.307)	0.711 (0.590)	25.87953
2	P^2 + Vit	0.548 (0.251)	0.090 (0.164)	0.492 (0.610)	0.769 (0.788)	25.99523
3	P + Vit^2	0.550 (0.249)	0.081 (0.139)	0.490 (0.611)	0.771 (0.745)	25.96141
4	P^2 + Vit^2	0.528 (0.343)	0.075 (0.091)	0.465 (0.544)	0.777 (0.717)	27.21449

Responses to environmental variables

When describing the relationship between the environmental variables and the different functional groups, we focussed only on effects with at least 95% posterior probability (Fig. 3.2). The proportion of marram grass in the near vicinity was only positively correlated with the abundance of root-feeding nematodes found in the roots, while it was negatively correlated with the abundance of omnivores found in the bulk soil. The spatial configuration of marram grass only affected the abundance of fungivorous nematodes found in the rhizosphere. Fewer predatory and fungivorous nematodes were found in the bulk soil of more vital marram grass tussocks. The biogeographical regions clearly affected the root and soil nematode functional abundances, with generally more nematodes found in the Boulonnais and the Wadden district, and fewer nematodes in the Renodunal district and in the UK. Finally, the presence of *Senecio* positively influenced all nematode abundances found in the bulk soil, except fungivore nematode abundance.

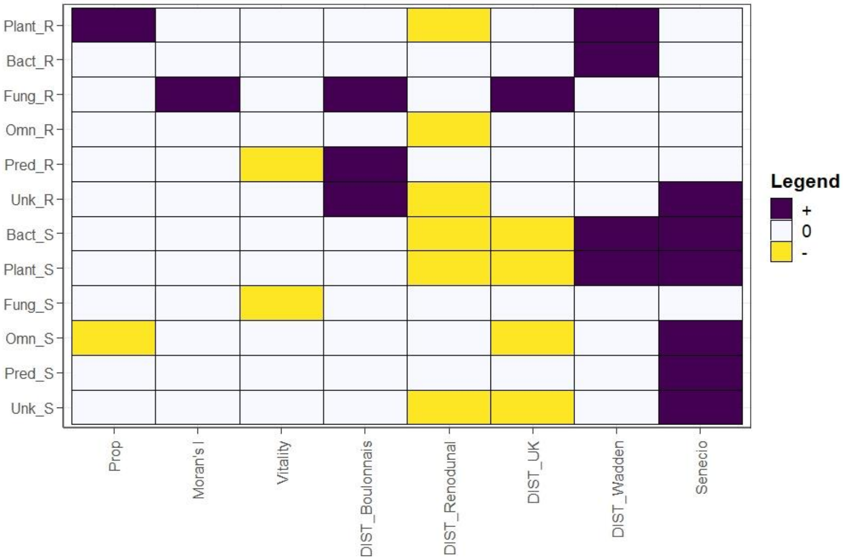


Figure 3.2 *The responses (β's) of the species to the environmental variables. Responses that are positive with at least 95% posterior probability are shown in purple and responses that are negative with at least 95% posterior probability are shown in yellow. Functional groups are indicated on the y-axis, codes as in Fig. 3.1.*

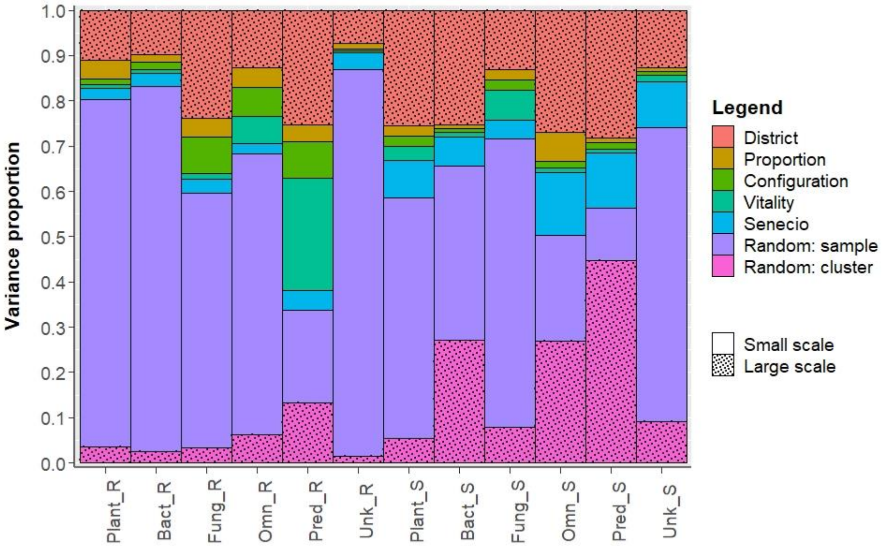


Figure 3.3 *Variance partitioning of the explained variation among the random and fixed effects in the HMSC model. The two random effects are based on the residual variation. Functional groups are indicated on the x-axis, codes as in Fig. 3.1.*

Variance partitioning (Fig. 3.3) showed that the regional variability explained by the biogeographic district accounted for (median) 18.9% ($F_{4,192}$ = 13.8) of the total variation. The local environmental variables explained 15.6% ($F_{4,192}$ = 11.4) together. Among the local environmental variables, the explained variation was distributed as follows: the presence of *S. inaequidens* explained 4.3 % ($F_{1,192}$ = 12.5), the proportional cover of marram grass 2.3 % ($F_{1,192}$ = 6.73), marram grass spatial configuration 1.6 % ($F_{1,192}$ = 4.68) and marram grass vitality 1.1 % ($F_{1,192}$ = 3.22). Finally, the residual variance on sample level scale captured 59.1%, while the random effect on transect unit scale covered 7.1%. Most variation is thus associated with single samples, demonstrating that either other unmeasured effects or stochasticity are driving most of the variation in the local nematode functional group composition. From the residual association matrix (Fig. 3.4), it is very clear that different nematode functional groups extracted from the roots are highly positively associated with each other, and that the same holds true for nematodes extracted from soil. Several weaker positive associations were found among nematode functional groups from bulk and rhizosphere soil.

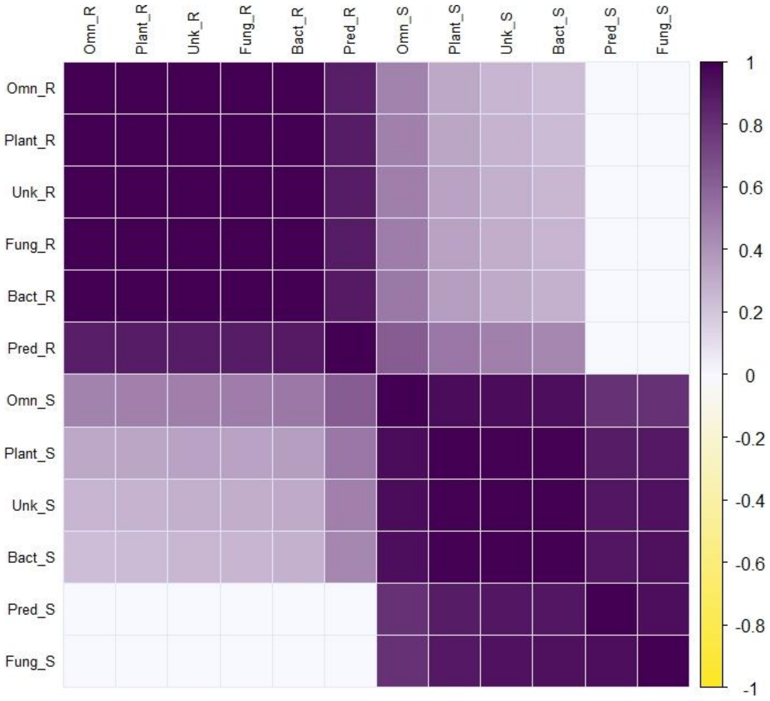


Figure 3.4 *Residual species association matrix that shows species pairs with a positive (purple) or negative (yellow) association. Associations are only shown if they had at least 95 % probability. Functional groups codes as in Fig. 3.1.*

3.5 Discussion

Compared to other terrestrial biomes, coastal dune areas are characterised by intermediate nematode abundances in the bulk soil with an average total of 6 nematodes per gram of soil, as expected (Costa et al. 2012, van den Hoogen et al. 2019). With an average of 1200 nematodes per gram of roots, nematode abundances found in marram grass roots and rhizosphere were on the higher end, but still within expectations (Van der Stoel et al. 2006, Vandegehuchte et al. 2010b).

The biogeographical districts differed significantly in terms of nematode abundances, with the lowest abundances in general found in the Renodunal district, while the UK had low nematode counts in bulk soil samples only. The differences between the districts could be related to complex changes in climate and soil characteristics (Mateille et al. 2011, van den Hoogen et al. 2019) or to unmeasured marram grass properties (defensive mechanisms or nutrient composition) possibly covarying with climate or soil characteristics. However, the ameliorating effect of the sea dampens climatic variability (Wiedemann and Pickart 2004) while dune ecosystems are homogenously resource-poor (Reijers et al. 2020). Thus, neither climate nor soil nutrients are likely to explain these results. We consequently expect these differences in nematode numbers to be mainly explained by a difference in soil acidity (Wu et al. 2011). However, since none of these parameters were measured, elaborating on the actual cause should be done cautiously. The variance partitioning clearly indicated that this regional factor greatly influenced nematode functional group abundances. Such a relationship was already known for other groups, i.e., plants and spiders (Lambinon et al. 1998, Bonte et al. 2003), and is here confirmed for soil nematodes. Overall, biogeographical districts unequally influenced the abundance of different nematode functional groups, consequently changing nematode functional diversity.

As expected, more root-feeding nematodes were found in marram grass roots when more marram grass was present in the near vicinity because of the higher resource concentrations in the form of marram grass roots. Additionally, this may partly be explained by the low plant diversity in marram grass-dominated dunes, where marram grass forms large quasi-monocultures, while diverse plant communities have been shown to decrease belowground herbivore loads (Cortois et al. 2017). Other functional groups were not correlated with the proportion of marram grass, except for the number of omnivores found in the bulk soil, which declined when there was more marram grass present. Assuming omnivorous nematodes are mainly affected by resource availability (Li et al. 2022), our results seemed to indicate that these nematodes are able to find more food in bare sand. Omnivorous nematode species are indeed able to live in bare sand, albeit together with an abundance of bacterivorous and fungivorous nematodes potentially serving as food source (McSorley 2011). Next to other nematodes, omnivorous nematodes are known to feed on numerous soil microbes ranging from algal filaments to protists, supplemented with fungal hyphae and bacteria when their primary food sources are unavailable (Orgiazzi et al. 2016). Increased competition for nutrients of these soil microbes with marram grass roots could decrease their numbers, consequently explaining the decrease in omnivorous nematode abundance when marram grass cover is higher.

We hypothesised nematode abundances to increase with an increasing clustering of marram grass because of the lower sand-capture efficiency (Reijers et al. 2019a, 2021, Bonte et al. 2021) and because the captured sand is thought to be largely free of nematodes. This was only true for fungivorous nematodes residing in the rhizosphere, while no correlations were found for other nematode functional groups. These results confirm that fungivorous nematodes are sensitive to disturbances of different origins, but thrive under more stable conditions (Orgiazzi et al. 2016). The mechanism behind this process is most likely linked to the development of fungi. Fresh wind-blown sand from the beach only contains low amounts of fungi (Mudryk et al. 2013). When sand accretion slows down, development of fungi around marram grass roots can be assumed to increase, while fungal development is minimal in bulk soil because it is probably not suitable for most hyphae formation (Rajaniemi and Allison 2009). Hence, fungivore nematode abundance only increased in the rhizosphere. The lack of correlations between other nematode groups and the spatial clustering of marram grass could point towards a relatively quick colonization of marram grass roots by soil nematodes after initial formation, confirming observations of other field studies (Van der Stoel et al. 2006).

Less vital marram grass tussocks are characterized by increasingly more dead stems and leaf litter deposition. This organic material, together with the high microbial biomass they support, provides additional habitat and feeding opportunities for many soil nematode groups (Rahman et al. 2009, van den Hoogen et al. 2019). Because of this increased resource availability, we expected a decrease in nematode abundances for all nematode functional groups with increasing vitality, except for root-feeding nematodes. Predatory and fungivorous nematodes were found in larger quantities in respectively the rhizosphere and bulk soil from less vital marram grass tussocks, hinting at the indirect importance of dead organic material for these nematode functional groups (Orgiazzi et al. 2016). Fungivorous nematodes benefit from an increase in fungi due to the availability of decaying organic material while predators might profit from increased prey abundances. On the other hand, predators could benefit from increased water retention underneath tussocks with more leaf litter (Preisser et al. 2006). Our results demonstrate that bacterivorous and omnivorous nematodes were able to find enough food, even when less dead plant material was available. Note that marram grass vitality is based on the aboveground part of the marram grass tussock. Including root vitality, which is shown to correlate with endoparasitic root-feeding nematode numbers (Vandegehuchte et al. 2010b), could furthermore help clarify drivers of specific nematode functional groups.

Contrary to our hypothesis, the presence of *Senecio inaequidens* had a positive rather than a negative effect on the abundance of nematodes in bulk soil, except for fungivores nematodes. The most likely explanation for these results is an increase in nutrient concentrations due to the presence of *S. inaequidens* in soils with initially low concentrations (Dassonville et al. 2008), especially since nematodes are known to positively react to increasing nutrient concentrations (McSorley 2011). Furthermore, results of research done on the relation between marram grass growth and the presence of *S. inaequidens* could also be largely explained by a probable increase in nutrients (Van De Walle et al. 2022b). This result indicates that chemical compounds, like pyrrolizidine alkaloids, are not able to accumulate and negatively affect soil nematode abundances in sandy environments. Alternatively, *Senecio* could negatively affect other organisms in the soil, among which the natural enemies of nematodes. If nematodes facilitate decomposition of organic matter of *Senecio*, this explanation is still in line with previous results (Van De Walle et al., 2022).

The analysis of the residual covariance among nematode functional groups shows that abundances of different functional groups tend to be positively associated within a given compartment (rhizosphere or bulk soil), once the effects of local biotic and abiotic factors have been taken into account (Fig. 4). This effect is quite likely the result of ecological filtering by compartments: some roots will harbour generally more nematodes of all functional groups while others will be symmetrically impoverished of all functional groups because local conditions affect all groups in the same way. The absence of negative covariances (Fig. 4) also suggests that the extent of locally good or bad conditions “seeps” to nearby compartments: if a root sample harbours a high abundance of nematodes, it is very likely that the nearby bulk soil sample will also do so. This hints at the fact that locally good/bad conditions occur at a scale larger than a single root or soil sample. It has been shown that root-feeding nematode activity can increase nutrient leakage from roots, which consequently increases microbial populations, in turn providing food for bacterivore and fungivore nematodes and even potentially their predators (Gebremikael et al. 2016). Marram grass-associated nematode functional abundances are thus positively covarying in natural foredunes. These results are in line with a global study done on the spatial structure of soil nematode functional groups (van den Hoogen et al. 2019). We cannot claim that all variables related to bottom-up structuring of nematode communities were included in the model, yet we used variables that can be thought to substantially capture the most important drivers. Variables such as root mass and leaf litter can be argued to correlate with marram grass vitality, while nutrient concentrations are thought to be quite similar among coastal dunes (Reijers et al. 2021). Assuming that the most important factors structuring nematode abundances were, at least indirectly, included in the model, these results hint at the importance of studying the interactions between functional nematode groups if we want to further develop our understanding of soil communities.

To conclude, our results indicate that local nematode functional group abundances are variable among biogeographic regions, something which was already known for other species groups and is here confirmed for soil nematodes. Within regions there is still much unexplained variation, analysis of which indicated spatial clustering of nematode abundances. Hence, if nematode pressure truly affects the local performance of marram grass in coastal dunes, this impact will be highly variable across space, which would clarify why the *Ammophila* problem observed under constant conditions in the lab is still not completely resolved in the field. Unravelling which factors and species interactions structure the clustering at very small spatial scales could help shed light on this matter. In light of the recent climate change, dunes are becoming more and more fixated by marram grass (Jackson et al. 2019), which would lead to an increase in root-feeding nematodes according to our research. Since these abundances are heterogeneous and highly spatially clustered, so would be their role and impact in dune development and succession.

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Author contributions

RVDW and DB analysed the data. RVDW conducted the practical work and wrote the first draft of the manuscript. All authors contributed substantially to interpretation of the results and revision of the manuscript.

Competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Chapter 4

Plant-associated invertebrate communities in coastal dunes are more related to reginal than to local environmental factors

Ruben Van De Walle, Ward Langeraert, Dries Benoit, François Massol, Martijn L. Vandegehuchte & Dries Bonte

Dunes covered by *C. arenaria.*

4.1 Abstract

Habitat heterogeneity is an important factor driving species richness and community composition at both small and large spatial scales. More heterogeneous habitats are generally linked with higher species richness, but at smaller spatial scales species interactions also become important determinants of local species richness. A key aspect of habitat heterogeneity is the structure of the vegetation, which can influence entire animal communities. This is especially the case for plant species with disproportionate community effects, i.e. keystone species. The European marram grass *Calamagrostis arenaria* is such a keystone species in coastal dunes.

In many stabilized dune ecosystems, sand dynamics have recently been restored because open dunes are expected to support more biodiversity. However, the link between dune vegetation cover and biodiversity is not well studied. Here, we studied how invertebrate communities associated with marram grass in coastal dunes in different regions are structured by the cover and vitality of marram grass, as well as by invertebrate species traits and phylogeny.

Invertebrate species richness mainly differed among large-scale biogeographic districts. At smaller scales, invertebrate species richness in marram-grass-dominated foredunes did not increase if vegetation cover was reduced from high to intermediate densities. Species' responses were not influenced by the included traits, however, they seemed to be phylogenetic structured by some unmeasured trait(s). Residual species associations pointed towards the existence of two distinct invertebrate communities.

Our results indicate that, despite the regional difference in species richness, managing of local marram grass properties could influence dune biodiversity, with a heterogenous mix of vital and less vital marram grass plants benefiting species richness. Open sand patches seemed less necessary for marram grass-associated invertebrates, however, they can still be important in other dune habitats (e.g., grey dunes or dune grasslands) or for conservation of specific species.

4.2 Introduction

Different processes can influence species richness and community composition at different spatial scales (Shmida and Wilson 1985, Heino et al. 2015). Speciation, extinction and migration events affect regional shifts in species composition (Qian and Kissling 2010, Götzenberger et al. 2012, Ovaskainen and Abrego 2020), whereas species interactions are supposedly more important at local scales (McGill 2010, Patrick and Swan 2011), although the relevant scale might depend on the type of interaction (Araújo and Rozenfeld 2014). For many invertebrate species in general, it is well established that vegetation is an important habitat feature influencing species richness and composition (Samways et al. 1996, Jonsson et al. 2009, Litt et al. 2014, Ebeling et al. 2018). However, plant species differ in their capacity to influence invertebrate communities. Species playing an important role in structuring communities, can be considered keystone species (Jones et al. 1994, Menge et al. 1994, Munzbergova and Ward 2002, Narango et al. 2020).

From the viewpoint of invertebrate communities, environmental heterogeneity encompasses both vegetation heterogeneity and other general variables such as land cover, soil characteristics, climate and topography (Stein et al. 2014). In general, more heterogeneous habitats support more species because of an increase in available niches (Stein et al. 2014), as long as increasing heterogeneity does not come at the cost of a diminished area per habitat type (i.e. the area-heterogeneity trade-off, Allouche et al. 2012). At the smallest spatial scale, species interactions are important in determining local species richness and composition (Choler et al. 2001, Munday et al. 2001, Anderson et al. 2002, Kurle et al. 2008), and they can either be facilitating (e.g., facultative mutualism or commensalism) or antagonistic (e.g., competition or predation). Nevertheless, the success of Hubbell’s neutral model (Rosindell et al. 2011) proves species composition to be independent from species interactions in some cases. Closely related species, which possibly harbour similar interaction traits (Witz 1990), might actively avoid each other at local spatial scales in order to lower competition for resources (Ronchetti et al. 1986), while still being linked to the same overall habitat characteristics, and thus positively associated at regional spatial scales (Mayfield and Levine 2010, Gerhold et al. 2015). Competition within plant-associated invertebrate communities can be mediated by the defence mechanism of the host plant itself. When the host plant alters its defence mechanisms qualitatively or quantitatively as a reaction to herbivory, this affects the whole community (van Dam et al. 2003, Leimu and Koricheva 2006). Plant-mediated competition among herbivores occurs when distinct herbivore species are differently affected by these changes (Masters et al. 1993).

Dynamic coastal dunes are an ideal system to study how vegetation heterogeneity structures invertebrate communities. These dunes are dominated by a few highly adapted plant species and a tractable number of invertebrate species (McLachlan 1991, Provoost and Bonte 2004), which are expected to depend to a large extent on the traits of the plants. Dune vegetation is increasing globally, with an observed stabilization of open sand dunes over the past decades (Provoost et al. 2011, Jackson et al. 2019, Gao et al. 2020). The European marram grass (*Calamagrostis arenaria*) is the principal ecosystem engineering species that stabilizes wind-blown sand in Western Palearctic dunes by forming large quasi-monocultures on sandy coasts (Huiskes 1979, Bonte et al. 2021). Because of this sand-capturing capability, marram grass has frequently been used in sand-stabilizing projects (van der Putten and Kloosterman 1991). More recently, stabilized dunes have been artificially re-mobilised because open dunes are expected to support more biodiversity (Darke et al. 2013, Konlechner et al. 2014). While the role of the abiotic environment and of belowground organisms in the ecology of marram grass have been studied quite well, how the vegetation structure influences the composition of aboveground invertebrate communities of marram grass-covered dunes is less known (but see Vandegehuchte et al. 2011, 2012).

Most studies linking coastal vegetation with animal richness investigated the effects of the vegetation zonation perpendicular to the shore (McLachlan 1991), i.e. the effect of the vegetation gradient between drift line and stable dune ecosystems. The pool of invertebrate species found within marram dunes specifically, is relatively small because of the high environmental stress due to salt spray, temperature variability and wind and sand dynamics (McLachlan 1991). Consequently, most species associate with marram grass because it ameliorates the physical stress and provides a sheltered habitat (McLachlan 1991, Bonte and Maelfait 2001, Maes et al. 2006). Depending on the local state of the dune, marram grass is vital when sand dynamics are strong, but the species loses vigour when sand burying ceases (Huiskes 1979, van der Putten and Troelstra 1990). Vital tussocks provide mainly fresh plant material while less vital tussocks provide a mixture of both live and dead plant material. Herbivore species richness and abundance are therefore expected to increase on vital plants, while detritus-feeding species should become more dominant when sand dynamics cease and plants start to decay. Consequently, invertebrate species richness is expected to peak in marram grass with intermediate vitality. These changes in vigour and sand dynamics are additionally related to changes in grass cover and spatial configuration. Increasing marram grass cover, either by planting or natural marram expansion (Webb et al. 2000), is expected to increase invertebrate species richness (Triantis et al. 2012). However, some dune-specialist invertebrates are known to use open sand, for instance for hunting or egg-laying, leading to some species preferring habitat patches with more bare sand (Provoost and Bonte 2004, Maes et al. 2006). Following the area-heterogeneity trade off (Kadmon and Allouche 2007, Allouche et al. 2012), a mix of open sand and vegetation is therefore likely to lead to more diversified arthropod communities in coastal dunes.

From an ecosystem functioning perspective, focusing on species traits rather than on individual species identity allows for more robust assessment of community structure and functioning (Cadotte et al. 2011, Gagic et al. 2015, Funk and Wolf 2016, Brose et al. 2019). This trait-based research focuses on identifying traits that enable species to respond to their environment in order to gain a more mechanistic understanding of the processes shaping species communities (McGill et al. 2006, Wong et al. 2019). A trait commonly associated with the environmental filtering of arthropods is body size (Wong et al. 2019), because it is linked with important features such as dispersal, predation and thermoregulation (Gravel et al. 2013, Hillaert et al. 2018, Pincebourde et al. 2021). Species can also be classified according to their assumed biotic interactions in so-called functional groups, which can be used to study interactions between functional groups rather than between actual species (Wong et al. 2019). All of these traits are ultimately shaped by evolution, hence, incorporating phylogenetic relationships to account for similarity in unmeasured traits (Futuyma and Kirkpatrick 2018) can further elevate our understanding of the processes shaping community assembly.

All of the above-mentioned processes affect species richness together and their influences can interact while doing so. The environment can, for example, influence species' dispersal (e.g., Clobert et al. 2009) or biotic interactions (e.g., Choler et al. 2001, Pellissier et al. 2018). Furthermore, phylogenetically related species likely have converging traits and occurrence patterns (Futuyma and Kirkpatrick 2018). We here aim to gain insights into the structure of invertebrate communities associated with marram grass in coastal dunes. In this context, we considered the local cover and vitality of marram grass as environmental predictors of species distributions while taking into account species co-occurrences and regional biogeographic variation. We asked the following research questions: I.) How much variation in species occurrence is due to environmental variables vs. random processes? How do these impacts change with scale? II.) How do species traits and phylogenetic relationships affect species responses to environmental variables? III.) How are species co-occurrence networks structured?

4.3 Material & Methods

Study area & design

Coastal dune areas along the Channel and the North Sea, encompassing the North of France, Belgium, the Netherlands and the United Kingdom, were studied. Sandy coasts with marram-dominated, yellow dunes (Natura 2000 habitat 2120, CORINE biotope 16.21) were selected and transects parallel to the coastline were marked. The mean transect length was 1212 +/- 786m. Along each transect, a number of samples were taken within the first 100 m from the seaward side of the foredunes. The number of samples along each transect depended on the length of the transect because individual samples were separated by at least 20 m. Each sample is centred on a marram grass (*Calamagrostis arenaria* (L.) Roth) tussock surrounded by more or less pure marram grass vegetation and bare sand (e.g., no shrubs, trees, or large quantities of other herbaceous species). Sampling units were picked to maximize the variation in (1) hight and vitality of the central marram grass tussock and (2) the spatial configuration of the surrounding marram grass cover.

Our study area comprised six distinct biogeographical districts, which differ in their soil characteristics because of their geological history (Bonte et al. 2003). These six districts are: Southern UK (UK-S), Northern UK (UK-N), the Boulonnais region in France from Camiers until Dunkerque, the Flemish dune region from Dunkerque until Knokke, the Renodunaal region from Cadzand until Bergen aan Zee, and the Wadden district in the Netherlands from Bergen aan Zee to Texel (Fig. 4.1).

Data collection

At each sampled marram grass tussock, aboveground invertebrates were sampled by sweep netting in and above the tussock for 15 seconds. Afterwards, ground dwelling invertebrates were collected manually at the base of the tussock for 5 minutes. Sampling was only performed on relatively sunny days so flying insects would be active. All specimens were stored in 70 % ethanol. Finally, the species were identified using a stereomicroscope and the number of individuals per taxon per sample were recorded. Altogether, 15 726 individuals from 632 taxonomic units were identified, among which 434 to species level, 96 to genus level and 102 to family level or higher.

Initial exploration revealed a large number of zeroes in the species abundances, even after combining the abundances of both catching methods into one single count per species per sample. Therefore, abundances were converted to occurrences (absence = 0, presence = 1). After excluding samples with missing environmental variables (see further) and taxa not identified up to species level, the 50 most common species that occurred in at least 20 samples were selected (Supp. Mat. 4.1). From the initial 638 marram grass tussocks sampled during the summers of 2017-2019, 588 samples nested within 44 transects (Fig. 4.1) were analysed using Joint species distribution modelling (JSDM).

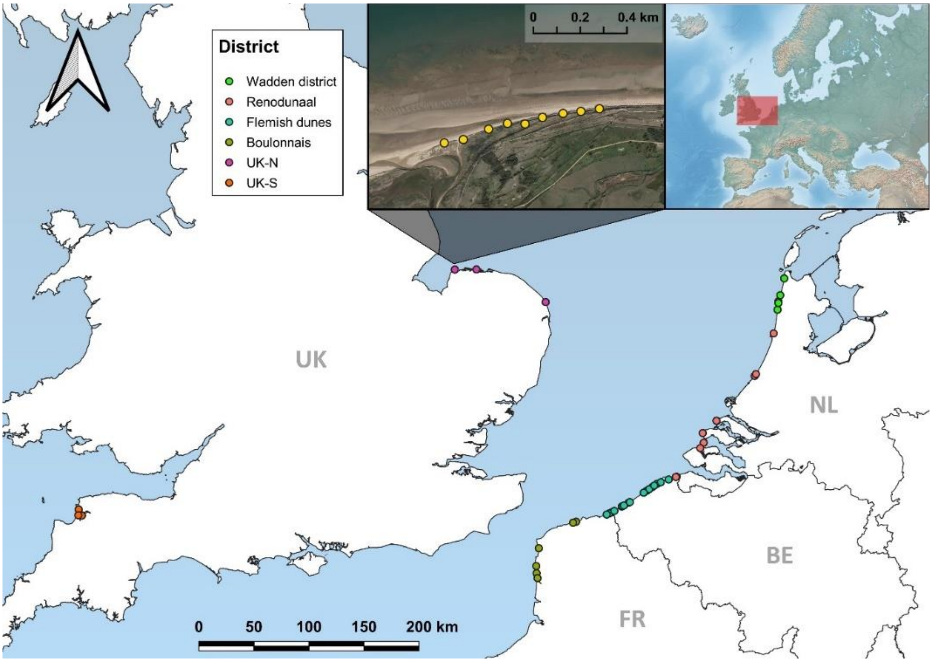

Figure 4.1 *Geographical scope of the study. Transects are indicated by dots and coloured per biogeographical district. The left inset shows an example of the sampling unit locations (yellow dots) within the indicated transect (Holme, UK) (satellite image: © 2022 Google). Figure made with QGIS v3.2.3- Bonn (QGIS Development Team 2018).*

Explanatory variables

For the JSDM, the following groups of explanatory variables were considered: (1) local environmental variables (at sample level), (2) regional environmental variables (spanning multiple transects), (3) species trait variables and (4) phylogenetic relationships (both at species level).

Local environmental variables. The proportional cover (P) of the surrounding marram grass and a measure for its spatial configuration (here, Moran's I), together with the vitality (V) of the central marram grass tussock were assessed. The proportional cover and spatial configuration of marram grass surrounding the central tussock were both quantified from vegetation maps of the coastal dune areas (Bonte et al. 2021). Calculations were done within a 50-m radius circle around each central marram grass tussock. Moran's I is a measure of spatial autocorrelation (Moran 1950, Bivand and Wong 2018), with negative values indicating an increasingly regular configuration, zero indicating a random configuration and positive values indicating an increasingly clustered configuration. Marram grass naturally grows in clusters (Bonte et al. 2021), so that Moran's I values in our data set varied from 0.7495 to 0.9801. Marram grass vitality was given a score (ranging from 0 to 4) based on the estimated % of green visible in a photograph of the central marram grass tussock.

Regional environmental variable. The biogeographic district (as described above) was included as the only large-scale environmental variable.

Species traits. The average size (in millimeters) and functional group of the adult individuals were included as trait variables (Supp. Mat. 4.1). Size is a continuous variable, while functional group is a categorical variable with four levels: (1) detritivore, (2) herbivore, (3) omnivore and (4) carnivore.

Phylogenetic relationships. Taxonomical information, as a proxy for phylogeny, was used to account for relatedness among species and to correct for any unmeasured phylogenetically structured traits. The taxonomical information for each species was obtained via the GBIF backbone taxonomy (GBIF Secretariat 2021) and modified to a taxonomical tree with equal branch lengths (Supp. Mat. 4.2).

Statistical modelling

Joint species distribution modelling, such as the Hierarchical Modelling of Species Communities (HMSC, Ovaskainen and Abrego 2020) method, allows to species occurrences with environmental variables at different scales while taking into account species traits and phylogenetic relationships (Poggiato et al. 2021). A HMSC model with the probit link function, was used to analyse occurrences of marram grass-associated invertebrates.

First, four models considering only environmental covariates were fitted and compared to determine whether the effects of P and V should include only the variable or also a quadratic term. These four JSDMs were fitted with either P and/or V as a quadratic term or not, together with spatial autocorrelation and the biogeographical district as environmental covariates. Continuous variables were centred around their mean (V around the median). Note that, although vitality was defined as an ordinal categorical variable, it was implemented as a continuous variable to ease interpretation and because ordinal variables are currently not supported by the Hmsc package. After confirming convergence for all four models, the 'best' model was selected using WAIC and used for the further model comparison and analyses (further referred to as model 1).

Model 1 estimated species niches based on environmental covariates, starting from the same expected value for the species niches. Model 2 extended model 1 by modelling the expected species niches in a species-specific way by including the invertebrate life-history traits described above. Closely related species might, on average, have more similar traits, some of which were potentially not measured. Using a phylogenetic tree, we can control for relatedness among species and account for any unknown, phylogenetically structured traits. In model 3, we further elaborated model 2 and included the phylogenetic tree by converting the tree into a phylogenetic correlation matrix. Model selection from models 1-3 was again used to select the final fixed effects model.

In the final step, model 4 was specified, which added a random effect structure to the final fixed effects model selected among models 1-3. This random effect structure was used to account for the spatial context of the study by implementing a random effect on the transect level, since sampling units within the same transect are expected to be more similar than between transects. A second random effect for the sampling unit was implemented in order to infer species co-occurrences (Ovaskainen and Abrego 2020).

For all models described above, the posterior distribution was sampled with four chains. HMSC specifically uses blocked Gibbs sampling (Tikhonov et al. 2020a) with Markov Chain Monte Carlo (MCMC) samples. For the models without random effects, each chain ran 300 000 iterations with a burn-in period of 100 000 samples and a thinning factor of 100. This resulted in 2000 posterior samples for each chain and a total of 8000 posterior samples per model. The models with random effects ran 1 500 000 iterations with a burn-in period of 500 000 samples and thinning factor 1000. Thus, each chain ran for 1000 posterior samples for a total of 4000 posterior samples per model. The default priors were used for all variables in all models.

R Statistical Software version 4.0.4 (R Core Team 2021) was used for all data analyses. Moran's I of marram grass surrounding the central tussock was calculated using the "moran.test" function from the "spdep" package (Bivand and Wong 2018). The Hierarchical Modelling of Species Communities was done using the R package "Hmsc" (Tikhonov et al. 2020b, 2021). Traceplots, autocorrelation plots and posterior densities were made and calculated using the 'mcmcplots' package (Curtis 2018). The 'rgbif' package v3.7.2 (Chamberlain et al. 2022) was used to extract taxonomical from the GBIF backbone taxonomy and the 'ape' package v5.6.2 (Paradis and Schliep 2019) was used for the construction of the taxonomic tree.

4.4 Results

Species richness varied from one to sixteen species per sample, with the richest samples on average found in the Flemish dunes (median = 7) and a lot of species only present in a minority of the study sites (average % occupied samples was 9.5 %) (Supp. Mat. 4.3). The most prevalent species were *Theba pisana* (O. F. Müller, 1774) (present in 36% of the samples), *Neophilaenus lineatus* (Linnaeus, 1758) (26%), *Demetrias monostigma* (Samouelle, 1819) (25%), *Meromyza pratorum* (Meigen, 1830) (22%) and *Tibellus maritimus* (Menge, 1875) (20%). The 50 most common species selected for this study covered two different phyla (Arthropoda and Mollusca), five classes, ten different orders, 31 different families and 48 genera (Fig. 4.2).

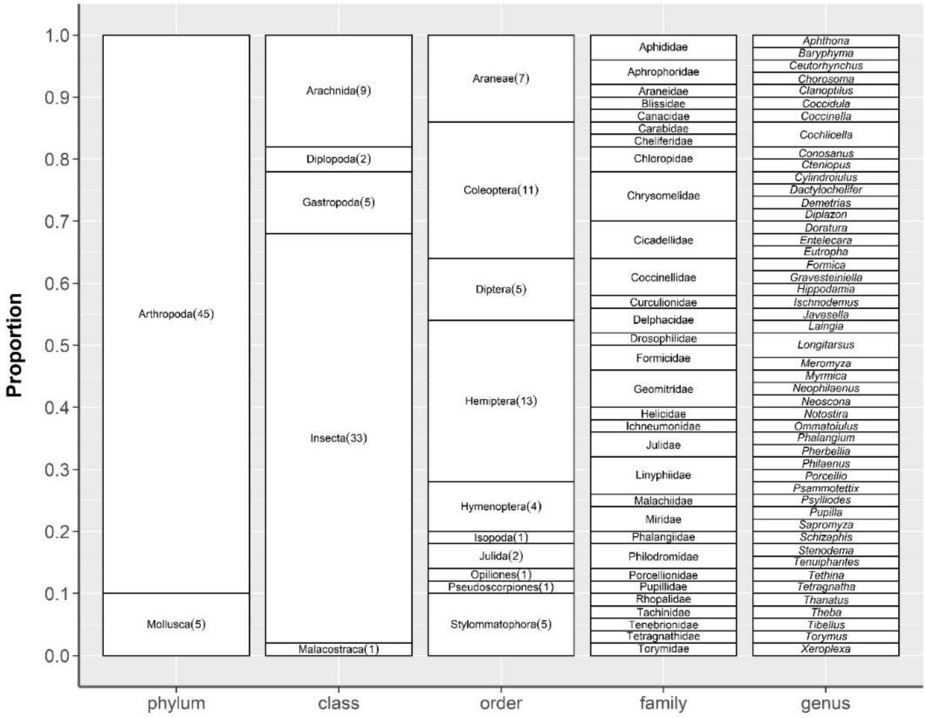

***Figure 4.2** Taxonomical scope of the species considered for analysis. For phylum, class and order, the numbers of species per group are indicated between parentheses.*

MCMC convergence & Model selection

MCMC convergence was satisfactory for all HMSC models without random effects (models 1-3). For these models, posterior densities for each parameter were very comparable between the different chains and autocorrelation between iterations was absent or low. The Gelman-Rubin potential scale reduction factors for all parameters in the different models were close to one (Supp. Mat. 4.4).

The environmental-variables-only model with both P and V as quadratic term had the lowest WAIC (12.56099) compared to the other environmental-variables-only models (respectively 12.57899, 12.61958 and 12.63496 for the models with only P^2, only V^2 or without quadratic term). Although the difference is minimal, this model formula was used for the rest of the analysis, since this also agrees with our knowledge of the study system. Adding trait variables to the model did not increase model fit (WAIC = 13.9554). However, correcting for phylogeny slightly did (WAIC = 12.5405). Adding the random effect in model 4 further lowered the WAIC of the model to 12.10181.

Based on the lowest WAIC and no large difference in explanatory or predictive power (Supp. Mat. 4.5), model 3 containing the environmental variables, together with species traits and phylogenetic data was used to add the random effect structure (model 4). Initially, model 4 additionally included the sample and transect random effects. However, the model did not converge with both included, so a final model with only the random effect on sample level was fitted. Diagnostic plots and potential scale reduction factors for this model were satisfactory for all but the estimated random effect. The trace plots of problematic random effect parameters showed outlying MCMC samples reached in turn by the different chains. Any of the outlying samples had a low posterior probability because outliers were infrequently sampled and only every 1000th MCMC sample was saved (thinning factor). Therefore, these outliers did not seem to have a big influence on the final posterior densities nor the expected values of the parameters. The potential scale reduction factor compares within and between chain variation, which explains the outlying values in Figure S.4D (Supp. Mat. 4). Some chains sample more outlying values which increases their within chain variance compared to the between chain variance. We conclude that, although convergence is not ideal, the posterior densities of all parameters in model 4 look well-defined and their expected values can be interpreted. We compared the outcome with the outcome of the model without random effect (model 3) to make sure no large differences were induced by including the random effect.

Species traits and phylogenetic signal

We found that the inclusion of species traits alone did not substantially improve model fit. However, in combination with phylogenetic data, model fit slightly improved (see above). Model 3 showed a strong phylogenetic signal with posterior median 0.72 and 95 % highest posterior density (HPD) interval between 0.38 and 0.98. This signal can be seen as inclusion of missing traits by which species react more (dis)similarly to their environment based on their phylogenetic affiliations.

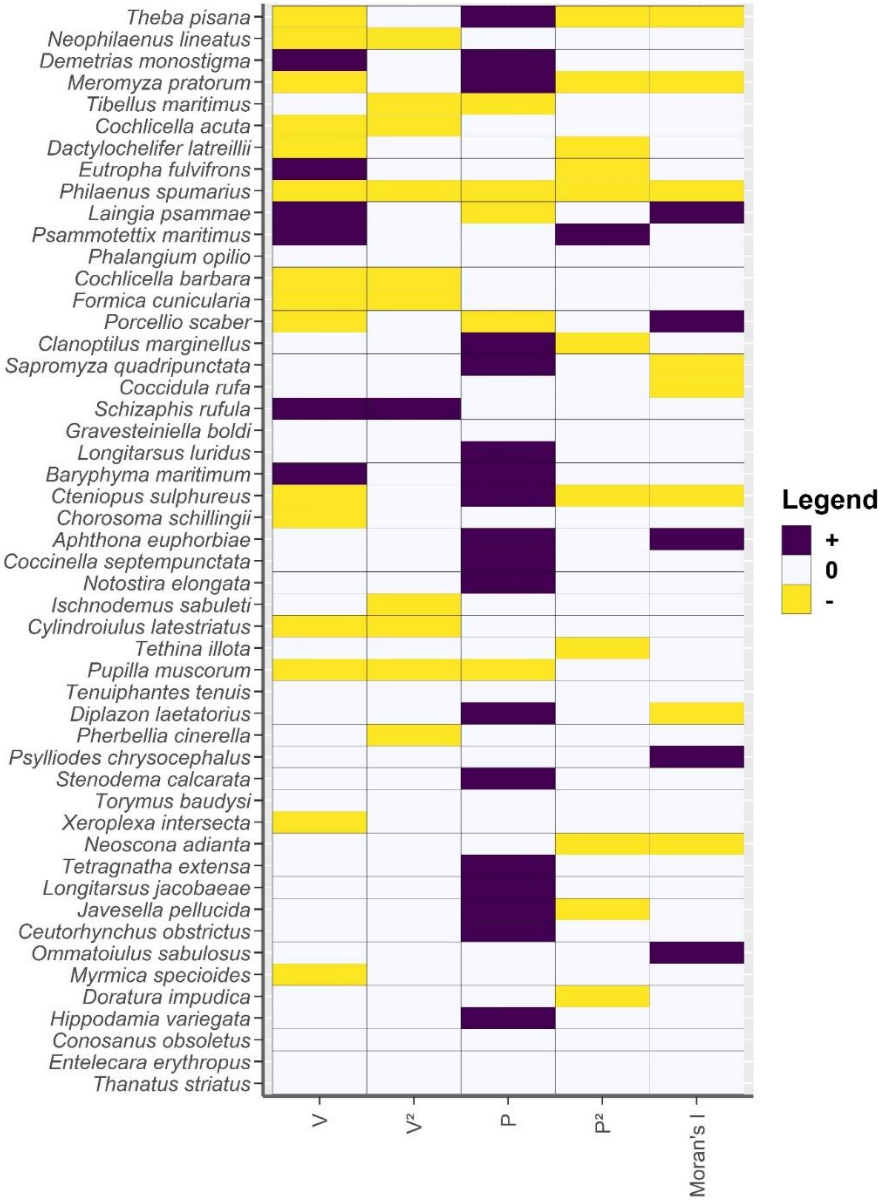

__Figure 4.3__ The responses of the species to environmental variables. V = vitality, P = proportional cover of surrounding marram grass. Responses that are positive with at least 95 % posterior probability are shown in purple and responses that are negative with at least 95 % posterior probability are shown in yellow. The species are ordered in decreasing prevalence from top to bottom.

Responses to environmental variables and variance partitioning

This and the following subsections treat the results of the final model, model 4. Only taking into account the responses with at least 95% posterior probability, our results clearly indicate strong effects of all environmental variables on species occurrences (Fig. 3). Model predictions of species richness over the environmental gradients were similar between the districts since no interactions between covariates were considered. Consequently, only the trends for the Flemish dunes, which had the clearest trends due to the high sample count and high species richness, are illustrated here. See Supp. Mat. 6 for the effects of the separate biogeographical regions.

At the local scale, the proportion and configuration of marram grass within a 50m radius affected species composition and occurrences (Fig. 4.3). Species richness increases with the proportion of marram grass up to intermediate proportion and then stays rather constant (Fig. 4.4A). Species richness decreased in highly clustered marram grass tussocks (i.e., higher Moran's I values; Fig. 4.4B). An optimal species richness is reached in marram grass tussock of intermediate vitality (Fig. 4.3 and Fig. 4.4C).

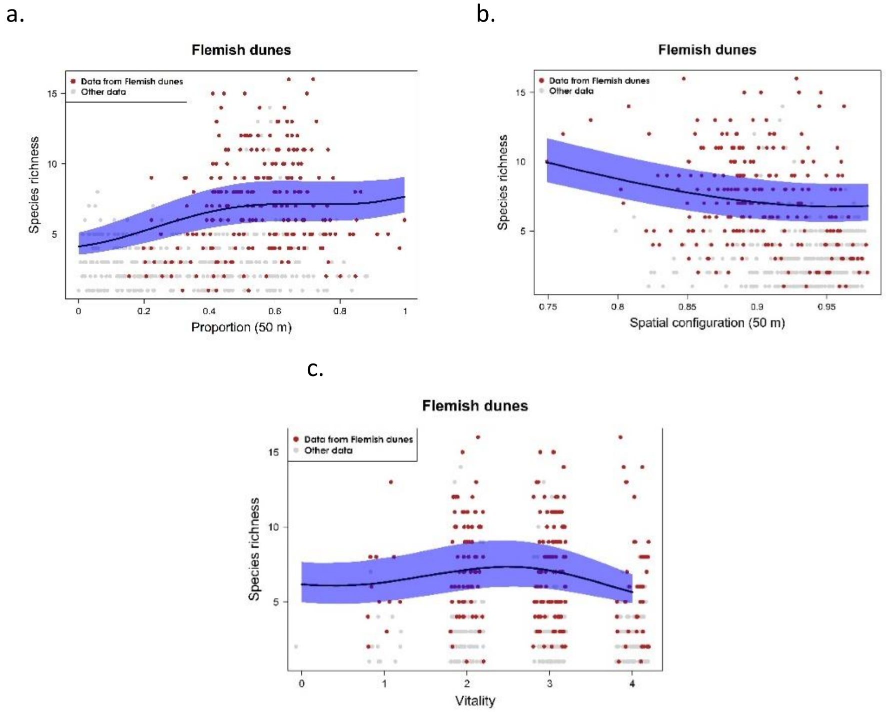

__Figure 4.4__ Model predictions of species richness over environmental gradients in the Flemish dune district. The posterior median (black line) and interquartile range (blue shade) are illustrated. A. Gradient in the proportional cover of marram grass. B. Gradient in spatial configuration of marram grass. C. Marram grass vitality gradient, data are jittered horizontally.

Variance partitioning (Fig. 4.5) showed that the explained variation by the fixed effects can mainly be attributed to regional variability captured by the biogeographical district, which explained on average (median) 60.5 % (Q1-Q3: 56.9-67.7 %) of the total variation. The local environmental variables together explained on average 25.9 % (18.3-32.1 %), with proportional cover of marram grass explaining 9.5 % (6.0-15.3 %), vitality of the marram grass 7.1 % (4.5-13.4 %), and the spatial configuration 3.2 % (1.9-5.1 %). The residual variation captured in the random effect still accounted for on average 11.3 % (6.7-17.2 %).

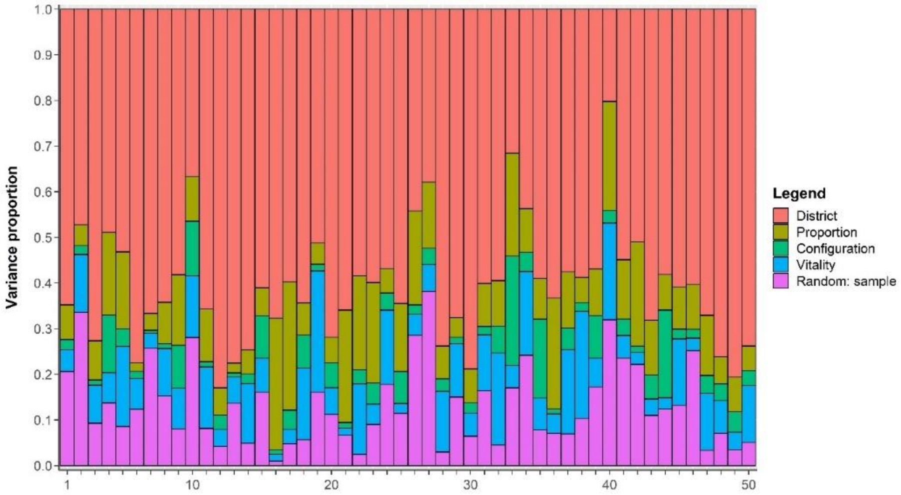

Figure 4.5 *Variance partitioning among the fixed effects in model 4. The residual variation is captured in the random effect. The species have been ordered from left to right according to decreasing prevalence.*

Species co-occurrence

The species-to-species association network showed a clear structure which can be organized in three groups (Fig. 4.6). The first group of species *Sapromiza quadripunctata* – *Ceutorhynchus obstrictus* (except *Tibellus maritimus* and *Gravesteiniella boldi*) tended to occur together but not with species from the second group *Eutropha fulvifrons* – *Demetrias monostigma* (except *Tethina illota* and *Ischnodemus sabuleti*). The second group tended to occur together but not with species from group 1. The remaining species (group 3) occurred independently from the other species.

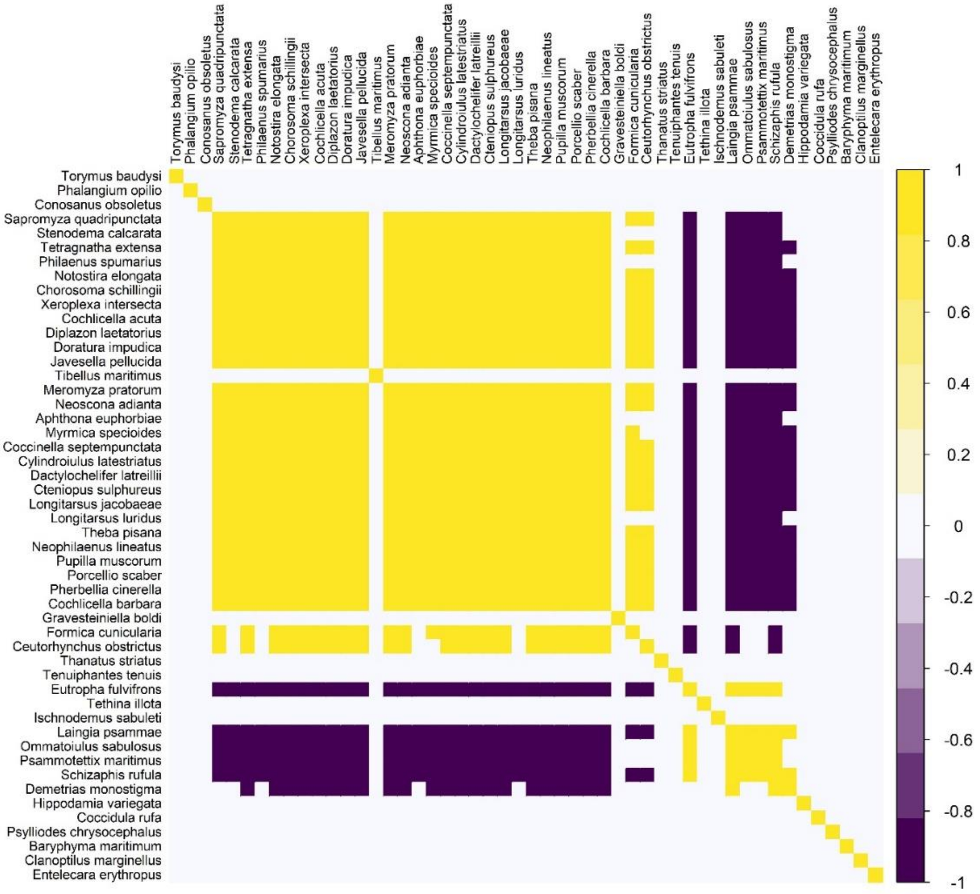

Figure 4.6 *Residual species association matrix that shows species pairs with a positive (yellow) or negative (purple) correlation. Associations are only shown if the correlation was positive/negative with at least 95 % probability.*

4.5 Discussion

The biogeographic district was the most important factor structuring marram grass-associated invertebrate community composition, accounting for around 60 % of the variation. Local-scale parameters, such as marram grass configuration and vitality, still significantly influenced aboveground invertebrate biodiversity, accounting for 26% of the variation. Stochastic processes were less important, only explaining 11% of the explained variation in species composition. Species traits seemed to increase model fit only after accounting for the phylogenetic relationship between species. The residuals of the model seemed to indicate the existence of two distinct communities inhabiting marram grass, with species of one community rarely co-occurring with species of the other.

The large portion of variation explained by the biogeographical district was potentially related to many unmeasured variables with a geographical structure such as the chemical composition of the sediment (lime in the soil, pH), a north-south gradient of climatic variables (e.g., temperature) and the management of coastal areas (Ager and Wallace 1966, Kooijman et al. 1998, Provoost and Bonte 2004). For example, lime concentrations are highest in the Flemish dunes and the Boulonnais region. Snails are strongly associated with lime-rich soils because they depend on it to grow their shells (Graveland and Van Der Wal 1996, Provoost and Bonte 2004). As expected, all five snail species in our study were more present in samples originating from the abovementioned districts. Alternatively, this observation could be explained by the covered north-south gradient, since these biogeographic regions are also the most southern. It furthermore makes a distinction between continental Europe and the UK. The occurrence of the generalist spider species *Tenuiphantes tenuis* could only be linked to this distinction, being found more in UK samples. Finally, since different countries (and thus by extension biogeographical districts) were sampled during different years, the district variable possibly captured variation in weather conditions among years. Insect populations and activity rates are known to fluctuate depending on weather conditions (Didham et al. 2020), which could explain the differences in species composition between districts. However, rerunning the final model with only data gathered during 2018 confirmed that the effect of the biogeographic district captured more than only yearly weather variation, since biogeographic district still explained 55% of the variation (Supp. Mat. 7).

Species richness was maximal in marram grass tussocks of intermediate vitality. This trend is driven by different species using either mainly fresh or dead plant material. For instance, both aphids (*Laingia psammae* and *Schizaphis rufula*) and one leafhopper species (*Psammotettix maritimus*) occurred more frequently on vital marram grass tussocks. However, the trend was less clear for other leafhoppers. Also predatory dune specialists (e.g. *Demetrias monostigma* (Weeda et al. 1991) and *Baryphyma maritimum*) seem to prefer more vital marram grass tussocks. Other species like the pseudoscorpion *Dactylochelifer latreilli*, the isopod *Porcellio scaber* and some snail species (*Cochlicella* sp. and *Pupilla muscorum*) preferred marram grass tussocks with more detritus, most likely because they use dead plant material as hiding place, food source or a combination of both. The hypothesized optimum in species richness with respect to marram grass vitality is thus confirmed to be driven by a mix of species using all available niches.

Marram grass vitality and spatial configuration are inherently intertwined in a natural setting, where marram grass grows vigorously in open dunes with moderate sand dynamics (Nolet et al. 2018). Under moderate sand burial, marram grass grows in a patchy distribution, optimizing sand trapping capacity (Reijers et al. 2021). If these dynamics persist for a while, sand accretion could slowly decrease because of increasing marram cover, which would consequently lower marram grass vitality (Huiskes 1979, Bonte et al. 2021). By implementing both parameters separately in the JSDM, we tried to disentangle their effects. The proportional cover of marram grass in a radius of 50 m can thus be seen as a biological parameter related to disturbance and sand fluxes and an overall measure of habitat availability for most foredune species. Species richness increased from low to intermediate cover and remained more or less constant from intermediate to high cover. The initial increase in species richness can be explained by an increase in habitat availability and consequently an increase in resources and niche space for species to exploit. Increased proportional cover of marram grass surrounding the examined tussock also reduces disturbance due to sand dynamics because it stabilizes open sand, leading to more species being able to colonize the tussock. Around intermediate proportional cover, an increase in vegetation no longer raised species richness, pointing towards competition among species becoming more important than habitat availability. For the associated invertebrate communities, marram grass tussocks can be seen as islands in an inhospitable sea of sand, where the theory of island biogeography (TIB) states that larger islands have higher species richness (MacArthur and Wilson 1967, Gravel et al. 2011). Hence, marram grass-associated invertebrate richness abides perfectly to the TIB.

Species richness within the studied tussock decreased when the surrounding marram grass occurred more clustered together. Since our measure for clustering was calculated independently from the vegetation cover, this means that distances between patches became generally larger with a higher clustering. Thus, these results match again perfectly with the TIB, which states that species richness of an island, or marram grass tussock in our case, will decrease with increasing isolation. On the other hand, increased marram grass clustering could be linked to a decrease in overall sand dynamics (Bonte et al. 2021, Reijers et al. 2021), something which is known to influence dune-specific species (Maes and Bonte 2006). However, marram grass only occurred clustered in our study (Bonte et al. 2021) and therefore, we can only deduce that species richness tends to decrease from highly clustered to maximally clustered marram grass configurations. Because of this low variability within marram grass clustering, it is not surprising that this variable explained the least amount of the variance in species occurrences of the small-scale environmental variables.

According to model selection, the inclusion of traits and especially phylogenetic data did only slightly improve model fit. Nevertheless, the phylogenetic signal appeared to be quite strong, indicating that related species react more similarly to their environment than distantly related species. These results pointed towards phylogenetically structured traits important for environmental filtering that were not included in our analysis (Abrego et al. 2017, Ovaskainen et al. 2017, Ovaskainen and Abrego 2020). Both pairs of species within the genera *Cochlicella* and *Longitarsus* do indeed correlate in a similar way to the environmental covariates. Because of the broad phylogenetic range of the included species (Brusca et al. 2016) and because of the limited number of traits included, it was not surprising that more predictive, phylogenetically structured, traits could have been identified (Burner et al. 2021). Nevertheless, the environmental factors were most important in explaining species presence or absence of marram grass-associated invertebrates, since including the phylogeny did not significantly improve model fit. Even though the arthropod phylogeny based on molecular and morphological data seem congruent (Giribet et al. 2001), we must acknowledge potential shortcomings regarding the taxonomy-based phylogeny used here, since it represented a simplification of species phylogenetic relations by using a tree with equal branch lengths. Whitfeld et al. (2012) found for example that the assumption of equal branch lengths hampers the ability to identify phylogenetic patterns in a plant community compared to estimating branch lengths from DNA sequences. We therefore cannot exclude that including more relevant traits and more accurate phylogenetic data could have revealed different conclusions.

The residual species co-occurrences seemed to indicate the existence of two groups of invertebrates that are positively co-occurring within group, but negatively between groups. The larger group contained generalist species which are not specifically associated with marram grass or even with dunes or warm habitats in general, such as *Coccinella septempunctata* (a ladybird), *Longitarsus jacobaeae* (a leaf beetle), *Notostira elongata* (a capsid bug), *Philaenus spumarius* (a spittlebug) and *Porcellio scaber* (a woodlouse). The smaller group mainly consisted of dune specialists who strongly depend on marram grass for their survival. For instance, *Laingia psammae* and *Schizaphis rufula* are two aphids almost exclusively associated with marram grass (Weeda et al. 1991, Vandegehuchte et al. 2010a), *Psammotettix maritimus* (a leafhopper) feeds monophagously on marram grass (Weeda et al. 1991) and *Eutropha fulvifrons* (a grass fly) uses marram grass as food plant (Nartshuk and Andersson 2013). The remaining species occurred independently from the other groups and from each other. This group seemed to consist largely of predatory (spider) species such as *Tenuiphantes tenuis*, *Thanatus striatus*, *Entelecara erythropus* and *Tibellus maritimus*. This result could point towards priority effects between specialist and generalist species, which entail that community assembly depends on the order and timing in which species join communities (Chase 2003, Fukami 2015, De Meester et al. 2016). This process is plant-mediated, with the host-plant becoming more suitable for either of the two communities, depending on the first species to arrive. Marram grass might, for instance, allocate more resources to the roots as a response to herbivory (Kaplan et al. 2008). Within this explanation, it is perfectly understandable that the remaining species not co-occurring with either group are mainly predators. Additionally, predators attracted by multiple prey species might influence species co-occurrences via apparent competition. Alternatively, this result could be explained by the effect of an environmental variable not included in the model. This result could, for instance, be linked with genetic differences between marram grass plants (Vandegehuchte et al. 2011) or with the succession in foredune vegetation (van der Putten et al. 1993), with the specialist group occurring in more pure marram grass patches and the generalist group occurring in patches with already some other plants growing in the vicinity.

Coastal dunes provide a variety of ecosystem services such as coastal protection, tourism, drinking water supply and biodiversity (Van der Biest et al. 2017). Here, we assessed how regional and local factors influenced invertebrate dune biodiversity and found that variation in species richness is large between different coastal regions. Nevertheless, managing local marram grass properties can influence dune biodiversity, which is already threatened (Provoost and Bonte 2004). Coastal dunes are characterised by a mixture of vegetation patches and open sand areas. Recent dune re-mobilisation projects are being carried out to restore biodiversity (Darke et al. 2013, Konlechner et al. 2014). Our results did not support a significant raise in biodiversity when vegetation cover is reduced from high to intermediate densities, at least not for invertebrate biodiversity in marram-grass-dominated foredunes. Providing a mix of vital and less vital plant material did seem to raise species richness, which does partly advocate the need for re-mobilisation of fixated dunes because marram grass becomes less vital in those dune parts (van der Putten et al. 1993). Additionally, dune re-mobilisation, especially the resulting open sand patches, can still be important in other dune habitats (e.g., grey dunes or dune grasslands) or for conservation of specific species (Bonte et al. 2000, WallisDeVries and Raemakers 2001, Maes and Bonte 2006, Batsleer et al. 2022). Furthermore, reinvigorating dune dynamics and growth can be crucial to increase coastal protection (Bonte et al. 2021, Reijers et al. 2021).

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Competing interests

The authors have declared that no competing interests exist.

Author contributions

MLV and D. Bonte designed the field work. RVDW and MLV conducted the practical work. WL and RVDW wrote the first draft of the manuscript. WL, D. Benoit, D. Bonte and RVDW analysed the data. WL made conceptual figure 1. All authors contributed substantially to interpretation of the results and revision of the manuscript.

4.6 Supplementary Materials

S4.1 Species list

Table S4.1 *The 50 most common invertebrate species found in the 2-seas-area. Sizes are based on literature or averaged measurements of multiple specimen of the same species (chapter 5). Functional group of the adult individuals are based on literature. The prevalence index ranges from 1 (the most prevalent species) to 50 (the least prevalent species) and is based on the fraction of occupied samples per species.*

Species	Order	Functional group	Size (mm)	Prevalence
Aphthona euphorbiae	Insecta	Herbivore	1.8	25
Baryphyma maritimum	Arachnida	Predator	2.2	22
Ceutorhynchus obstrictus	Insecta	Herbivore	2.8	43
Chorosoma schillingii	Insecta	Herbivore	15	24
Clanoptilus marginellus	Insecta	Herbivore	5.75	16
Coccidula rufa	Insecta	Predator	3.2	18
Coccinella septempunctata	Insecta	Predator	6.7	26
Cochlicella acuta	Gastropoda	Herbivore	15	6
Cochlicella barbara	Gastropoda	Herbivore	11	13
Conosanus obsoletus	Insecta	Herbivore	5	48
Cteniopus sulphureus	Insecta	Herbivore	7.8	23
Cylindroiulus latestriatus	Diplopoda	Detritivore	18	29
Dactylochelifer latreillii	Arachnida	Predator	2.5	7
Demetrias monostigma	Insecta	Predator	4.5	3
Diplazon laetatorius	Insecta	Predator	5.5	33
Doratura impudica	Insecta	Herbivore	4.9	46
Entelecara erythropus	Arachnida	Predator	1.9	49
Eutropha fulvifrons	Insecta	Herbivore	2.25	8
Formica cunicularia	Insecta	Omnivore	3.9	14
Gravesteiniella boldi	Insecta	Herbivore	3.1	20
Hippodamia variegata	Insecta	Predator	4.4	47
Ischnodemus sabuleti	Insecta	Herbivore	4.6	28
Javesella pellucida	Insecta	Herbivore	4.25	42
Laingia psammae	Insecta	Herbivore	2.4	10
Longitarsus jacobaeae	Insecta	Herbivore	3	41
Longitarsus luridus	Insecta	Herbivore	1.7	21
Meromyza pratorum	Insecta	Detritivore	5.5	4
Myrmica specioides	Insecta	Omnivore	4	45
Neophilaenus lineatus	Insecta	Herbivore	6	2

Neoscona adianta	Arachnida	Predator	6.5	39
Notostira elongata	Insecta	Herbivore	7.6	27
Ommatoiulus sabulosus	Diplopoda	Detritivore	22.5	44
Phalangium opilio	Arachnida	Predator	5.25	12
Pherbellia cinerella	Insecta	Detritivore	4	34
Philaenus spumarius	Insecta	Herbivore	6.1	9
Porcellio scaber	Malacostraca	Detritivore	11.25	15
Psammotettix maritimus	Insecta	Herbivore	4.7	11
Psylliodes chrysocephalus	Insecta	Herbivore	3.5	35
Pupilla muscorum	Gastropoda	Herbivore	2.7	31
Sapromyza quadripunctata	Insecta	Detritivore	4.2	17
Schizaphis rufula	Insecta	Herbivore	1.9	19
Stenodema calcarata	Insecta	Herbivore	7.5	36
Tenuiphantes tenuis	Arachnida	Predator	2.75	32
Tethina illota	Insecta	Detritivore	2.5	30
Tetragnatha extensa	Arachnida	Predator	9	10
Thanatus striatus	Arachnida	Predator	4	50
Theba pisana	Gastropoda	Herbivore	18.5	1
Tibellus maritimus	Arachnida	Predator	8.2	5
Torymus baudysi	Insecta	Predator	2.5	37
Xeroplexa intersecta	Gastropoda	Herbivore	9.5	38

S4.2 Phylogeny of the invertebrate data

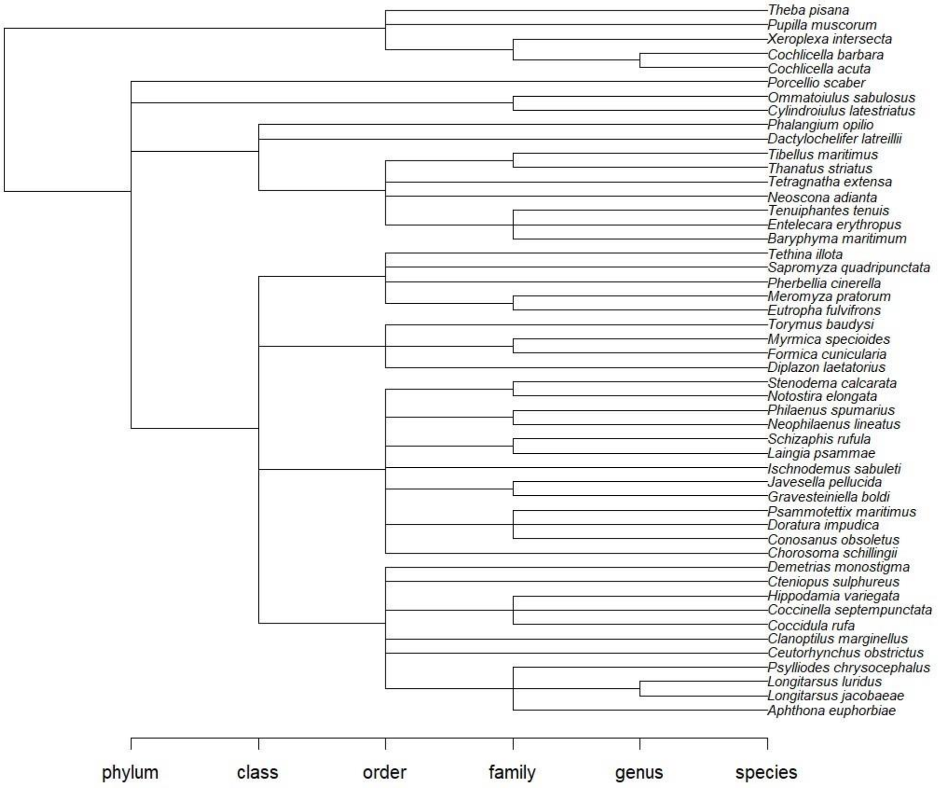

Figure S4.2 *The phylogenetic tree with equal branch lengths based on taxonomical classification used in the JSDM.*

S4.3 Species richness

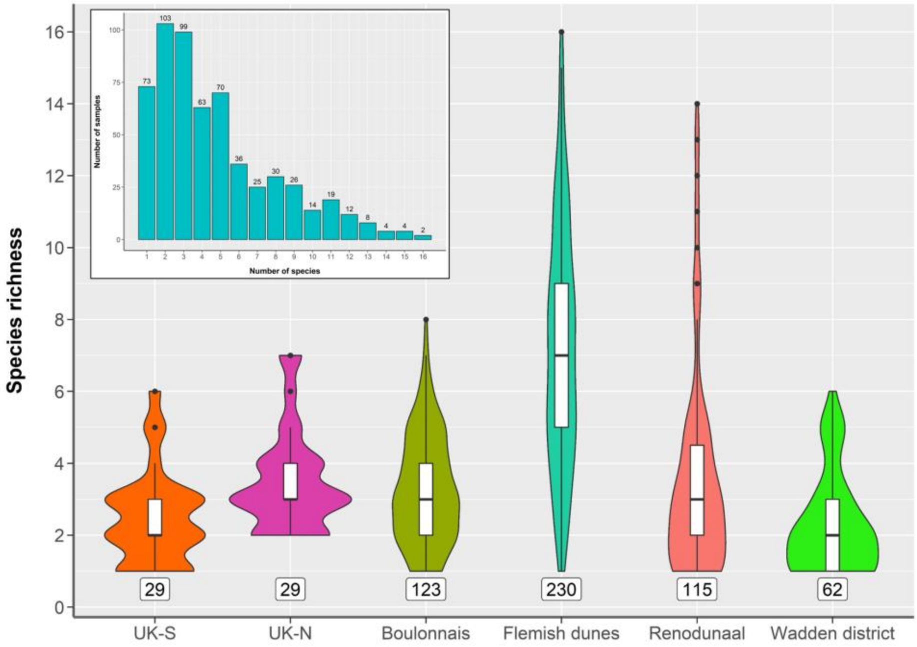

Figure S4.3 *Species richness in the different districts. The number below the violin plots indicates the number of sampling units per district. Inset shows overall distribution of species richness per sampling unit.*

S4.4 The potential scale reduction factors

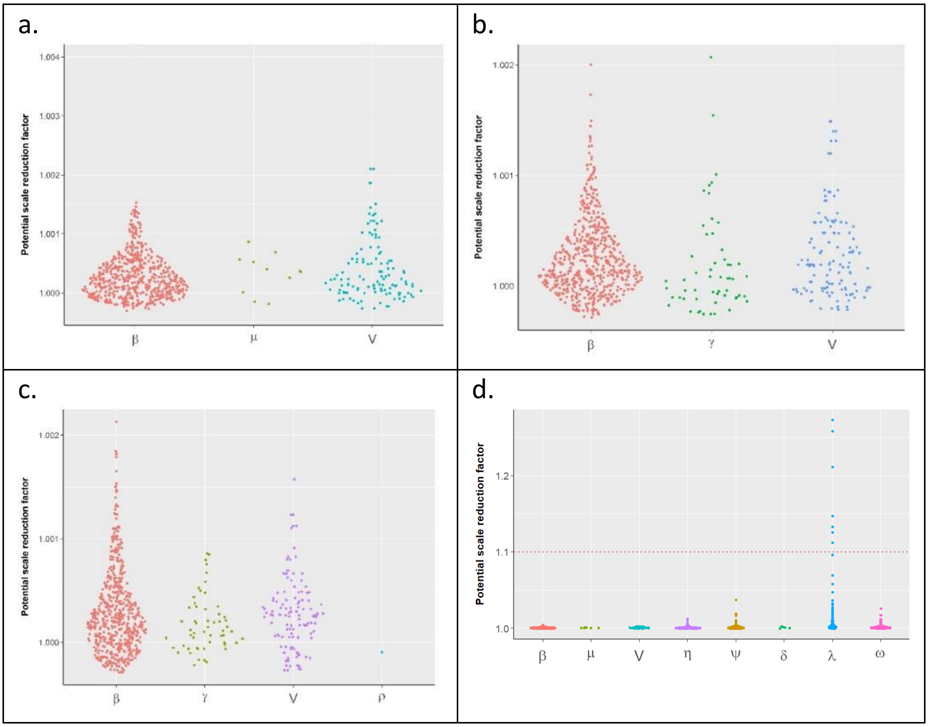

Figure S4.4 *Potential scale reduction factors for all parameters in the different models. A. Model 1 with environmental variables. B. Model 2 with environmental and trait variables. C. Model 3 with environmental variables, trait variables and phylogenetic data. D. Model 4 with environmental variables and random effects on sampling unit level.*

S4.5 Explanatory and predictive power

Models 1-3 showed for most species a clear difference between the averages of fitted values for presences and absences (Tjur's R^2) and predicted presences and absences better than expected by chance (AUC). Both measures are always higher for the explanatory power than for the predictive power. The median Tjur's R^2 is highest for model 2, and the median AUC is highest for model 1. The differences between the models are however relatively small. Indeed, when we plot the exploratory and predictive power for both measures between the different models, we see no clear higher Tjur's R^2 or AUC for more complicated models.

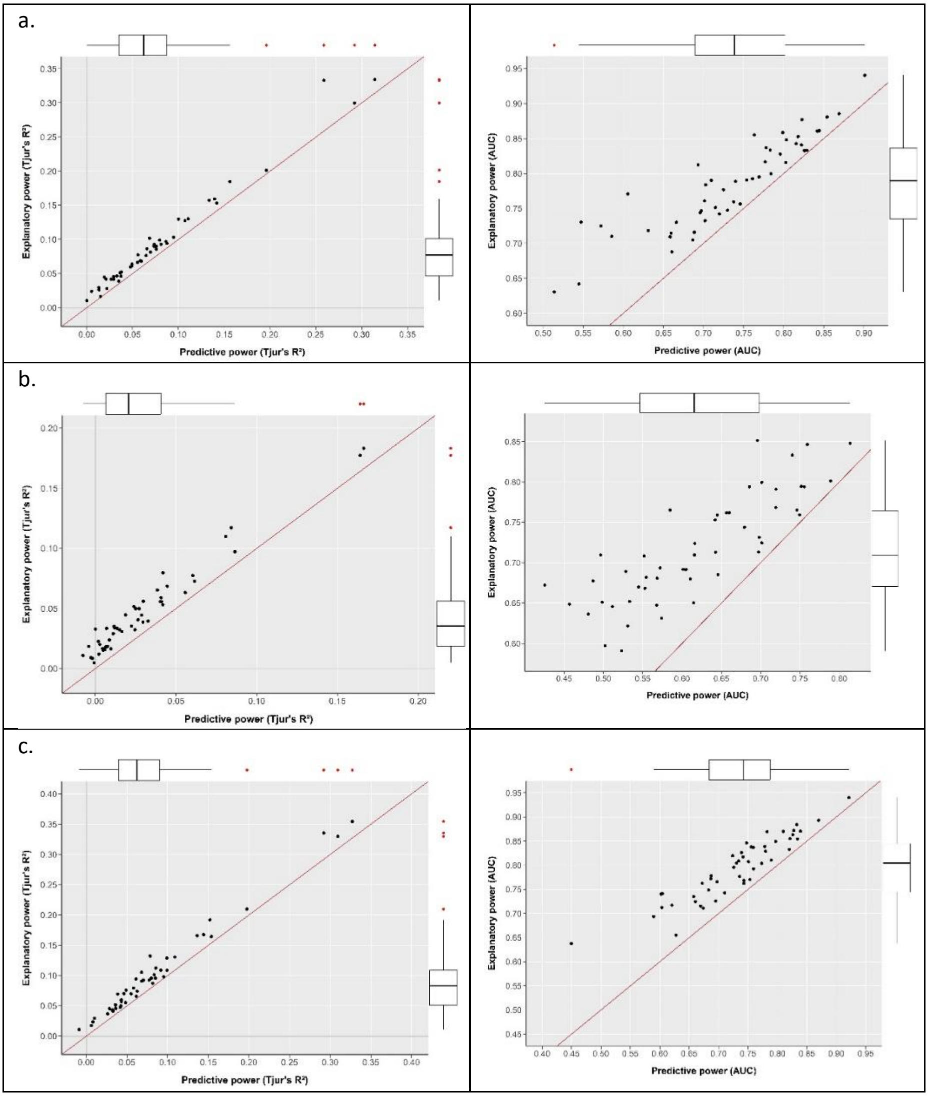

Figure S4.5 *Explanatory and predictive power based on Tjur's R2 (left) and AUC (right). Predictive power is based on 2-fold cross-validation.* ***A.*** *Model 1 with environmental variables.* ***B.*** *Model 2 with environmental and trait variables.* ***C.*** *Model 3 with environmental variables, trait variables and phylogenetic data.*

S4.6 Predictions for other biogeographical districts

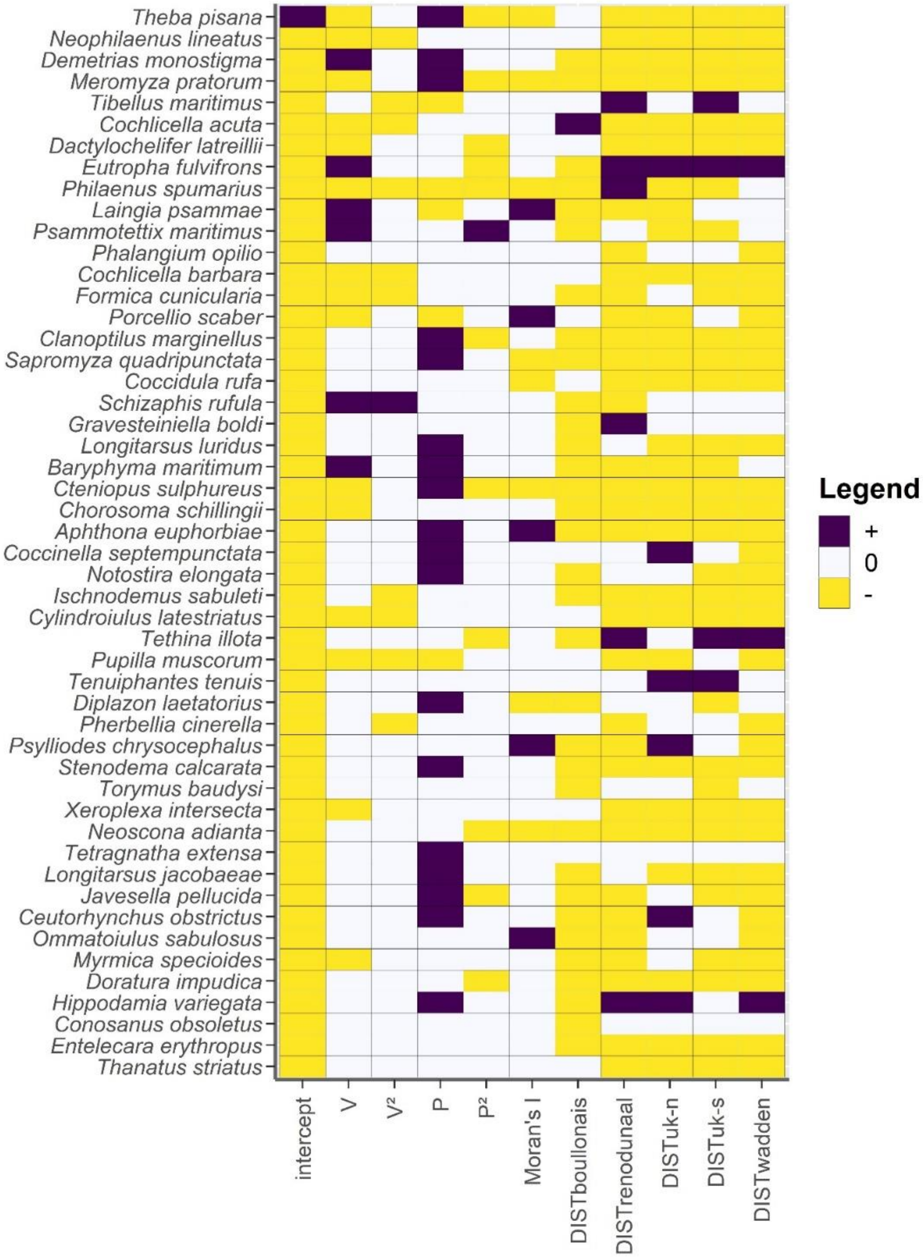

Figure S4.6 *The responses of the species to all variables included in the JSDM. V = vitality, P = proportional cover of surrounding marram grass. Responses that are positive with at least 95 % posterior probability are shown in purple and responses that are negative with at least 95 % posterior probability are shown in yellow. The species are ordered in decreasing prevalence from top to bottom.*

S4.7 Variance partitioning for model 4 with only 2018 biodiversity data

Model 4 based on only the data gathered during 2018. This data set included 286 data points spread over 4 biogeographic regions. The effects of the environmental variables were less pronounced because of the drastic reduction in data points. Nevertheless, variance partitioning again indicated biogeographic district to be the most important variable (56.5 %).

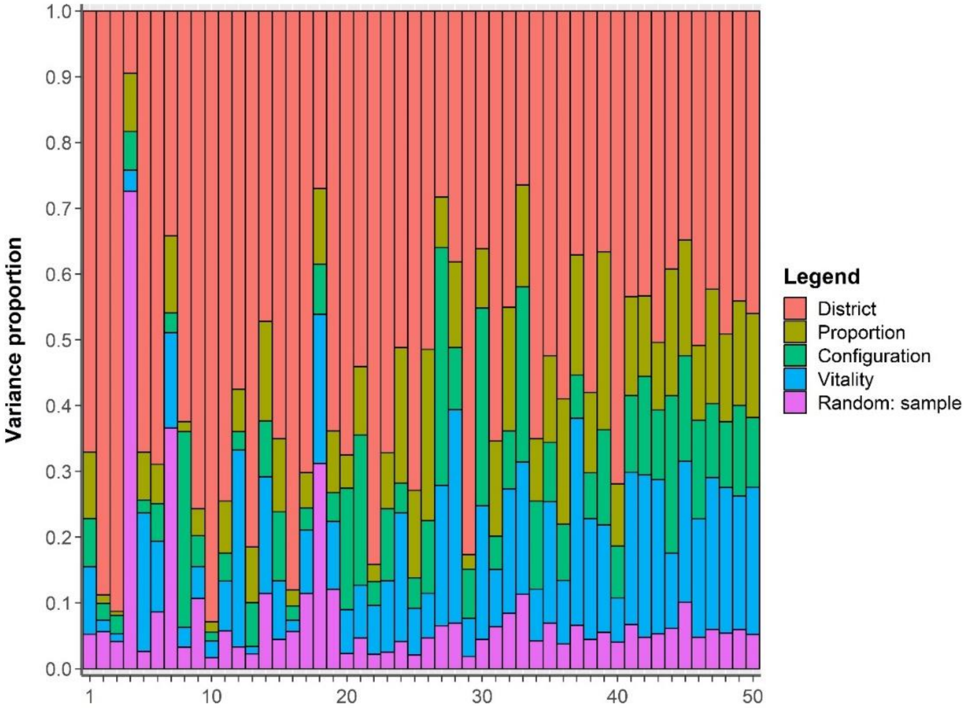

Figure S4.7 Variance partitioning among the fixed effects in model 4. The residual variation is captured in the random effect. The species have been ordered from left to right according to decreasing prevalence.

Chapter 5

Arthropod food webs predicted from body size ratios are improved by incorporating prey defensive properties

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*Shared first authorship

Illustration of a possible food web in marram grass.

Adapted from: Van De Walle R, Logghe G, Haas N, Massol F, Vandegehuchte ML, Bonte D (2023) Arthropod food webs predicted from body size ratios are improved by incorporating prey defensive properties. Journal of Animal Ecology.

5.1 Abstract

Trophic interactions are often deduced from body size differences, assuming that predators prefer prey smaller than themselves because larger prey are more difficult to subdue. This has mainly been confirmed in aquatic ecosystems, but rarely in terrestrial ecosystems, especially in arthropods.

Our goal was to validate whether body size ratios can predict trophic interactions in a terrestrial, plant-associated arthropod community and whether predator hunting strategy and prey taxonomy could explain additional variation.

We conducted feeding trials with arthropods from marram grass in coastal dunes to test whether two individuals, of the same or different species, would predate each other. From the trial results, we constructed one of the most complete, empirically derived food webs for terrestrial arthropods associated with a single plant species. We contrasted this empirical food web with a theoretical web based on body size ratios, activity period, microhabitat, and expert knowledge.

In our feeding trials, predator-prey interactions were indeed largely size-based. Moreover, the theoretical and empirically based food webs converged well for both predator and prey species. However, predator hunting strategy, and especially prey taxonomy improved predictions of predation. Well-defended taxa, such as hard-bodied beetles, were less frequently consumed than expected based on their body size. For instance, a beetle of average size (measuring 4 mm) is 38% less vulnerable than another average arthropod with the same length.

Body size ratios predict trophic interactions among plant-associated arthropods fairly well. However, traits such as hunting strategy and anti-predator defences can explain why certain trophic interactions do not adhere to size-based rules. Feeding trials can generate insights into multiple traits underlying real-life trophic interactions among arthropods.

5.2 Introduction

Biodiversity is in a worldwide crisis, with unprecedented declines in the species richness of many taxa (Ceballos et al. 2015). An understudied aspect of this biodiversity crisis is the loss of species interactions (Fortuna et al. 2013). These interactions even disappear at faster rates compared to species loss (Valiente-Banuet et al. 2015) and therefore contribute substantially to the degradation of ecosystem functions and services (Griffiths et al. 2016, Keyes et al. 2021). Not only mutualistic interactions, such as pollination and facilitation (Montoya et al., 2012; Traveset et al., 2018), but also trophic interactions, such as herbivory and predation, can have important effects on ecosystem functioning (Schmitz 2008, Lavorel et al. 2013). To realistically gauge the effect of disappearing trophic interactions, a precise quantification and understanding of food web structure is necessary (Novak et al. 2011). This is, however, challenging for smaller and less studied organisms such as invertebrates, even though they often attain high numbers and diversity in natural systems (Traugott et al. 2013, Gongalsky 2021).

Body size is generally used to identify potential trophic interactions, with the assumption that predators usually feed on prey that are (slightly) smaller than themselves (Gravel et al. 2013). Body size further constrains the potential diet of a species between a lower and upper limit (Cohen et al. 1993, Hirt et al. 2020). On the one hand, prey that are much larger than the predator will be very difficult to handle and subdue, with pack-hunting and host-parasite systems as notable exceptions (Kalinkat et al. 2013, Hirt et al. 2020). Very small prey items, on the other hand, would not yield sufficient energy to compensate for the invested effort, except if harvesting can be done efficiently (Naisbit et al. 2012). However, ratios between predator and prey body sizes can vary greatly between and within taxonomic entities (Brose et al. 2006, Naisbit et al. 2011).

Empirical evidence on predator-prey size ratios is growing fast. Nevertheless, data is still scarce for terrestrial invertebrates (Traugott et al. 2013, Gongalsky 2021) despite mentionable efforts (Brose et al. 2008, Eitzinger et al. 2018, Miller-ter Kuile et al. 2022). Furthermore, a positive relationship between body size and trophic level is usually very clear in both marine and freshwater environments (Sholto-Douglas et al. 1991, Boukal 2014), but less pronounced in terrestrial ecosystems (Brose et al. 2006, Potapov et al. 2019). The difference is due to inherent dissimilarities between aquatic and terrestrial ecosystems: first, the range of body sizes of the main terrestrial and aquatic primary producers (vascular plants vs. unicellular algae respectively) is different (Shurin et al. 2005, Brose et al. 2006, Perkins et al. 2019, Potapov et al. 2019); second, many terrestrial invertebrate predators have developed strategies to handle larger prey species by use of toxins or suctorial mouth parts (Brose et al. 2006). Thus, whereas some small terrestrial herbivores consume large plants (e.g. most aphids and caterpillars) and some small terrestrial predators can attack relatively large prey (e.g. small spiders killing large insects), most aquatic prey are fed upon by larger predators, in turn fed on by even larger predators and so on (Potapov et al., 2019).

Apart from body size differences, hunting strategy is another factor influencing the likelihood of predator-prey interactions (Miller et al. 2014, Brose et al. 2019, Potapov et al. 2022). Ambush predators use the element of surprise to hunt prey that happen to pass by (Nentwig and Wissel 1986, Kersch-Becker et al. 2018, Hirt et al. 2020). Ambush predators are incentivized to attack a larger range of prey species since their overall encounter rates are lower than those of active predators, as the former stay stationary for longer periods of time (invertebrates and ectotherm vertebrates) or occupy a smaller territory (endotherm vertebrates) (Strand and Obrycki 1996, Hirt et al. 2020). Active predators, however, confront their prey head-on, a strategy that is more successful with a larger body size (Nentwig and Wissel 1986, Hirt et al. 2020).

The outcome of a predation event is not only influenced by the predator, but also by the prey species. Prey use different mechanisms to try to escape predation, ranging from evasive behaviour (e.g. leaf- and grasshoppers, gazelles) to the development of defensive properties such as camouflage (e.g. owls, stick insects), hard body armour (e.g. beetles, turtles) or chemical defences (e.g. dart frogs, shield bugs) (Peschel et al. 2006, Jeschke et al. 2008). There is considerably more selective pressure to specialize towards particular prey species than there is to develop specific defensive traits against particular predator species, because it is more necessary to avoid overlap of resources than it is to avoid sharing natural enemies (Rossberg et al. 2006). As a consequence, defence mechanisms seem to be largely uniform across each arthropod taxonomic group (Witz 1990). Some studies even suggest that prey phylogeny is more important than body size when determining predator-prey interactions (Naisbit et al. 2012).

Food webs are important tools to study ecosystem functioning (Montoya et al., 2006; Thébault et al., 2007). Despite some notable exceptions (e.g. McLaughlin et al., 2010), empirical studies on terrestrial arthropod food webs are mostly restricted to one-on-one interactions (e.g. among specific pest species and their main predators) or highly simplified food webs from agricultural systems or extreme environments (e.g. Curtsdotter et al., 2019; Digel et al., 2014; Sint et al., 2019). Size-based predictions of predator-prey interactions from soil food webs were shown to provide useful insights into the realised food web structure, but their accuracy can be optimized by including species traits (Potapov 2022). Furthermore, validation of the assumed interactions between species is still needed for such soil food webs (Potapov 2022, Potapov et al. 2022).

In general, food webs can be constructed by compiling fundamental trophic niches, which include all pairwise trophic interactions that a species can potentially establish with other species (Torres-Campos et al. 2020). These niches can be inferred from literature or ratios between putative prey and predator body sizes (e.g. Hines et al., 2019). Not all potential interactions are, however, necessarily realized in a given food web (Torres-Campos et al. 2020). Predator and prey species can for instance be separated in space or time (e.g. through differences in seasonal activity, microhabitat choice or behaviour) or potential prey can have defensive properties that deter predators from attacking (Ruxton et al., 2004; Torres-Campos et al., 2020).

Additionally, smaller juveniles might eat smaller individuals and even species that are no prey for larger adults (Cuff et al. 2021). Since average adult body size is often used for the construction of food webs, interactions by juveniles or exceptionally large or small individuals are usually ignored (Gongalsky 2021). Realised food webs can thus be more complex than those based on adult size, which begs the question to what extent a purely size-based approach is adequate to construct food webs in terrestrial ecosystems (Petchey et al. 2008). Food webs can be based on realized interactions through isotope studies, field observations or gut content analyses (mostly through DNA metabarcoding) (e.g. Jacob et al., 2011; Miller-ter Kuile et al., 2022). However, these methods have some shortcomings, the most important one being the inability to distinguish predating and scavenging when gut content is used as a proxy for realized interactions (Kamenova et al. 2017, Miller-ter Kuile et al. 2022).

In order to reconstruct a natural but practically tractable food web, we focused on the arthropod community associated with a keystone plant species of coastal sand dunes: marram grass (*Calamagrostis arenaria*). This grass is an engineering species of coastal foredunes where harsh conditions, such as salt spray, strong winds and extreme absolute temperatures, restrict the number of species that are capable of surviving in this unique ecosystem (McLachlan, 1991). Nevertheless, species communities in marram grass dunes are much more diverse and complex than those in most agricultural systems, making this ecosystem appropriate for studying the reliability of size-based food web construction (Moore 1994).

The aim of this study is to assess whether the arthropod food web in marram grass dunes can be accurately predicted through the assessment of body size ratios. This was done by constructing two food webs representing the trophic interactions in marram grass dunes. A theoretical food web was constructed based on body size ratios, expert knowledge and literature data on microhabitat, phenology and trophic interactions. The second food web was derived from experimental feeding trials with arthropod pairs in small vials. We hypothesise that the theoretical food web based on body size ratios is able to predict trophic interactions, but would be improved by incorporating species traits like prey defences and predator hunting strategy.

5.3 Material & Methods

Construction of the theoretical food web

To construct the arthropod food web of marram grass dunes, we used data from coastal dune areas along the Channel and the North Sea, covering the North of France, Belgium, the Netherlands and the United Kingdom (Supp. Mat. 5.1). Arthropods were sampled by sweep-netting and manually searching the base of 638 marram grass tussocks during the summers of 2017-2019. In total more than 15 000 specimens were caught and identified, using a stereomicroscope. The overarching food web was constructed by pooling the data of all sites and countries. Interactions between two species were based on the species' feeding ecology, body size differences between predator and prey, microhabitat (i.e. whether the species reside primarily among the marram grass leaves or on the ground at the base of the tussock), seasonal activity periods (all collected from literature; see Supp. Mat. 5.2 for a full overview of the used literature) and expert knowledge. This method has been used before (e.g. Hines et al., 2019). We refer to the resulting network as the theoretical food web.

Construction of the empirical food web

Collection of arthropods

During the summer of 2019, 718 arthropod individuals belonging to 155 different species were collected in several marram grass dune areas along the Belgian coast: 93 individuals were caught in De Panne (51.0949°N, 2.5635°E; 27/07), 107 in Wenduine (51.2972°N, 3.0717°E; 03/08), 270 in Blankenberge (51.3205°N, 3.1446°E; 06/07, 15/07, 10/08 and 24/08) and 248 in Oostduinkerke (51.1368°N, 2.6997°E; 03/07, 17/08 and 31/08). All arthropods were caught in marram grass tussocks (*Calamagrostis arenaria*) by hand or aspirator. After sampling, all arthropods were deprived of food for at least 24h to create a baseline, except for aphids (Sternorrhyncha), leafhoppers (Auchenorrhyncha) and true bugs (Heteroptera), which were provided with small pieces of marram grass to avoid mortality. Water was presented to all individuals in the form of a small ball of wet paper.

Pairwise feeding trials

Feeding trials were used to test pairwise interactions between and within species. These trials were conducted in 60 mL vials that were closed off with mesh to allow free air flow. The bottom of each arena was covered in sand originating from coastal dunes to simulate a slightly more natural environment. Neither marram grass, nor any other form of structure was added to exclude any influence these could have on the interaction. Water was provided on a daily basis. Each trial consisted of two randomly chosen individuals interacting with each other. These could also be individuals from the same species but with different sizes, in order to test for cannibalism. Additionally, the pairs of interacting individuals could be any combination of herbivores, omnivores and carnivores. However, two strict herbivores were never paired. Testing of two predators (either omnivores or carnivores) was included to study intra-guild predation. At later stages of the experiment, some specific interactions were tested in order to maximize the number of tested potential links.

After introducing the arthropods to the vial, it was stored in a shady area at room temperature and left alone. The outcome of the trials was checked and recorded daily with minimal interference. Trials were terminated when at least one of the two interacting individuals had died, i.e. there was no fixed time limit for the trials. In case two known carnivores (e.g. two spiders, either belonging to the same or two different species) did not consume each other, the same trial was counted twice: once with individual one as predator and individual two as prey and vice versa. The dead arthropod was stored in 70% ethanol for later identification, whereas the surviving individual, after being deprived of food for at least one day, could be re-used for subsequent trials. At the end of the series of experiments, all tested arthropods were identified with a stereomicroscope to the most detailed taxonomic resolution according to morphology and/or life stage. This resulted in 617 specimens identified to species level, 63 to genus level and 38 to family level. The food web that resulted from pooling the pairwise trophic interactions will be referred to as the experimental food web.

Determining body size

Since it was not possible to determine the dry weight of individuals, we used body length as an alternative measure for body size (Ganihar 1997, Martin et al. 2014, Moretti et al. 2017). Before the start of each trial, a digital photograph of every individual was taken with a camera mounted on a stereomicroscope and used to measure its body length using ImageJ version 1.52a (Schneider et al. 2012). Body length was measured from cephalon to abdomen, excluding appendages such as antennae, chelicerae, legs or wings. The body length across all tested species and individuals ranged from 1.6 to 12.3 mm (Supp. Mat. 5.4).

Statistical analyses

Data preparation

Predators were categorized as active or ambush hunter. A separate third category for web-building spiders was included because the use of a web possibly enables spiders to catch larger prey (Enders 1975, Nentwig and Wissel 1986) and spiders appeared as outliers in size-based automated food web construction attempts (Bohan et al. 2011). However, since almost all web-building spiders did not construct a web during the feeding trials, this category served more as a correction for the absence of a web, i.e. we expect lower prey size for web-building spiders in the context of standardized experiments in which web-building was not possible. Since closely related species are known to have similar defence mechanisms, order-level taxonomy of the prey was used as a proxy for defensive traits. Because of large differences in defence mechanism within the order of the Hemiptera, suborders Sternorrhyncha (reproduce rapidly to survive), Heteroptera (chemical defence mechanisms) and Auchenorrhyncha (escape predation by rapid movement) were used instead.

42 feeding trials were omitted form the data, because predation could not be reliably determined, e.g. it seemed likely that the “predator” was scavenging or an individual escaped. After removing these data points, the data set consisted of 586 trials, of which 170 ended in predation and 416 did not.

Testing pairwise interactions in the lab

To test the link between predation success, predator/prey body size ratio, hunting strategy of the predator (ambush, active, web-building) and prey taxonomy, we used generalized linear mixed models with a logit link function and binomial distribution. The outcome of the feeding trial, i.e. success (1) or failure (0), was used as response variable, while the log-transformed length of the prey (included for the purpose of correction) and the log-transformed predator/prey size ratio together with categorical variables for hunting strategy and prey taxonomy were used as explanatory variables. Orders that included fewer than 15 tested individuals (Blattodea, Collembola, Dermaptera, Diptera, Hymenoptera, Isopoda, Myriapoda, Neuroptera, Opiliones, Orthoptera, Trombidiformes and Sternorrhyncha), were grouped together into a single category due to convergence issues. This artificial group was then used as a baseline for the comparison with the other included groups (Araneae, Auchenorrhyncha, Coleoptera, Heteroptera, Pseudoscorpionida and Psocoptera). The importance of hunting strategy and prey taxonomy for predator-prey interactions was determined by modelling them as fixed effects, with or without an interaction with the predator-prey body size ratio. According to model selection based on the corrected Akaike Information Criterion (AICc), several models could be considered to best describe the data (Supp. Mat. 5.3). The model with the lowest AICc was used because model averaging does not allow post-hoc comparison for prey taxonomy and hunting strategy.

The model used to analyse the data from the feeding trials was:

success ~ log(Length prey) + log(Length predator/Length prey) + Hunting strategy + Prey taxonomy + log(Length predator/Length prey)*Hunting strategy

Post hoc tests with Tukey adjustments were used to compare different levels of the fixed effects. Individual ‘prey ID’ was used as a random variable to correct for re-using some prey individuals in different trials. ‘Predator ID’ was included as a random variable in the initial models but excluded from final models because it explained almost no variation.

Comparing the empirical and theoretical food webs

Some species were not represented in both food webs, since the theoretical food web was based on biodiversity data and the experimental food web depended on the sampled species. The exclusion of these species resulted in the two final food webs containing the same 85 species (Fig. 5.1; see Supp. Mat. 5.4 for the full species list).

The number of interactions in the subset theoretical food web was much higher than in the empirical food web (726 vs. 143 interactions) because not all possible interactions could be tested in the experimental trials. Therefore, only interactions that were tested in the feeding trials were selected and compared between both food webs (Fig. 5.1). The interactions were classified into four categories of agreement, with the first and second digit indicating whether or not the interaction was observed in the theoretical or the empirical food web respectively: (1-1) interactions that did or (0-0) did not occur in both food webs, (0-1) interactions that were only observed during the feeding trials or (1-0) interactions only described in the theoretical food web. These categories were linked to the taxonomy of the prey and predator species separately via the construction of mosaic plots. The mosaic plot helps visualise the observed and expected interactions more clearly. The relative frequency of the prey taxonomic groups within each category of agreement between the two food webs are represented by the size of the boxes. We use 0-0 and 1-1 to represent the theoretical and experimental food web agreeing on the absence or presence of an interaction, respectively. 0-1 represents a link that is not present in the theoretical food web but happened during the experimental trials, while 1-0 means the opposite. Over- or under-representation of a taxon in one of the categories is determined by the size of standardized residuals (Meyer et al., 2006) and is indicated by the colouring of the boxes: blue indicates over- while red indicates under-representation. The statistical significance of the residuals is eventually indicated by the shading (legend of Fig. 5.5).

Since we were interested in the presence or absence of interactions between different species, the length of the arthropods was not needed in this analysis, which allowed us to include 12 extra lab trials (for which we could not reliably determine the size of one of the tested individuals due to wrong scale bars on the photographs), resulting in a data set with 598 tested interactions.

R version 4.0.4 (R Core Team 2021) was used to perform all data analyses. Generalized linear mixed models (glmm) were fitted with 'lme4' (Bates et al. 2015) and 'lmerTest' (Kuznetsova et al. 2017). The 'anova' function was used to perform likelihood ratio tests between nested models. The 'emmeans' function, with Tukey adjustment of p-values, from 'emmeans' package (Lenth 2022) was used to assess and test parameter differences between categories of hunting strategies and taxonomic groups. The 'emtrends' function from the same package was used to test differences in the effect of predator-prey body size ratio between different hunting strategies. Network metrics were calculated using the 'igraph' package (Csardi and Nepusz 2006). Mosaic plots were made with the 'mosaicplot' function of the R base package 'graphics' (R Core Team 2021). Gephi software (Bastian et al. 2009) was used for network visualization.

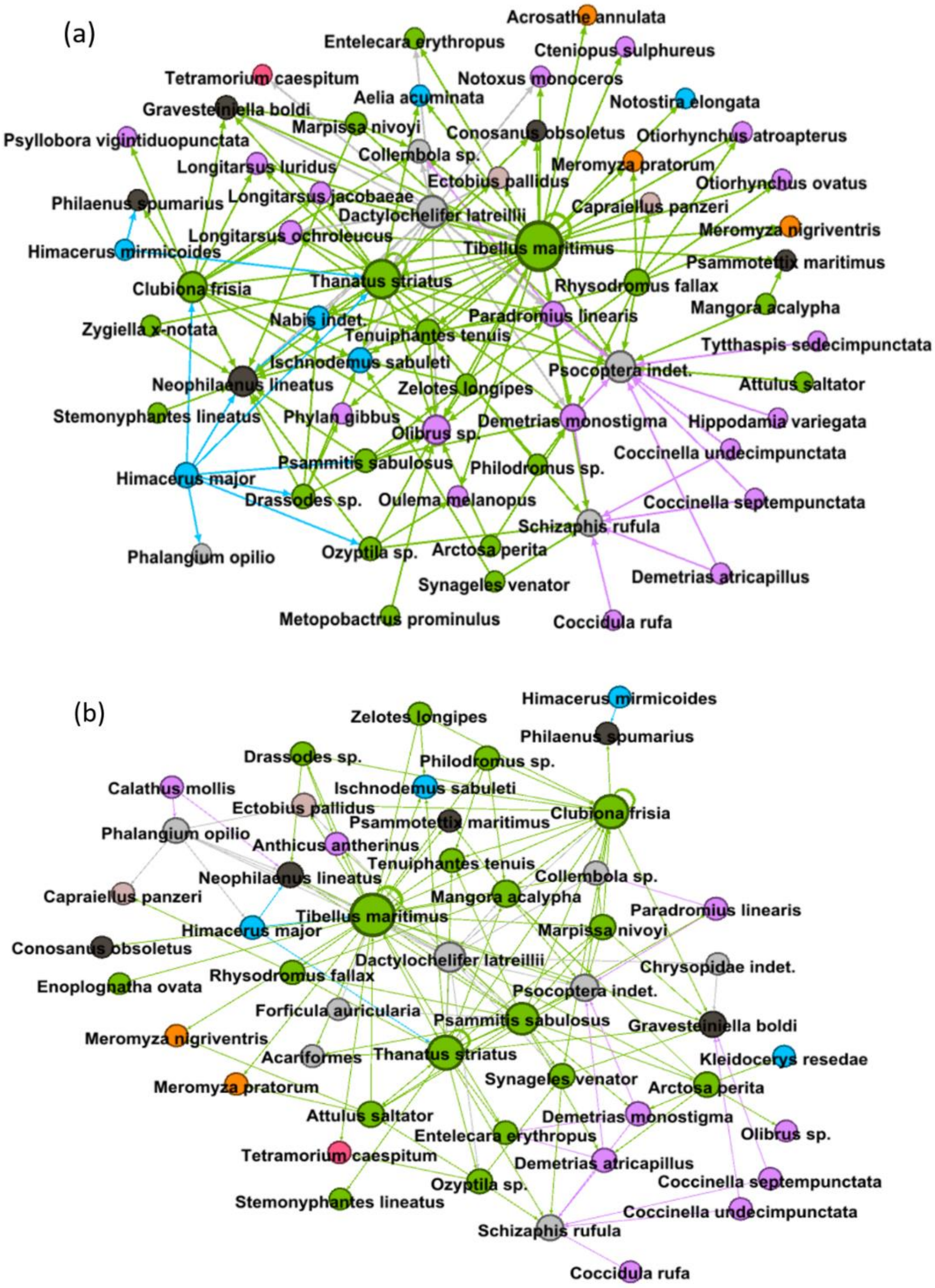

Figure 5.1 (a) *The theoretical food web and* ***(b)*** *the empirical food web. Node colours indicate the species' taxonomic group: beetles (purple), spiders (green), true bugs (blue), leaf hoppers (black), flies (orange), ants (pink), cockroaches (beige), other (grey). Interaction arrows point from predator to prey and the colour indicates predator taxonomic group.*

5.4 Results

Pairwise interactions

On average, the body size ratio between (potential) predator and prey was larger for successful predation events compared to trials where predation did not happen (Fig. 5.3). The probability of successful predation depended on the ratio of predator to prey size (LRT, χ^2_1 = 10.27, p = 0.001), but was generally lower when the prey was larger (LRT, χ^2_1 = 9.43, p = 0.002). Overall, the results indicated that individual predators prefer to consume prey that are ca. 20% shorter than themselves (Fig. 5.2).

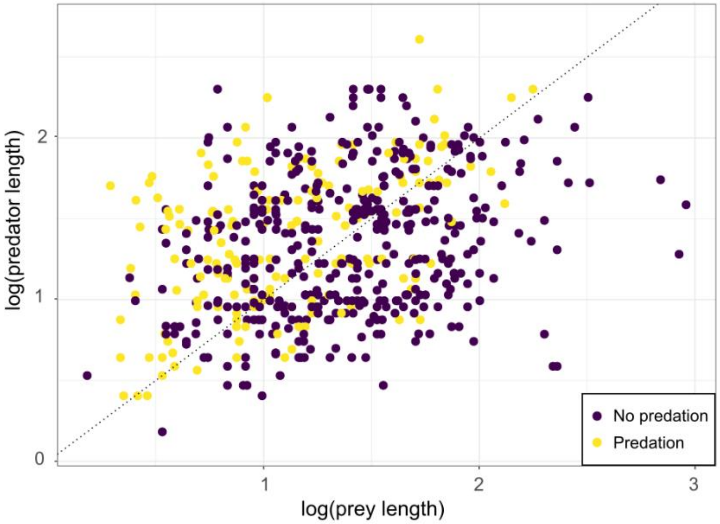

__Figure 5.2__ Overview of (potential) predator and (potential) prey size for all tested pairwise interactions. Colours indicate whether or not predation occurred.

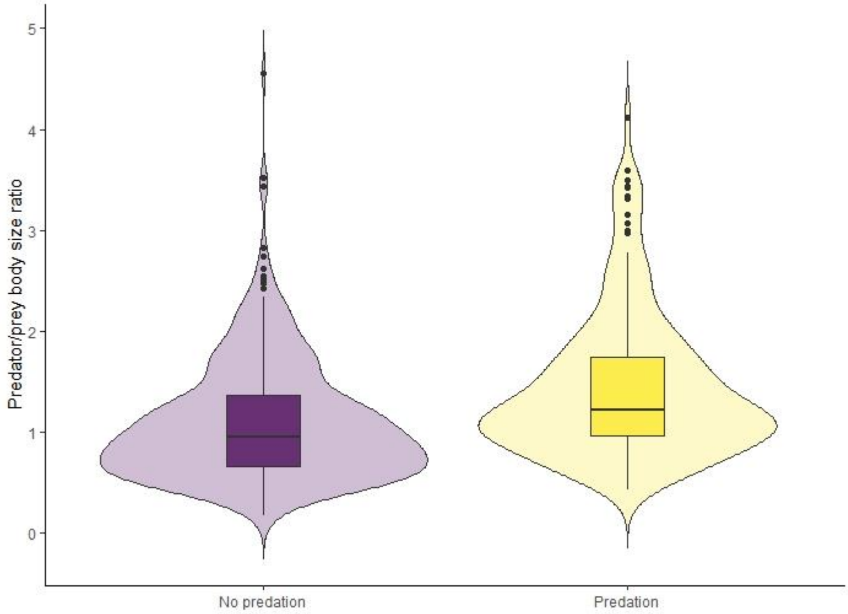

Figure 5.3 *Box- and violin plots represent predator-prey body size ratio in relation to the outcome of the feeding trials. Boxes represent median, 1st and 3rd quartiles. Whiskers represent 1.5 times the interquartile range.*

The probability of predation was further influenced by predator hunting strategy (LRT, $\chi^2_2 = 13.43$, $p < 0.001$) and prey taxonomy (LRT, $\chi^2_6 = 110.3$, $p < 0.001$), while the interaction between predator hunting strategy and body size ratio did not significantly increase the goodness-of-fit (LRT, $\chi^2_2 = 4.37$, $p = 0.113$). Active (z ratio = 3.182, p = 0.004) and ambush hunters (z ratio = 2.932, p = 0.009) engaged more into predation compared to web-building spiders; however, no difference was found between the first two hunting strategies (z ratio = 0.420, p = 0.907). Nonetheless, differences between active and ambush hunting strategy were found when only spider data was used for the analysis (Supp. Mat. 5.6). Post-hoc comparisons among taxonomic groups showed that barklice (Psocoptera), leafhoppers (Auchenorrhyncha) and spiders (Araneae) are most likely to be preyed upon when tested during the feeding trials, while beetles (Coleoptera) and *pseudoscorpions (Pseudoscorpionida) are least likely to be consumed (Fig. 5.4, Supp. Mat. 5.5).*

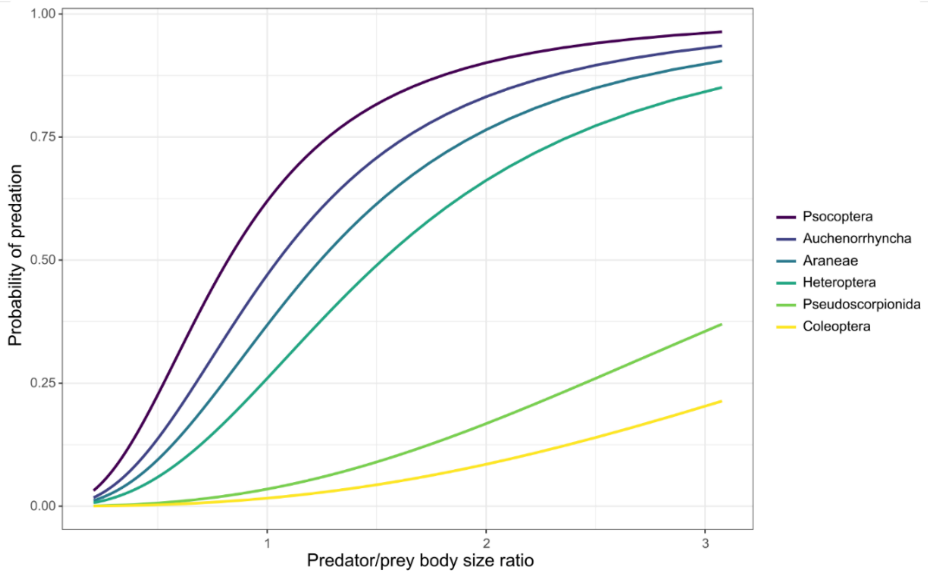

Figure 5.4 *Effect of prey taxonomic group on the relationship between predation probability and predator-prey body size ratio.*

Food web comparison

The theoretical (based on body size ratios and expert knowledge) and experimental food webs (based on the feeding trials) agreed on most interactions (436/598 or 72.9%; 370 interactions were absent and 66 were present in both food webs), although there were still some discrepancies between the two (81 interactions that were present only in the theoretical and 81 interactions only in the empirical food web).

Spiders were captured by more species during the feeding trials than was expected from the theoretical food web. In contrast, beetles were consumed by fewer species than expected (Fig. 5.5). The vulnerability of leafhoppers, aphids, springtails (Collembola) and barklice were well estimated (Fig. 5.5). Finally, Fig. 5.5 suggests that Hymenoptera and Neuroptera were, like spiders, eaten by more species than expected. However, these results are based on 2 and 1 observation(s) respectively, so they should be interpreted with caution.

As predators (Fig. 5.6), spiders and beetles again show the most remarkable results. For spiders, the theoretical and experimental food webs often disagreed (Fig. 5.6). This means that spiders were more often able to subdue prey in the feeding trials than expected based on expert knowledge and body size ratios and conversely, some of the prey indicated for spiders in the theoretical food web were not attacked. Unlike the mismatch between the two food webs regarding beetles as prey, expectations for beetles as predators based on the theoretical food web corresponded rather well to the feeding trials (Fig. 5.6). Finally, pseudoscorpions were less frequently able to kill their prey during the feeding trials than expected from the theoretical food web (Fig. 5.6).

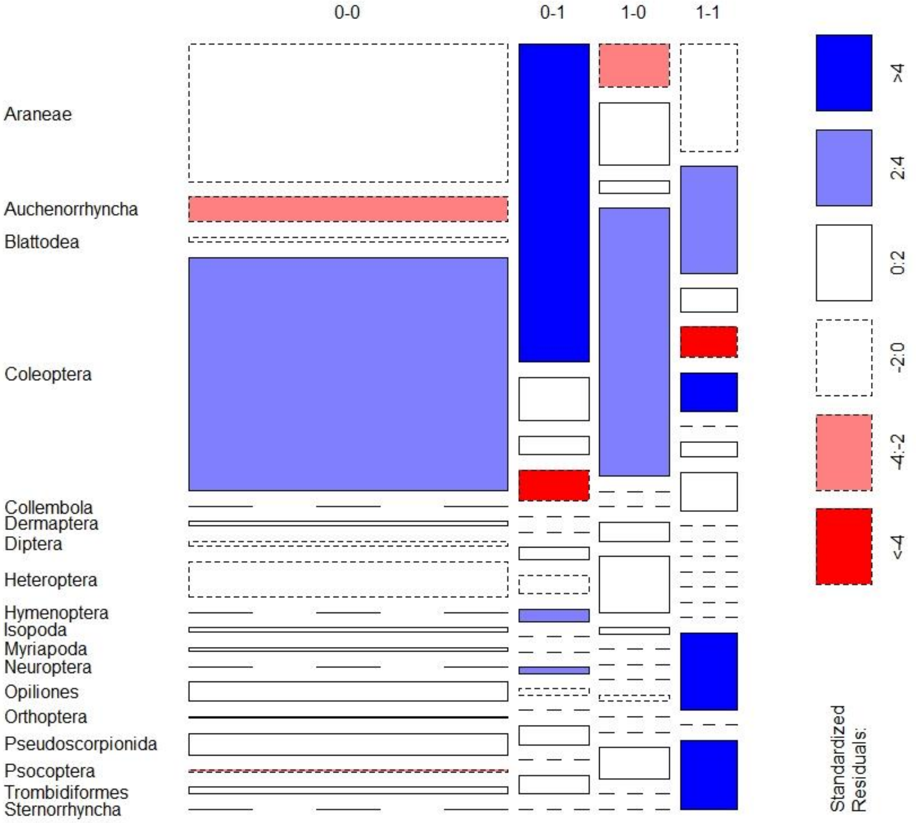

Figure 5.5 *Mosaic plot representing the relative frequency of the prey taxonomic groups within each category of agreement between the two food webs. 0-0 and 1-1 represent the theoretical and experimental food web agreeing on the absence or presence of an interaction respectively. 0-1 represents a link that is not present in the theoretical food web but happened during the experimental trials, while 1-0 means the opposite. The relative frequency is indicated by the area of the boxes. Blue colouration indicates over- while red indicates under-representation. Example: a blue 0-1 box indicates that the taxon is consistently more eaten during the feeding trials compared to what was expected from the theoretical food web. Shading represents the statistical significance (light colours for α = 0.05 and dark colour for α = 0.0001).*

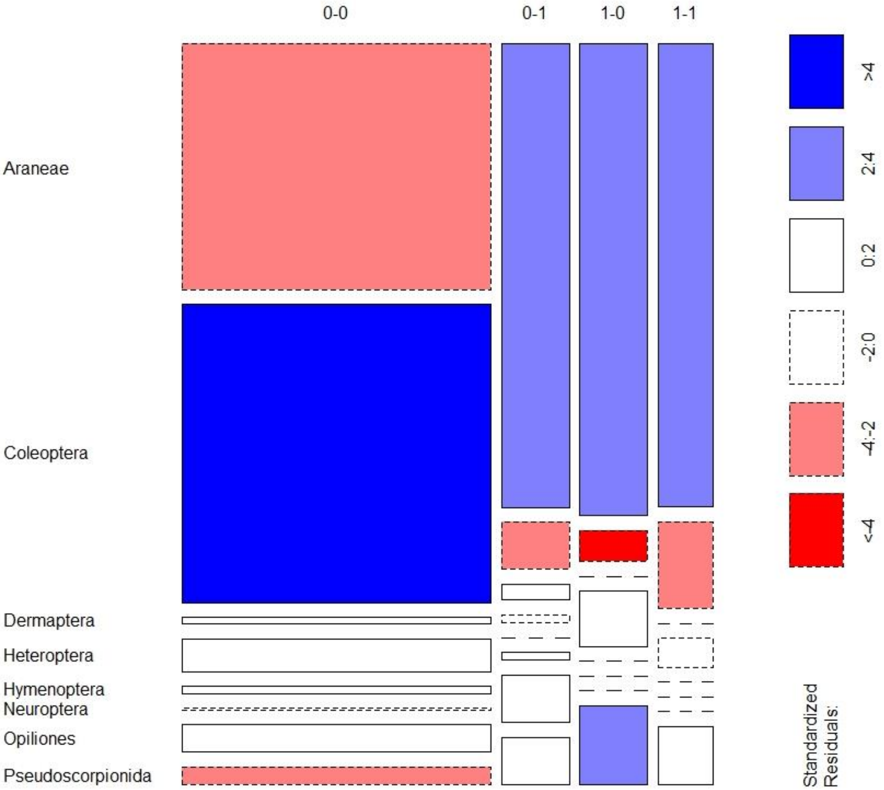

Figure 5.6 *Mosaic plot representing the relative frequency of the predator taxonomic groups within each category of agreement between the two food webs. Coding and colours are as in Figure 5.5.*

5.5 Discussion

Overall, the theoretical food web based on body size, activity period, microhabitat and expert knowledge converged quite well with the food web based on experimental feeding trials for both predator and prey species. Additionally, the pairwise feeding trials confirmed the general consensus that predators are typically larger than their prey (Cohen et al. 1993, Brose et al. 2006). Potential prey with a body length larger than 80% of that of the predator were in most cases not attacked.

Despite these results, several mismatches between the two food webs for some taxonomic groups were highlighted by the mosaic plots.

First, the vulnerability of certain prey taxa such as beetles (Coleoptera) and pseudoscorpions is consistently overestimated in the theoretical food web. This is likely due to their defensive traits, which deter large predators from attacking (Ruxton et al. 2004, Wang et al. 2018, Shinohara and Takami 2020). Our feeding trials provide some indirect evidence for this hypothesis by indicating prey taxonomy as an important predictor of their outcome. While prey taxonomy is linked with a spectrum of traits, we postulate that the most relevant trait for our study is defence strategy. For instance, hard exoskeletons like those of beetles effectively lower the predation probability, even when attacked by a much larger predator (Peschel et al. 2006, Wang et al. 2018). Taxonomic groups without any particular defensive structures, such as aphids and springtails, were frequently consumed, further supporting this hypothesis. Apart from their strong exoskeleton, Coleoptera also have low protein content (Reeves et al. 2021), which could further explain why they were not predated very often. The low predation probability of pseudoscorpion prey might illustrate that, sometimes, offence is the best defence. Pseudoscorpions do not have a hard exoskeleton, but are venomous and can rapidly paralyze or even kill a potential predator (von Reumont et al. 2014). Because predators without alternative prey in our experimental setup still refused to consume these well-defended prey, their defences will likely be even more effective in nature. In case of prey species relying more on evasive behaviour, probabilities of predation were likely inflated in our trials since consistent escape was futile.

About 60% of the spider trials and 50% of the pseudoscorpion trials that were differently classified by the theoretical food web, had a beetle as prey species, which resulted in lower-than-expected predation rates (Fig. 6). Since spiders are considered generalist predators, predictions for interactions between spiders and beetles were mainly based on size differences between predator and prey, but in reality, it appears difficult for spiders to kill even smaller beetles. For pseudoscorpions, however, interactions with beetles are mentioned in some studies (Harvey 1986, Del-Claro and Tizo-Pedroso 2009). However, Harvey (1986) mentioned beetle larvae rather than adults as prey for pseudoscorpions. In nature, beetle adults are probably mainly predated by larger vertebrate predators (Petracci 2002, Oosten 2016, O’Connor et al. 2019).

Second, spiders both ate more prey and were preyed upon more frequently –i.e. intraguild predation was more prevalent– during the feeding trials than expected based on the theoretical food web. This may be explained by the inclusion of microhabitat, a factor known to affect spider diet (Potapov et al. 2022), in the theoretical food web. For the feeding trials, arthropod species were matched randomly. Consequently, two (spider) species living in different microhabitats could be placed together, resulting in more frequent spider-on-spider predation. Given their high protein content and relatively soft exoskeleton (Reeves et al. 2021), spiders make high risk – high reward prey for other predators. Targeting smaller spider individuals might help mitigate this risk. Our data support this, since we noticed unpredicted links in the feeding trials between predators that were substantially larger than their prey, contributing to the overall size-conditionality of predator-prey relationships. Since it is known that young spiders disperse more than adults (Humphrey 1987), it can be expected that they encounter adult spiders inhabiting other microhabitats, i.e. that these interactions, though rare, do occur in nature.

Our feeding trials limited the natural behaviour of the species and consequently their predation success. For instance, ambush predator species are known to have more successful predation events when facing larger-bodied prey than actively hunting species [spiders (Nentwig and Wissel 1986, Verdeny-Vilalta et al. 2015), mammals (Hirt et al. 2020)]. This hypothesis was supported for spiders, but not across all considered taxa. We speculate that this may be due to the absence of structural complexity within the vials resulting in decreased ambush predation success, since the predator could not really hide. The positive effect of structural complexity on predation success is known from terrestrial systems (Mullin et al. 1998, Donadio and Buskirk 2016), but it is especially well established in aquatic systems (Flynn and Ritz 1999, Schultz et al. 2009), where predators are even reported to switch from ambush to active hunting according to the structural complexity (Říha et al. 2021). Web-building spiders can be considered a specific type of ambush predator, using webs to tackle larger prey (Enders 1975, Nentwig and Wissel 1986). However, since almost all web-building spiders did not build a web during our experiment, a significantly lower chance of predating any prey species was observed for these spiders. Direct observations of insects caught in the web, or gut content DNA metabarcoding; Schrojenstein Lantman et al., 2021) offer better possibilities to study the prey species diversity of web-building spiders, but then have as disadvantage that sizes are difficult to assess after consumption.

Trophic interactions involving prey without structural defence traits were well predicted because, as discussed above, these species could not evade predation. Consuming such prey species is easy if predators are able to find the prey in a natural environment. Our results therefor imply that existing information about size, feeding behaviour, life cycle and niche differentiation can be used to generate a coarse yet useful estimate of the trophic interactions among arthropods. We demonstrated this for terrestrial arthropods in marram grass dunes, but we support the wider applicability of such theory-based food web estimates in similar habitats. Size-structured predation remains an important factor when considering intra-guild predation, and can only be quantified by direct methods such as feeding trials, because indirect methods based on molecular markers cannot correct for intraspecific variation in body size. We therefore encourage the use of this under-rated method to study intraspecific variation within traits influencing trophic interactions; because “Humans are different; why do we think arthropods are the same?” (adapted from Gongalsky, 2021).

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Competing interests

The authors have declared that no competing interests exist.

Author contributions

RVDW, GL, NH, MLV and DB designed the lab experiment. GL, NH and RVDW conducted the practical work. GL and RVDW wrote the first draft of the manuscript. RVDW and FM analysed the data. All authors contributed substantially to interpretation of the results and revision of the manuscript.

Data availability

The raw data are available via Zenodo at https://doi.org/10.5281/zenodo.7546960 (Van De Walle et al. 2023).

5.6 Supplementary material

S5.1 Sampling locations for the theoretical food web

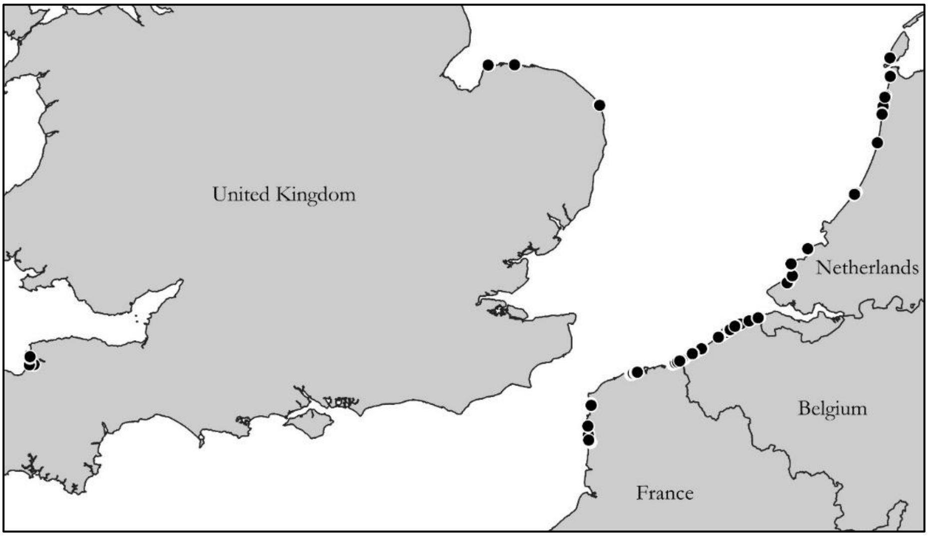

Figure S5.1 *Overview of all biodiversity samples taken along the Channel and the North Sea. 206 samples were taken along the Belgian coast, 184 along the French coast, 188 along the Dutch coast and 60 along the coast of the United Kingdom.*

S5.2 Literature list used for theoretical food web

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S5.3 Model selection

Table S5.3 *The coefficients, number of model parameters (df), AICc values, relative AICc (ΔAICc; i.e., difference between each model's AICc and the minimum AICc) and Akaike weights for all models.*
HS = predator hunting strategy, R = ration = predator/prey body size, PT = prey taxonomic group.

Intrcpt	HS	log(ratio)	log(prey)	PT	hs*log(R)	pt*log(R)	df	logLik	AICc	ΔAICc	weight
1,11	+	1,35	-1,14	+	+		14	-256,86	542,45	**0**	0,336
1,14	+	1,06	-1,13	+			12	-259,04	542,63	**0,177**	0,307
1,14	+	1,39	-1,19	+	+	+	20	-251,03	543,54	**1,094**	0,194
1,17	+	1	-1,19	+		+	18	-253,61	544,43	**1,976**	0,125
-0,5	+	1,97		+	+		13	-261,57	549,78	7,329	0,009
-0,55	+	2,23		+	+	+	19	-255,32	549,99	7,542	0,008
-0,48	+	1,66		+			11	-263,81	550,09	7,639	0,007
2,08	+		-1,77	+			11	-264,18	550,81	8,36	0,005
-0,53	+	1,81		+		+	17	-258,04	551,16	8,713	0,004
0,49		1,45	-0,81	+			10	-265,76	551,9	9,449	0,003
0,49		1,51	-0,87	+		+	16	-260,42	553,79	11,338	0,001
-0,58		1,81		+			9	-268,45	555,21	12,755	0,001
-0,65		2,03		+		+	15	-262,86	556,57	14,115	0
1,45			-1,57	+			9	-276,77	571,86	29,407	0
-0,49	+			+			10	-282,82	586,02	43,574	0
-0,71				+			8	-292,24	600,73	58,276	0
0,78	+	0,84	-1,43				6	-314,19	640,53	98,078	0
0,72	+	1,13	-1,43		+		8	-312,35	640,94	98,492	0
1,55	+	NA	-1,88				5	-317,12	644,34	101,892	0
0,21		1,31	-1,17				4	-320,15	648,37	105,918	0
-1,28	+	1,95			+		7	-319,34	652,87	110,424	0
-1,21	+	1,63					5	-321,45	653	110,547	0
-1,29		1,81					3	-325,14	656,32	113,868	0
1,19			-1,78				3	-328,06	662,17	119,717	0
-0,87	+						4	-340,99	690,06	147,608	0
-1							2	-349,67	703,36	160,909	0

S5.4 Species list

Table S5.4 *Overview of all species that were used to construct both the theoretical and experimental food web, with their respective body length ranges. Note that this table does not include all species that were used in the experimental trials.*

Nr.	Taxonomic group	Species	Min body length (mm)	Max body length (mm)
1	Araneae	*Agroeca cuprea*	3.8	3.8
2	Araneae	*Arctosa perita*	3.3	5.4
3	Araneae	*Attulus saltator*	2.4	2.4
4	Araneae	*Clubiona frisia*	4.3	6.1
5	Araneae	*Drassodes sp.*	5.1	7.5
6	Araneae	*Enoplognatha ovata*	3.6	4.8
7	Araneae	*Entelecara erythropus*	1.4	2.3
8	Araneae	*Floronia bucculenta*	3.5	3.5
9	Araneae	*Mangora acalypha*	1.2	2.8
10	Araneae	*Marpissa nivoyi*	4.3	5.0
11	Araneae	*Metopobactrus prominulus*	1.8	1.8
12	Araneae	*Ozyptila sp.*	2.2	3.3
13	Araneae	*Philodromus sp.*	2.5	3.5
14	Araneae	*Psammitis sabulosus*	2.0	4.7
15	Araneae	*Rhysodromus fallax*	3.2	5.1
16	Araneae	*Stemonyphantes lineatus*	3.1	4.2
17	Araneae	*Synageles venator*	2.3	3.5
18	Araneae	*Tenuiphantes tenuis*	1.6	3.1
19	Araneae	*Thanatus striatus*	1.6	4.4
20	Araneae	*Tibellus maritimus*	1.5	10.0
21	Araneae	*Zelotes longipes*	2.7	5.3
22	Araneae	*Zygiella x-notata*	6.1	6.1
23	Auchenorrhyncha	*Conosanus obsoletus*	5.0	5.0
24	Auchenorrhyncha	*Gravesteiniella boldi*	1.6	4.6
25	Auchenorrhyncha	*Neophilaenus lineatus*	5.2	6.8
26	Auchenorrhyncha	*Philaenus spumarius*	5.5	6.3
27	Auchenorrhyncha	*Psammotettix maritimus*	4.7	4.7
28	Blattodea	*Capraiellus panzeri*	3.2	7.0
29	Blattodea	*Ectobius pallidus*	3.6	5.1
30	Coleoptera	*Aleochara bipustulata*	5.4	6.2
31	Coleoptera	*Amara spreta*	7.5	7.5
32	Coleoptera	*Anthicus antherinus*	2.8	3.8

33	Coleoptera	*Anthicus bimaculatus*	3.5	3.5
34	Coleoptera	*Calathus mollis*	6.9	7.4
35	Coleoptera	*Coccidula rufa*	2.9	4.5
36	Coleoptera	*Coccinella septempunctata*	4.8	7.1
37	Coleoptera	*Coccinella undecimpunctata*	4.4	4.8
38	Coleoptera	*Cteniopus sulphureus*	6.6	9.1
39	Coleoptera	*Demetrias atricapillus*	4.8	5.9
40	Coleoptera	*Demetrias monostigma*	4.1	5.5
41	Coleoptera	*Hippodamia variegata*	3.8	5.2
42	Coleoptera	*Longitarsus jacobaeae*	3.0	3.0
43	Coleoptera	*Longitarsus luridus*	1.7	1.7
44	Coleoptera	*Longitarsus ochroleucus*	2.3	3.2
45	Coleoptera	*Notoxus monoceros*	3.7	4.4
46	Coleoptera	*Oedemera lurida/virescens*	6.8	6.8
47	Coleoptera	*Olibrus sp.*	2.0	2.5
48	Coleoptera	*Otiorhynchus atroapterus*	8.3	10.9
49	Coleoptera	*Otiorhynchus ovatus*	5.0	5.0
50	Coleoptera	*Oulema melanopus*	5.1	5.1
51	Coleoptera	*Paradromius linearis*	4.2	6.8
52	Coleoptera	*Phylan gibbus*	6.7	7.3
53	Coleoptera	*Propylea quatuordecimpunctata*	4.7	4.7
54	Coleoptera	*Psyllobora vigintiduopunctata*	3.5	3.5
55	Coleoptera	*Rhyzobius chrysomeloides*	3.2	4.2
56	Coleoptera	*Tachyporus hypnorum*	4.0	4.6
57	Coleoptera	*Tytthaspis sedecimpunctata*	2.7	3.7
58	Coleoptera	*Xanthomus pallidus*	6.1	7.3
59	Collembola	*Collembola sp.*	3.0	3.0
60	Dermaptera	*Forficula auricularia*	9.2	10.9
61	Diptera	*Acrosathe annulata*	8.9	8.9
62	Diptera	*Meromyza nigriventris*	5.0	6.1
63	Diptera	*Meromyza pratorum*	4.9	6.1
64	Diptera	*Sphaeroceridae indet.*	2.4	2.5
65	Heteroptera	*Aelia acuminata*	7.4	9.0
66	Heteroptera	*Himacerus major*	5.5	8.4
67	Heteroptera	*Himacerus mirmicoides*	6.3	7.2
68	Heteroptera	*Ischnodemus sabuleti*	2.6	6.8
69	Heteroptera	*Kleidocerys resedae*	3.9	4.4

70	Heteroptera	*Nabis sp.*	6.2	6.6
71	Heteroptera	*Nabis ferus*	6.9	6.9
72	Heteroptera	*Notostira elongata*	7.8	7.8
73	Heteroptera	*Scolopostethus affinis*	3.8	3.8
74	Hymenoptera	*Lasius fuliginosus*	4.4	4.6
75	Hymenoptera	*Tetramorium caespitum*	3.6	3.8
76	Isopoda	*Armadillidium vulgare*	12.2	12.2
77	Isopoda	*Porcellio scaber*	7.1	7.5
78	Myriapoda	*Ommatoiulus sabulosus*	17.1	19.3
79	Neuroptera	*Chrysopidae sp.*	5.1	7.1
80	Opiliones	*Phalangium opilio*	1.9	7.3
81	Orthoptera	*Chorthippus sp.*	12.3	12.3
82	Pseudoscorpionida	*Dactylochelifer latreillii*	1.9	3.7
83	Psocoptera	*Psocoptera sp.*	1.3	2.5
84	Sternorrhyncha	*Schizaphis rufula*	1.8	2.0
85	Trombidiformes	*Acariformes sp.*	1.8	2.7

S5.5 Post-hoc tests

Table S5.5.1 *Post-hoc comparison of the coefficients of the different hunting strategies. P-values are Tukey corrected. Positive values indicate that the first hunting strategy is more likely to eat the prey than the second hunting strategy. Significance level is indicated with ***.*

Hunting strategies	estimate	SE	Z ratio	p-value
Active – Ambush	0.135	0.321	0.420	0.9073
Active – Web	2.352	0.739	3.182	0.0042***
Ambush – Web	2.217	0.756	2.932	0.0094***

Table S5.5.2 *Post-hoc comparison of the coefficients of the interaction between different hunting strategies and log-transformed predator-prey body size ratio.*

Hunting strategies	estimate	SE	Z ratio	p-value
Active – Ambush	0.717	0.614	1.168	0.4724
Active – Web	2.194	1.157	1.896	0.1397
Ambush – Web	1.477	1.224	1.207	0.4489

Table S5.5.3 *Post-hoc comparison of the coefficients of different prey taxa. Negative values indicate that the first taxon is eaten less than the second and vice versa. Significance level is indicated with ***.*

Prey order	**Estimate**	**SE**	**Z ratio**	**p-value**
Other - Araneae	0.0785	0.363	0.216	1.0000
Other - Auchenorrhyncha	-0.3745	0.458	-0.817	0.9833
Other - Coleoptera	3.5693	0.628	5.681	<.0001 ***
Other - Heteroptera	0.6059	0.503	1.204	0.8930
Other - Pseudoscorpionida	2.8587	0.933	3.063	0.0357 *
Other - Psocoptera	-1.0209	0.799	-1.277	0.8626
Araneae - Auchenorrhyncha	-0.4530	0.393	-1.154	0.9111
Araneae - Coleoptera	3.4908	0.592	5.896	<.0001 ***
Araneae - Heteroptera	0.5274	0.456	1.156	0.9103
Araneae - Pseudoscorpionida	2.7802	0.905	3.073	0.0346*
Araneae - Psocoptera	-1.0994	0.739	-1.487	0.7526
Auchenorrhyncha - Coleoptera	3.9438	0.660	5.975	<.0001 ***
Auchenorrhyncha - Heteroptera	0.9804	0.508	1.931	0.4597
Auchenorrhyncha - Pseudoscorpionida	3.2332	0.962	3.361	0.0137 *
Auchenorrhyncha - Psocoptera	-0.6463	0.821	-0.787	0.9862
Coleoptera - Heteroptera	-2.9634	0.666	-4.449	0.0002 ***
Coleoptera - Pseudoscorpionida	-0.7106	0.965	-0.736	0.9904
Coleoptera - Psocoptera	-4.5902	0.925	-4.960	<.0001 ***
Heteroptera - Pseudoscorpionida	2.2528	0.969	2.324	0.2325
Heteroptera - Psocoptera	-1.6268	0.862	-1.888	0.4882
Pseudoscorpionida - Psocoptera	-3.8796	1.142	-3.398	0.0121 *

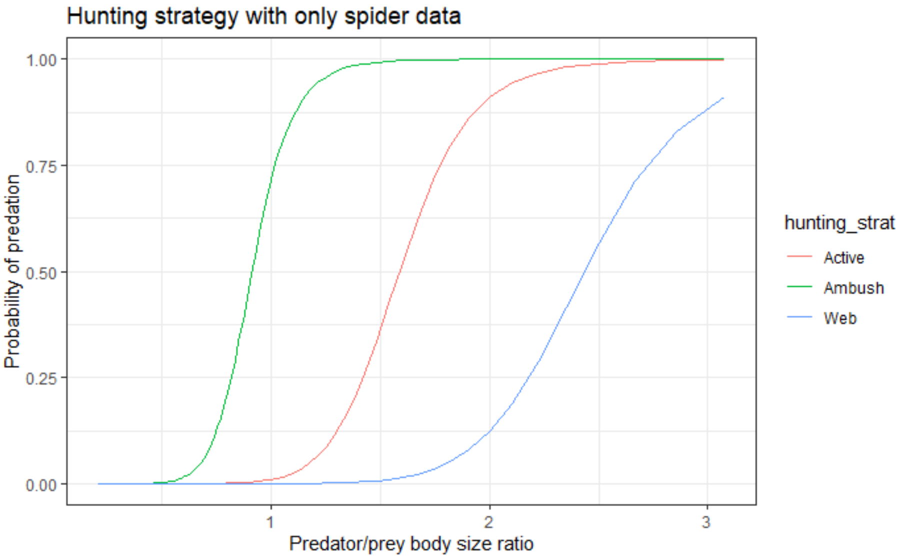
S5.6 Hunting strategy with only spider data

Data set with 437 observations: 325 active hunters, 40 ambush predators and 72 web-building spiders.

Model used: success ~ log(Prey) + log(Predator/Prey) + Hunting strategy

Table S.6: Post-hoc comparison of different hunting strategies for the model where only spider data is used. P-values are Tukey corrected.

Hunting strategies	estimate	SE	Z ratio	p-value
Active – Ambush	-5.53	2.30	-2.399	0.0434
Active – Web	4.27	2.02	2.120	0.0858
Ambush – Web	9.80	3.22	3.043	0.0066



6. General discussion

6.1 Overview of main conclusions

During the four years of my PhD, I have explored different factors influencing dune biodiversity. More specifically, I studied the occurrence of an invasive plant species and the possible consequences of its spread. Furthermore, I researched the correlations between different regional and local variables with below- and aboveground invertebrate biodiversity. Furthermore, I used the arthropod community found in marram grass dunes to validate whether body size ratios can predict trophic interactions. I will start this discussion with a short overview of the main conclusions from the previous chapters. Next, I will discuss these results in the framework of plant-mediated interactions. Linking chapter 3 and 4, I try to gauche whether we observed trends explainable by above-belowground interactions. I continue with a discussion on the implications of my work for conservation, where I dive deeper into how marram grass could be managed to ensure the survival of the invertebrate biodiversity characteristic for this ecosystem. Furthermore, I try to estimate how beneficial marram grass dunes, planted as nature-based solutions for coastal protection, could be for dune biodiversity. Finally, I will end this work with discussing some of the future perspectives and opportunities

Chapter 2

By mapping the occurrence of narrow-leaved ragwort (*Senecio inaequidens*) in coastal foredunes, it became clear that *Senecio* is capable of establishing under relatively dynamic sand conditions. Competition with marram grass lowered the probability of occurrence only slightly. On the other hand, growing in *Senecio*-altered soils clearly increased marram grass performance, even though it could not overrule the omnipresent negative effect of the soil biota. We hypothesised this positive abiotic soil modification to be an elevation in nutrient concentrations because of *Senecio* leaf litter decomposition.

Chapter 3

Total nematode numbers in sandy soils are clearly concentrated around marram grass roots, where plant-feeding nematodes accounted for the largest portion of the nematode community. In bulk soil, bacterivorous nematodes were generally more abundant. Nevertheless, overall abundances of most functional groups were highly correlated. The biggest difference in nematode numbers among samples could be explained by the biogeographic region in which the sample was taken. Within the region, marram grass properties affected the associated nematode community only slightly, while nematode communities in the bulk soil correlated most with occurrence of the invasive plant species *S. inaequidens*. Overall, there still seemed to be quite some stochasticity structuring nematode communities in our samples.

Chapter 4

Biogeographic region is most important in determining aboveground invertebrate species richness associated with marram grass tussocks. Local marram grass parameters still influenced above-ground invertebrate diversity quite substantially, while stochasticity seemed least important in structuring the marram-associated community. From the marram grass parameters, vitality of the sampled tussock and the proportional cover surrounding it both displayed an optimum for species richness, while increased clustering was correlated with a decrease in species richness. Furthermore, phylogenetic data rather than species body length or feeding guild helped to improve model fit. From the residual species-associations, it seemed that invertebrate communities in marram grass tussocks can be subdivided into specialist and generalist communities.

Chapter 5

Prey were on average 20% smaller than their predators in successful trials. Our pairwise feeding experiments thus indicated that inferring trophic interactions from body size ratios is a good practice for terrestrial arthropods. However, expectations were consistently off for some taxa. Notably, spiders were eaten more, while beetles were eaten less than expected. Including phylogenetic data, with a focus on the prey species, could help improve such predictions. This is especially important for species of whom little is known about their ecology, such as many arthropod groups.

6.2 Plant-mediated interactions

Our results do not allow to make explicit statements about plant-mediated interaction between species separated in space or time. Alternatively, I will try to combine the results from chapters 3 and 4 and discuss them within the established framework of aboveground-belowground interactions. The results of the chapters can be linked via the marram grass variables and their correlations with above- (chapter 4) or belowground (chapter 3) invertebrate biodiversity. In the coastal foredunes studied, both aboveground species richness and belowground herbivore abundance increased with an increasing marram grass cover. This is in line with the results from Vandegehuchte et al. (2010), who found that adverse interactions between root and foliar herbivores established in a controlled marram grass microcosm were not detected under natural field conditions. The influence of other, more dominant, factors structuring herbivore populations, such as plant vitality, was suggested as a viable explanation (Vandegehuchte et al. 2010b). Aboveground species richness displayed a shallow maximum in marram grass tussocks of intermediate vitality, but was otherwise fairly constant. Since functional groups did not affect this relationship, we can assume that invertebrate predator species richness follows the same trend. Belowground, less predatory and fungivore nematodes were found in the rhizosphere of vital marram grass tussocks. If either the above- or belowground herbivore community is top-down regulated, changes in predator abundances due to marram grass vitality might indeed subsequently influence the induced effects of above- or belowground herbivores. In the introduction, it was established that above-belowground interactions can vary greatly with regards to their direction and magnitude, thus mutualistic effects between both herbivore communities cannot be completely excluded, as these have been shown in literature too (Johnson et al. 2009, Kaplan et al. 2009), albeit not for marram grass specifically.

I did not previously combine these two biodiversity indices into one analysis because the response variables are fundamentally different, i.e., species occurrences for the aboveground biodiversity vs. functional group abundances for the belowground biodiversity. Moreover, both response variables were discussed in previous chapters in different frameworks, using a more trait based approach for nematode counts, while a more detailed ecological approach was used for the aboveground invertebrate species diversity. On a technical note, it would probably not have been feasible to combine them in the first place, taking into consideration that the HMSC model with the transect as random effect (chapter 4) did not converge and that using both data sets for a combined analysis would drastically reduce our sample size (because no missing data is allowed in HMSC Ovaskainen and Abrego 2020)) and thus the chance of overall convergence for an even more complicated model.

For the belowground invertebrate biodiversity studied in chapter 3, only nematodes were considered, although insect larvae, e.g. moth (*Noctua pronuba*) or beetle larvae (*Otiorrhynchus atroapterus*), are also known to feed on marram grass roots (Weeda et al. 1991). Including information on larval stages could have helped to deepen our understanding of the intricate relationship between marram grass and its associated invertebrates.

Plant-mediated interactions between species separated in time are called priority effects. The outcome of these effects often depends on the particular order of arrival of the species on the plant, or in the community in general (Chase 2003). The two distinct invertebrate communities observed in the residual species co-occurrences in chapter 4 could point towards priority effects. The mechanisms driving priority effects are considered to be either niche preemption or niche modification (Fukami 2015). Niche preemption, i.e., a reduction in the amount of resources attainable for latter arriving species, seems unlikely to explain this observation because marram grass is very abundant and grows in dense quasi mono-cultures. Additionally, niche preemption has to be exceptionally strong to prevent colonization by late-arriving species and is normally linked with lowered species abundances rather than complete exclusion (Fukami 2015). Thus, niche conversion, via changes in the chemical profile of marram grass, seems a more plausible explanation. These changes are probably not caused by the production of secondary metabolites, but are rather the consequence of increased allocation of foliar resources towards the roots as a reaction to leave herbivory (Kaplan et al. 2009). We have to assume that this reaction can be induced by either specialist or generalist, who are able to cope with it while the other group is not, for this explanation to work. Predator species, less affected by these processes because they are mediated by the host plant, seemed to be less correlated to either of the distinct groups. Nevertheless, a few spiders and predatory beetles seem to co-occur together with the generalist group, hinting at the importance of tritrophic interactions (van der Putten et al. 2001), where sequestration of secondary metabolites by specialised herbivores are known to influence predatory species (Opitz and Müller 2009, Zhang et al. 2019). Another explanation could be that these predators avoid specialist species because they are occurring on young plants, which differ in their nutritional conditions. The predatory beetle *Demetrias monostigma* is considered a dune specialist (although it is not strictly dependent on marram grass; Weeda et al. 1991, Provoost and Bonte 2004) and occurs more together with other dune specialist. This could indicate that it is better adapted to the specific chemical composition (either increase chemical defences or altered nutritional values) of specialist dune herbivores.

6.3 Implications for conservation

Identifying the factors structuring biodiversity is important when trying to conserve natural habitats. The most important factor determining aboveground species richness in our data set was the biogeographic region in which the sample was taken (chapter 4). As mentioned before, this parameter correlates with a lot of variables that can be related to climate, soil characteristics, temporal variation in species populations etc. Identifying which variables drive the significance of this parameter would be most helpful for biodiversity. However, these regional variables are often harder to manage or not even manageable at all (e.g., the climate). Consequently, I opted to focus instead on the influence of the local conditions because these results are more applicable. Knowing how vegetation structures biodiversity is important, considering dune managers can try to steer dune vegetation growth accordingly. This knowledge is, furthermore, crucial if we would like to reconcile biodiversity conservation with coastal protection.

Dune vegetation is increasing globally, consequently stabilizing open sand dunes during the past decades (Provoost et al. 2011, Jackson et al. 2019, Gao et al. 2020). More recently, stabilized dunes are artificially re-mobilised because open dunes are expected to support more biodiversity (Darke et al. 2013, Konlechner et al. 2014). This instigated a scientific debate with at its core the question whether the cause of this dune stabilisation is natural or mainly human-induced (Delgado-Fernandez et al. 2019, Pye and Blott 2020, Austin and Walker-Springett 2021, Cooper and Jackson 2021). However, in the whole discussion, the link between dune vegetation cover and biodiversity is largely ignored. I will try to link the invertebrate diversity in coastal dunes with the local cover and vitality of marram grass based on my research.

Knowing which dunes support the highest biodiversity might allow dune managers to maintain foredunes in the most suitable way for conservation purposes. On a local scale, marram grass parameters were correlated with biodiversity living on both the leaves and the roots. In chapter 4, most aboveground invertebrate species were found in foredunes that were covered for 50 % or more by marram grass with intermediate vitality. According to these results, re-mobilising vegetated dunes by removing vegetation seems futile, since a reduction from high to intermediate cover will not significantly raise species richness. Contrarily, if too much vegetation is removed, species richness could be reduced. On the other hand, sand dynamics are expected to be lower in dune areas with higher vegetation cover and, additionally, we showed that plant-feeding nematode abundances increased with marram grass cover. Taken together, lowered sand dynamics in combination with higher nematode abundances will consequently decrease marram grass vitality in highly vegetated dunes, something which is already well-established (Huiskes 1979, Van der Stoel et al. 2002). Hence, reducing vegetation cover in stabilized dunes with withering marram grass could allow sand dynamics to increase, therefore reinvigorate marram grass. This could consequently have a positive effect on biodiversity, since marram grass of intermediate vitality harboured the highest species richness.

We found that aboveground invertebrate species richness was higher in less clustered marram grass configurations (see chapter 4), thus our data suggests that regular growing marram grass might possibly be even better for biodiversity. This could be leveraged to further raise aboveground invertebrate species richness in coastal foredunes, assuming this trend is linear (see further). However, to maintain less clustered marram grass configurations would require constant disturbance or management, since marram grass grows clustered under natural conditions. Before the eradication by Myxomatosis in the 1950s, rabbit populations reduced vegetation via herbivory and by uprooting whole plants (Provoost et al. 2011). Allowing more people in coastal dunes, especially in countries like the Netherlands and the UK, where this is now largely prohibited, could also create more disturbance. Even though samples were taken in 44 different dune areas, all of them were covered by (highly) clustered marram grass configurations. Consequently, this variable had only a small influence on species richness and trying to estimate how species richness will change in regularly growing marram grass are extrapolations outside the scope of our sampled data. Thus, caution is warranted because the actual trend in regular distributed marram grass could be different from the trend within only clustered marram grass configurations. Nevertheless, since this is the situation we have to work with, we might as well try to learn as much as we can from natural marram grass configurations.

Our statistical approach enabled us to disentangle species specific responses to marram grass variables (Poggiato et al. 2021), which allows us to study the species' ecology in more detail. For instance, the beetle *Cteniopus sulphureus* belongs to the

Tenebronidae, a family which mainly includes detritivores in marram grass dunes (Weeda et al. 1991). The amount of detritus found in a marram grass tussock will increase as our measure for vitality decreases and this beetle species did indeed display a negative correlation with marram grass vitality. We could thus assume that this species from the Tenebronidae family is also a detritivore. A disadvantage of our study is the unintentional exclusion of larger and more mobile dune species such as *Oedipoda caerulescens* (a grasshopper) and *Cicindela maritima* (a carabid beetle) due to sampling only in and above marram grass tussocks. These species are known to more habitually use open sand for their daily activities (Maes et al. 2006). The optimal species richness along the vegetation cover gradient might thus have been more pronounced if we would have been able to include such species. Our results need to be interpreted accordingly, namely as a proof-of-principle rather than specific conservation guidelines. Knowledge of species' specific ecology is still important for dune managers and coastal conservation.

I want to stress the distinction between species diversity and species abundance. The discussion above was done based on predictions for species richness, i.e., the number of species occurring on marram grass, and not for species abundances, i.e., the number of individuals of a certain species occurring on marram grass. Initially, we did measure abundances for the aboveground invertebrate community. However, we did not use them since many species were either missing completely from numerous samples or were only present in very low numbers, and this zero-inflated data set caused problems with the statistical model (see chapter 4). Nevertheless, it can be expected that species richness and species abundances are highly correlated (McLachlan 1991) and that measures beneficial for species richness will also benefit species abundances.

Another faunal group we completely ignored by focussing on invertebrate species richness, are the larger vertebrate taxa. Although most large vertebrates such as birds and mammals do not stay in marram grass permanently, they are known to temporarily make use of it for feeding (McLachlan 1991). We can thus expect that an increase in invertebrate diversity will also benefit larger animals. However, the perceived magnitude of the spatial scales highly depends on the taxa considered. For instance, invertebrates are smaller than vertebrate species and thus have, in general, a lower dispersal capacity (Tews et al. 2004, Soininen 2016). This makes that local scale for a vertebrate species could imply considerable barriers for an invertebrate species. Keeping in mind 'scale' is perceptual and thus taxon-specific is important for nature conservation.

Non-native species are reported as (part of) the cause of numerous extinction in the past (Bellard et al. 2016) and currently still pose a huge threat to species from all taxonomic groups worldwide (Dueñas et al. 2021). They are proven countless times to not influence specific species but rather communities as a whole, with impacts ranging from positive to negative depending on the context (Katsanevakis et al. 2014, Guy-Haim et al. 2017), although the overall effect seems to be slightly negative (Guy-Haim et al. 2017). Resident species are especially affected when the invasive species are ecosystem engineers, restructuring physical stress (Guy-Haim et al. 2017). We found a high probability of establishment of *Senecio inaequidens* in almost all sampled natural marram dunes (chapter 2), meaning that it is only a matter of time before it spreads to other dune areas along the European coast. I will discuss the consequences of *Senecio* (or invasive species in general) establishment on the belowground community in the next section, since nematode abundances are tightly linked with marram grass vitality, sand dynamics and consequently dune growth and coastal protection. The possible effect of *S. inaequidens* establishment on aboveground diversity was not tested because we thought it more important in structuring the belowground community (Scherber et al. 2003, Kowalchuk et al. 2006, Caño et al. 2009). Even though we showed that *Senecio* plants are able to establish in marram dunes, no large numbers were observed during our field work. Consequently, I do not think *Senecio* establishment would drastically alter aboveground invertebrate richness. The nearby presence of *Senecio* plants could increase insect pollinator richness because of a spill-over effect caused by the nectar of the flowers of adult *Senecio* plants. Nevertheless, there still exists the possibility of a decrease in herbivore richness due to dune species not being adapted to the chemical compounds of *S. inaequidens*. However, native *Senecio* species (e.g., *Senecio jacobaea*) do also occur in close proximity to the foredunes, namely in grey dunes. If anything, I would suspect a slight increase in the occurrence of the beetle *Longitarsus jacobaeae*, which is observed to switch from its native host *S. jacobaea* to feed on *S. inaequidens* plants (Scherber et al. 2003) and which was already found frequently in our samples.

6.4 Implications for coastal protection

Coastal dunes protect vast amounts of the worlds sandy shoreline against floods and sea level rise. Marram grass is crucial for dune growth at sandy coasts south of latitude 63 °N (Huiskes 1979). I will here discuss the consequences of potential invasive species establishment and nematode numbers on marram grass health and spatial configuration; and the consequences of those changes in the marram grass variables for coastal protection in both natural and human-made dunes.

As already mentioned in section 6.3, the probability of *S. inaequidens* spreading to other natural dune areas is high. Fortunately, according to our other results, the direct consequences of *Senecio* expanding its range seem to be limited, as marram grass performed better in Senecio-altered sand in our growth experiment (chapter 2), while nematode numbers in the field survey (chapter 3) mainly increased in the bulk soil, and less in the rhizosphere of marram grass. Increased nematode abundances could potentially increase the net negative effect from the soil community experienced by marram grass. However, biodiversity in S*enecio*-altered soils did not significantly differ from unvegetated sand in their effect on marram grass performance during our growth experiment, thus an increased pressure on marram grass seems unlikely. Yet, an increase in nematode abundances in the field was observed. The combination of these results hint at marram grass being more capable of handling more stressful conditions - higher nematode numbers - under increased nutrient concentrations, an idea that was already expressed before (Reijers et al. 2020). Our results furthermore indicate that soil biodiversity as a whole was not reduced, which contradicts other studies on both *S. inaequidens* and other *Senecio* plants reporting adverse effects (Kowalchuk et al. 2006, Harkes et al. 2017). This could be explained by the high permeability of sandy soils, which prevents the chemical defence compounds to build up. Consequently, these plant defence chemicals cannot reach high enough concentrations to significantly alter the soil community.

Marram grass has a rich history of being used to stabilize sandy coasts both in (e.g., van der Putten and Kloosterman 1991, Weeda et al. 1991) and out of Europe (e.g., Wiedemann and Pickart 1996, Hilton et al. 2005). Manually planting marram grass or even artificially creating whole dunes might become more necessary in the future due to the coast line retreating more inland, where it is confronted by the continual urbanization of coastlines, resulting in a dramatic restraint of coastal areas, especially in Europe (Keijsers et al. 2015, Bonte et al. 2021). This coastal squeeze in combination with the projected sea-level rise have increasingly raised the interest in dunes as coastal protections, especially within the ‘Nature-based solutions’ framework. Marram grass used to be frequently planted in a homogeneous way, minimizing spatial autocorrelation (van der Putten and Kloosterman 1991), even though it occurs clustered together in natural foredunes (Bonte et al. 2021). More recently, experiments are being set up to test the capacity of different marram grass spatial configurations for dune growth (e.g., Derijckere et al. 2022). Since most stabilization projects still plant marram grass in a homogeneous way, I will discuss the implications of my results for nature-based solutions assuming low spatial autocorrelation (i.e. Moran’s I close to zero) and a low to intermediate proportional cover of the surrounding marram grass.

In artificially planted dunes, the establishment of invasive species in general, and for *Senecio inaequidens* in particular, will largely depend on the density of the planted marram grass. Probability of establishment will be high if marram grass is only sparsely planted and it will gradually decrease with an increasing cover. However, since we only sampled a few marram grass tussock in dunes with low autocorrelation and intermediate cover, the lower probability of establishment might be caused by the low sample size. Establishment probability in dunes with such specific configurations might thus be higher than estimated from our data. On the other hand, high tolerance for sand burial is a prerequisite in order to extrapolate our results to other invasive plant species in the first place. Focusing on *S. inaequidens* specifically, I do not think that it will cause a lot of problems when it establishes, since our field data hinted at marram grass being the better competitor and our growth experiment showed an increased performance of marram grass in *Senecio*-altered soils. However, should the increased marram grass growth in combination with an increased vegetation cover due to *S. inaequidens* drastically lower local aeolian sand transport, dunes could become vegetated, and thus stabilized, more rapidly. Accordingly, dunes would be lower overall and marram grass would be succeeded more rapidly by other vegetation less capable of driving dune formation.

Artificial dunes created for coastal defence purposes would more or less be void of fauna just after planting. During the colonization process, priority effects might influence the invertebrate species composition assembling on different tussocks, with specialist or generalist dune species grouping together. If no natural dunes are located nearby, chances of generalist species arriving first are higher, which might be detrimental for later arriving dune specialist if the species co-occurrence observed in chapter 4 is indeed caused by a mechanism initiated by generalist herbivore species feeding on marram grass. An alternative explanation we suggested was that the marram grass specialists occurred more frequently in pure marram grass patches (with no other plants growing nearby). If this is the case, artificial dunes could increase population numbers of dune specialists. The way marram grass is planted at regular intervals seems to be ideal for dune invertebrates because it lowers the distance between different marram grass plants. Invertebrate numbers will initially be low, partly because of the low marram grass cover. Nevertheless, their numbers might be assumed to steadily increase as the marram grass cover of the artificial dune increases over time, until a fully mature dune is established.

Since we have no data mechanistically linking the spatial configuration of marram grass with dune growth, making statements about the optimal starting configurations for both biodiversity and coastal protection is speculative. From data published from a simulation model and remote sensing (Bonte et al. 2021), the optimal spatial configuration for dune growth seems to be an intermediate cover with low clustered marram grass. This configuration would be good for biodiversity as well, although a higher cover would be even better. However, since dune growth seems to decrease drastically when marram grass cover increases, optima for coastal protection and biodiversity seem to be only partly overlapping. Protection of the coast will evidently be the first priority when developing nature based solutions. Fortunately, our results indicate that dune biodiversity, more specifically invertebrates associated with marram grass, will also benefit from these artificially created ecosystems.

6.5 Perspectives and opportunities

The dune grass *Calamagrostis arenaria* is frequently used to stabilize aeolian sand dynamics while simultaneously increasing coastal protection against sea level rise and storm surges. During these practices, marram grass is planted with little regards for biodiversity. With this thesis I tried to gain better insights into the profound relationship between invertebrate species associated with both marram grass' roots and leaves, and their host plant.

Both above- and belowground invertebrate communities displayed a strong biogeographical structuring. This signal was especially strong in aboveground invertebrates, while belowground nematodes seemed to be additionally structured by random, stochastic processes. These regional differences in biodiversity could be explained by a number of confounding gradients such as soil pH, climate, human use and management of dune areas, dune age etc. Owing to the tempering effect of the sea on climate extremes (Wiedemann and Pickart 2004), coastal vegetation has been described as “azonal” because it is largely homogenous across Europe (Del Vecchio et al. 2018, Torca et al. 2019, Giulio et al. 2020). Consequently, it could be postulated that climate only affects biodiversity to a lesser extent. Nevertheless, disentangling the role played by these different factors could further increase our understanding of invertebrate communities.

JSDMS are more and more used to analyse large, ecological data set. We ran into a convergence issue when trying to model a random effect on transect level in chapter 4. This convergence issue was mainly caused by outlying MCMC samples reached in turn by the different chains, resulting in a potential scale reduction factor (i.e., Gelman Rubin diagnostic) higher than 1.1. Although, admittedly, I do not understand all the details regarding the mathematics behind it, I think this upper limit could be relaxed slightly, especially since the posterior densities of all parameters looked well defined when plotted. Ecological data is furthermore known to be skewed by the observation of few common and many rare species (Begon et al. 2006, Levin et al. 2009, Mittelbach and McGill 2019), which challenges correct statistical modelling of these systems (Ferrier and Guisan 2006, Ovaskainen and Soininen 2011). Consequently, relaxation of this parameter might even facilitate the use of JSDMs in ecology.

The already installed artificial dunes linking marram grass spatial configuration with dune growth will provide a very important next step in reconciling coastal protection and biodiversity. Such projects will enable dune managers to artificially create dunes that are optimal for dune growth from the start. These set ups could furthermore allow to test for the priority effects our results indicated by following up the invertebrate biodiversity in a newly created environment. Maybe such field experiment will show that marram grass specialists colonize young plants and are gradually displaced by generalist as the plant matures and becomes better at defending itself (e.g., due to an increase in silica in the leaves)? Dune research will probably be driven forward in the coming years due to the interest for dunes as coastal protection. Consequently, these are exciting times to be a dune ecologist!

Something I became increasingly more aware of during my research, is how relatively little is known about small, inconspicuous species such as arthropods and nematodes. Papers about threatened species are mainly focussing on vertebrates or plants (e.g., Bellard et al. 2016, Dueñas et al. 2021), while info on invertebrate species is sometimes only included secondarily, because it is able to explain trends found in vertebrate species (e.g., Graveland and Van Der Wal 1996). Furthermore, ecological information is still limited for a lot of insect taxa (Wong et al. 2019). For instance, insect larvae were excluded from the aboveground analysis because ecological information on the larval stage of some species was limited or non-existing. This is unfortunate, considering insect species are very numerous and are linked with a variety of ecosystem services (Wagner et al. 2021). So for my final perspective, I would want to stress the importance of doing ecological research on small species in order to compensate for the historical “vertebrate bias” (Titley et al. 2017), because increasing our fundamental understanding of the ecological processes shaping diverse biological communities is crucial for their survival and nature conservation.

6.6 Conclusion

The results presented in this thesis hold several implications for both nature conservation and coastal protection. We observed a high change of occurrence of *S. inaequidens* in coastal dunes, especially in less vegetated areas. Managers of artificial dunes should be made aware of the increased potential for establishment of invasive species in sparsely planted dunes. Our growth experiment indicated that the occurrence of invasive species could accelerate dune stabilization and vegetation succession, which would end the process of dune formation prematurely, leaving our coasts more vulnerable than intended. Field surveys along the coast of West Europe linked a heterogenous landscape, where marram grass tussocks of varying vitality are intertwined with bare sand patches, with the highest species richness. These bare sand patches are indirectly beneficial for biodiversity, via marram grass itself, because too densely covered marram dunes harboured significantly more root-feeding nematodes, which could potentially lower marram grass vitality. Some specific dune species can also benefit directly from bare sand patches. Large differences in marram grass-associated diversity between the sampled biogeographic regions nevertheless remain unsolved.

Summary

Humans are drawn to coastal dunes since time immemorial. They used the vegetation growing in the dunes to feed their cattle, make utensils out of different parts of the plants and sometimes it was even used as a food source (e.g., *Hippophae rhamnoides*). Currently, coastal vegetation is increasingly used for coastal protection purposes, especially because the sea level is rising and extreme storm surges are predicted to increase as a consequence of the ongoing climate change. Vegetation in sandy coastal habitats worldwide, such as mangroves or salt marshes, naturally protect the lower laying hinterland. This is accomplished by gradually building up the land at the sea-land interface by locally lowering wind or water dynamics, causing the suspended sediment to settle, after which it is stabilized by the vegetation.

European marram grass, *Calamagrostis arenaria*, is the keystone plant species in the process of dune formation in European dunes. It thrives vigorously in dynamic dunes with a lot of wind-blown sand, yet, it slowly withers away when locked up in a completely vegetated, stabilized dune. This constant need for sand burial in order to grow arises from a negative effect caused by the associated soil biota. Different nematode species are thought to be the principle cause of this effect, although other factors such as fungi and nutrient concentrations are also zealously studied. Nevertheless, a complete mechanistic understanding of the process is still lacking today.

Today, the creation of artificial dunes is mainly done by first depositing sand on the beach and subsequently stabilizing it by planting marram grass. Marram grass is planted in a regular pattern on artificial dunes, notwithstanding it occurs more clustered together in nature. If more and more regular dunes appear along our coastline, how will this affect dune biodiversity? In an attempt to answer this question, I studied how the spatial configuration of marram grass influences the marram grass-associated biological communities.

In a first study (chapter 2), we investigated the potential of an invasive plant species (*Senecio inaequidens*) to further spread throughout European coastal dunes. The possible effects of *S. inaequidens* establishment on natural dune formation, by altering marram grass performance, were additionally evaluated. Our results indicated a relatively high probability of establishment for *S. inaequidens* in natural dune configurations, hinting at a high tolerance for sand burial. Nevertheless, marram grass seemed to be the stronger competitor in natural foredunes, lowering the probability of establishment in areas with high marram grass cover. Furthermore, marram grass performance was enhanced in *Senecio*-altered sand, possibly owing to higher nutrient concentrations. If such increased plant growth is a general phenomenon, further expansion of *S. inaequidens* could accelerate natural succession in European coastal dunes.

In chapter 3, we tried to disentangle the factors structuring nematode functional abundances in foredunes using joint species distribution modelling (JSDM). Research relating nematode numbers to marram grass is relevant because nematodes are thought to cause a decline in vigour when marram grass is not constantly cover by a thin layer of sand. We found that stochasticity among plants was the most important factor in explaining nematode functional abundances, which all occurred extremely clustered together. Identifying which factors possibly explain this stochasticity might help to clarify why the decline in marram grass performance observed under constant conditions in the lab, is still not completely resolved in the field.

Next, in chapter 4, we studied the aboveground invertebrate biodiversity associated with marram grass. More specifically, we investigated how invertebrate communities were influenced by regional and local variables, while taking into account species traits and phylogenetic relationships. We were especially interested in the effect of marram grass cover and vitality because, recently, vegetation was removed in stabilized foredunes under the pretence of being beneficial for dune biodiversity. Our results did not support a significant raise in biodiversity if vegetation cover would be reduced from high to intermediate densities, at least not for biodiversity in marram grass dominated foredunes. Residual species-associations indicated that generalist species did not inhabit the same marram grass tussock as dune specialist, hinting at the existence of two distinct communities. Further experiments or field work are necessary to confirm a causal relationship.

Species occupying the same habitat patch do not just live together, they interact. That is why, in the last research chapter, we focussed specifically on the arthropod community found in the marram grass tussocks and tested whether body size ratios can accurately predict trophic interactions between them. Assuming larger predators eat smaller prey, we additionally investigated whether predator hunting strategy and prey taxonomy could explain possible deviations from this general rule. To do this, we constructed an empirical food web based on pairwise feeding trials and contrasted this with a theoretical food web based on body size ratios, literature and expert knowledge. Our feeding trials confirmed that predator-prey body size ratio is a good predictor for trophic interactions. Nevertheless, phylogenetically structured anti-predator defences could explain why certain trophic interactions do not adhere to size-based rules.

The results presented in this thesis hold several implications for both nature conservation and coastal protection. Managers of artificial dunes need to be aware of the increased potential for establishment of invasive species to establish in sparsely planted dunes. Occurrence of invasive species could accelerate dune stabilization and vegetation succession, which would end the process of dune growth prematurely, leaving our coasts more vulnerable than intended. Coastal managers for the sake of biodiversity best aim for a heterogenous landscape, where marram grass tussocks of varying vitality are intertwined with bare sand patches. Large differences in marram grass-associated diversity between the sampled biogeographic regions nevertheless remain unsolved.

Coastal dunes are a marvellous ecosystem filled with underappreciated lifeforms, such as nematodes and arthropods. Further insights in their ecology are needed as the dramatic global decline in species richness and abundance is knocking out many species and interactions on which services such as pest control and nutrient cycling depend.

Samenvatting

Mensen voelen zich sinds jaar en dag aangetrokken tot kustduinen. Vroeger werd de duinvegetatie gebruikt om het vee te voederen, werden delen van andere planten gebruikt om gebruiksvoorwerpen te maken en nog andere soorten dienden als voedselbron voor de mens (bijvoorbeeld duindoorn, *Hippophae rhamnoides*). Momenteel wordt kustvegetatie in toenemende mate gebruikt voor kustbescherming, en vooral vanwege de voorspelde gevolgen van de aanhoudende klimaatverandering, zoals de zeespiegelstijging en een verhoogd aantal extreme stormvloeden. Veel vegetatie in zandige ecosystemen wereldwijd, vb. mangroves of slikken en schorren, beschermt het achterliggende land op natuurlijke wijze tegen de zeespiegelstijging. Dit gebeurt door het land geleidelijk aan op te hogen door lokaal de wind- of waterdynamiek voldoende te verlagen. Daardoor kan het opgeloste sediment neerslaan, waarna het door de vegetatie wordt vastgehouden.

Europees helmgras, *Calamagrostis arenaria*, is de belangrijkste plantensoort in het proces van duinvorming aan de Europese kust. Het gedijt uitstekend in dynamische duinen met veel opwaaiend zand, maar verdort langzaam als het vast zit in een volledig begroeide en gestabiliseerde duin. Deze constante behoefte aan vers zand om te kunnen groeien, wordt toegeschreven aan het effect van bodemorganismen. Er wordt aangenomen dat nematoden (wortelaaltjes) de hoofdoorzaak zijn van dit effect, hoewel ook andere factoren zoals schimmels en nutriëntenconcentraties ijverig worden bestudeerd. Het mechanisme van dit proces is nog altijd niet volledig ontrafeld.

Het aanleggen van kunstmatige duinen gebeurt momenteel door eerst het strand op te hogen met zand en dat vervolgens te stabiliseren door helmgras aan te planten. Hierbij wordt helmgras nog steeds in een regelmatig patroon aangeplant, hoewel het in de natuur meer gegroepeerd voorkomt. Hoe biodiveristeit gedijt in deze meer regelmatige duinen is amper onderzocht. In een poging deze vraag te beantwoorden, onderzoek ik in dit proefschrift hoe de ruimtelijke configuratie van helmgras een rol speelt bij het structureren van de biologische gemeenschap gevonden in helmgras.

In een eerste studie (hoofdstuk 2) onderzochten we het potentieel van een invasieve plantensoort (bezemkruiskruid, *Senecio inaequidens*) om zich verder te verspreiden binnen de Europese kustduinen. De mogelijke effecten van een verdere verspreiding van bezemkruiskruid op de natuurlijke duinvorming, door de groei van helmgras te beïnvloeden, werden eveneens onderzocht.

Onze resultaten wezen op een relatief hoge vestigingskans van bezemkruiskruid in natuurlijk voorkomende helmgras configuraties, wat kan wijzen op een hoge tolerantie voor zandbegraving van bezemkruiskruid. Desalniettemin leek helmgras de sterkere concurrent te zijn in natuurlijke kustduinen, wat de kans op vestiging deed dalen in gebieden met een hogere bedekking van helmgras. Bovendien groeide helmgras beter in zand verzameld onder het bezemkruiskruid, wat mogelijks wijst op hogere nutriëntenconcentraties vrijgekomen uit het organisch materiaal. Als een dergelijke verhoogde plantengroei een algemeen verschijnsel is, zou verdere uitbreiding van bezemkruiskruid de natuurlijke successie in de Europese kustduinen kunnen versnellen.

In hoofdstuk 3 hebben we geprobeerd om de effecten van verschillende factoren die de functionele aantallen van nematoden in kustduinen beïnvloeden, van elkaar te onderscheiden. Onderzoek naar nematoden in helmgras is relevant omdat er wordt aangenomen dat ze de groeikracht van helmgras verminderen als het niet constant bedekt wordt met een dun laagje zand. Helmgrasbedekking kon slechts een klein deel van de natuurlijke variatie in het aantal gevonden nematoden verklaren. Door de achterliggende factoren van deze variatie in nematoden aantallen te identificeren, kan worden onderzocht waarom de verminderde groei van helmgras, geobserveerd onder constante omstandigheden in het labo, nog niet volledig is uitgeklaard in het veld.

Vervolgens hebben we in hoofdstuk 4 de bovengrondse biodiversiteit aan ongewervelden, gevonden in het helmgras, bestudeerd. Meer specifiek onderzochten we hoe deze werden beïnvloed door regionale en lokale variabelen, rekening houdend met soortspecifieke kenmerken en fylogenetische relaties. We waren vooral geïnteresseerd in het effect van helmgrasbedekking en -vitaliteit omdat onlangs vegetatie werd verwijderd in gestabiliseerde duinen onder het mom gunstig te zijn voor de duinbiodiversiteit. Volgens onze resultaten zou de biodiversiteit in helmduinen niet toenemen als de vegetatiebedekking zou worden gereduceerd van hoge naar gemiddelde dichtheden. Door associaties tussen soorten te bekijken, vonden we dat generalistische soorten niet dezelfde helmgraspol verkiezen als duinspecialisten, wat duidt op het bestaan van twee verschillende gemeenschappen. Verdere experimenten of veldwerk zijn nodig om een causaal verband te onderzoeken.

Soorten die hetzelfde leefgebied bezetten, leven niet alleen samen, ze interageren ook met elkaar. Daarom hebben we in het laatste hoofdstuk getest of trofische interacties tussen geleedpotigen nauwkeurig kunnen voorspeld worden op basis van de verhoudingen tussen de lichaamsgrootte van de prooi en het roofdier. Ervan uitgaand dat grotere roofdieren kleinere prooien eten, hebben we daarnaast onderzocht of de jachtstrategie van het roofdier en de taxonomie van de prooi mogelijke afwijkingen van deze algemene regel kunnen verklaren. Om dit te doen, hebben we een empirisch voedselweb geconstrueerd op basis van paarsgewijze proeven en dit vervolgens vergeleken met een theoretisch voedselweb op basis van lichaamsgroottes, literatuur en expertise. Onze proeven bevestigden dat de verhouding tussen de lichaamsgrootte van roofdier en prooi een goede indicatie is voor trofische interacties. Desalniettemin zouden fylogenetisch gestructureerde verdedigingsmechanismen tegen roofdieren kunnen verklaren waarom bepaalde trofische interacties zich niet houden aan deze regel.

De resultaten gepresenteerd in dit proefschrift hebben verschillende implicaties voor zowel natuurbehoud als kustbescherming. Beheerders van kunstmatige duinen moeten zich bewust zijn van de verhoogde kans op vestiging van invasieve soorten in spaarzaam aangeplante duinen. De vestiging van invasieve soorten zou de duinstabilisatie en vegetatiesuccessie kunnen versnellen, waardoor het proces van duingroei voortijdig zou worden beëindigd, met lagere duinen als gevolg. Hierdoor zouden onze kusten kwetsbaarder kunnen worden. In het belang van biodiversiteit streven beheerders van duingebieden best naar een heterogeen landschap, waar helmgraspollen van verschillende vitaliteit worden afgewisseld met kale zandplekken. Grote verschillen in biodiversiteit gevonden in helmgraspollen tussen de bemonsterde biogeografische regio's blijven echter onopgelost.

Kustduinen zijn een prachtig ecosysteem vol ondergewaardeerde soorten, zoals nematoden en geleedpotigen. Het verder verwerven van ecologische inzichten in hun biologie is noodzakelijk aangezien de soortenrijkdom wereldwijd drastisch achteruit gaat. Samen met deze soorten verdwijnen ook de ecosysteemdiensten waarvoor zij verantwoordelijk zijn, zoals ongediertebestrijding en het recycleren van nutriënten.

Résumé

Les humains sont attirés par les dunes côtières depuis des temps immémoriaux. Ils utilisaient la végétation poussant dans les dunes pour nourrir leur bétail, fabriquer des ustensiles à partir de différentes parties des plantes et parfois même l'utiliser comme source de nourriture (par exemple, *Hippophae rhamnoides*). Actuellement, la végétation côtière est de plus en plus utilisée à des fins de protection côtière, notamment parce que le niveau de la mer monte et que les ondes de tempête extrêmes devraient augmenter en raison du changement climatique en cours. La végétation des habitats côtiers sablonneux du monde entier, tels que les mangroves ou les marais salants, protège naturellement l'arrière-pays de faible altitude. Ceci est accompli grâce à l'accumulation progressive de terre à l'interface mer-terre ce qui ralentit localement la dynamique du vent ou de l'eau, provoquant le dépôt des sédiments en suspension, après quoi ils sont stabilisés par la végétation.

L'oyat ou ammophile d'Europe, *Calamagrostis arenaria*, est l'espèce végétale clé dans le processus de formation des dunes européennes. Il prospère vigoureusement dans les dunes dynamiques avec beaucoup de sable soufflé par le vent, mais il se dessèche lentement lorsqu'il est enfermé dans une dune complètement végétalisée et stabilisée. Ce besoin constant d'enfouissement dans le sable pour croître provient d'un effet négatif causé par le biote du sol associé. On pense que différentes espèces de nématodes sont la principale cause de cet effet, bien que d'autres facteurs tels que les champignons et les concentrations de nutriments soient aussi étudiés de manière importante. Néanmoins, une compréhension mécaniste complète du processus fait encore défaut aujourd'hui.

Aujourd'hui, la création de dunes artificielles se fait principalement en déposant d'abord du sable sur la plage et en stabilisant ensuite la dune en plantant de l'ammophile. L'ammophile est plantée selon un schéma régulier sur des dunes artificielles, bien qu'elle soit plus regroupée dans la nature. Si de plus en plus de dunes régulières apparaissent le long de notre littoral, comment cela affectera-t-il la biodiversité des dunes ? Pour tenter de répondre à cette question, j'ai étudié comment la configuration spatiale de l'ammophile influence les communautés biologiques associées à l'ammophile.

Dans une première étude (chapitre 2), nous avons étudié le potentiel d'une espèce végétale envahissante (*Senecio inaequidens*) à se propager davantage dans les dunes côtières européennes. Les effets possibles de l'établissement de *S. inaequidens* sur la formation naturelle des dunes, en modifiant les

performances de l’ammophile, ont également été évalués. Nos résultats ont indiqué une probabilité relativement élevée d’établissement de *S. inaequidens* dans les configurations de dunes naturelles, suggérant une tolérance élevée à l’enfouissement dans le sable. Néanmoins, l’ammophile semble être le concurrent le plus fort dans les avant-dunes naturelles, réduisant la probabilité d’établissement dans les zones à forte couverture d’ammophile. De plus, la performance de l’ammophile est améliorée dans le sable modifié par *Senecio*, peut-être en raison de concentrations plus élevées de nutriments. Si une telle augmentation de la croissance des plantes est un phénomène général, une expansion supplémentaire de *S. inaequidens* pourrait accélérer la succession naturelle dans les dunes côtières européennes.

Dans le chapitre 3, nous avons essayé de démêler les facteurs structurant les abondances fonctionnelles des nématodes dans les avant-dunes à l’aide de la modélisation conjointe de la distribution des espèces (JSDM). Lier les abondances de nématodes à l’ammophile est une recherche pertinente car on pense que les nématodes provoquent une baisse de vigueur lorsque l’ammophile n’est pas constamment recouverte d’une fine couche de sable. Nous avons constaté que l’aléa entre les plantes était le facteur le plus important pour expliquer les abondances des groupes fonctionnels de nématodes, qui se sont toutes révélées extrêmement regroupées. L’identification des facteurs pouvant expliquer cet aléa pourrait aider à clarifier pourquoi la baisse des performances de l’ammophile observée dans des conditions constantes en laboratoire n’est toujours pas complètement résolue sur le terrain.

Ensuite, au chapitre 4, nous avons étudié la biodiversité aérienne des invertébrés associée à l’ammophile. Plus précisément, nous avons étudié comment les communautés d’invertébrés étaient influencées par des variables régionales et locales, tout en tenant compte des traits des espèces et des relations phylogénétiques. Nous nous sommes particulièrement intéressés à l’effet de la couverture et de la vitalité des ammophiles car, récemment, la végétation a été supprimée dans les avant-dunes stabilisées sous prétexte d’être bénéfique pour la biodiversité des dunes. Nos résultats n’ont pas démontré une augmentation significative de la biodiversité lorsque la densité du couvert végétal était réduit d’élevée à intermédiaire, du moins pas pour la biodiversité dans les avant-dunes dominées par l’ammophile. Les associations d’espèces résiduelles ont indiqué que les espèces généralistes n’habitaient pas la même touffe d’ammophile que les spécialistes des dunes, suggérant l’existence de deux communautés distinctes. D’autres expériences ou travaux de terrain sont nécessaires pour confirmer toute relation causale.

Les espèces occupant la même parcelle d'habitat ne vivent pas seulement ensemble, elles interagissent. C'est pourquoi, dans le dernier chapitre de recherche, nous nous sommes concentrés spécifiquement sur la communauté d'arthropodes trouvée dans les touffes d'ammophiles et avons testé si les rapports de taille corporelle pouvaient prédire avec précision les interactions trophiques entre ces espèces. En supposant que les prédateurs mangent des proies plus petites, nous avons également étudié si la stratégie de chasse des prédateurs et la taxonomie des proies pouvaient expliquer les écarts possibles par rapport à cette règle générale. Pour ce faire, nous avons construit un réseau trophique empirique fondé sur des tests de prédation par paires d'espèces et l'avons comparé à un réseau trophique théorique fondé sur les rapports de taille corporelle, la littérature et les connaissances d'experts. Nos tests en laboratoire ont confirmé que le rapport taille corporelle prédateur-proie est une bonne variable prédictive des interactions trophiques. Néanmoins, des défenses anti-prédateurs structurées phylogénétiquement pourraient expliquer pourquoi certaines interactions trophiques ne respectent pas les règles fondées sur la taille.

Les résultats présentés dans cette thèse ont plusieurs implications pour la conservation de la nature et la protection côtière. Les gestionnaires de dunes artificielles doivent être conscients du potentiel accru d'établissement d'espèces envahissantes dans les dunes peu plantées. La présence d'espèces envahissantes pourrait accélérer la stabilisation des dunes et la succession végétale, ce qui mettrait fin prématurément au processus de croissance des dunes, laissant nos côtes plus vulnérables que prévu. Les gestionnaires côtiers, dans l'intérêt de la biodiversité, devraient viser un paysage plus hétérogène, où des touffes d'ammophiles de vitalité variable sont entrelacées avec des plaques de sable nu. De grandes différences dans la diversité associée à l'ammophile entre les régions biogéographiques échantillonnées restent néanmoins non résolues.

Les dunes côtières sont un merveilleux écosystème rempli de formes de vie sous-estimées, telles que les nématodes et les arthropodes. Des connaissances supplémentaires sur leur écologie sont nécessaires car le déclin mondial spectaculaire de la richesse et de l'abondance des espèces élimine de nombreuses espèces et interactions dont dépendent des services tels que la lutte antiparasitaire et le cycle des nutriments.

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Thank you to the post-corona squad for reanimating the social life at the TEREC. It was refreshing to once again be able to chat about science and ecology in real life at the lab instead of doing it via a Teams meeting. Thank you Bram C., Cesare, Charlotte T., Charlotte V.D., Garben, Felipe, Femke, Katrien, Marina and Silvija. Furthermore, I want to thank you all for the more casual occasions such as the biological excursions, the writing week, coffee and lunch breaks, the paintball, after hours drinks and parties; I really enjoyed them! I wish you all the best of luck with finishing your PhDs and with the rest of you (scientific) careers. If you ever need anything or you just want to go grab a drink, you know where to find me.

Garben and Femke, I want to thank you additionally for the support throughout the years, but especially during corona. I really enjoyed both the meetings with Dries (talking about science) and the ones without him, where we just had a coffee (talking about other stuff, but also science). Garben, I first met you when I supervised your master thesis. You were already back then a very independent guy, so I didn’t had to do much ;-) After your master, you went on to do a PhD under supervision of Dries, which lead to us publishing your master thesis as part of my PhD. I want to hereby thank you for this wonderful cooperation! Femke, you were at the TEREC when I started and you will be finishing your PhD very soon. Consequently, we discussed and complained to each other about the similar thoughts, feelings, frustrations we had at that time in our journey, but especially in the end. Thank you for your enthusiasm about ecology and science, your healthy portion of criticism towards it (which lead to a paper!), thank you for your never-ending energy to help me with various questions about scientific writing, QGIS, ecology in general, … but most of all, thank you for being my friend at work! I hope we will still be able to match our schedules in the future to go on some more excursions together with Garben, because those were awesome!

Bram V. and Jonathan, thank you for representing EON during the lunchbreaks and parties! I really enjoyed talking to you guys about science and other stuff.

When I did not work from home or in Ghent, I worked at the Centre d'Infection et d'Immunité de Lille. Thank you Priscille for having me in your lab. Thank you Julien Lombard and Jonathan Chatagnon for switching to English when we were talking, it was greatly appreciated.

Now that I have thanked everyone professionally, I would, of course, also like to thank my friends and family.

In plaats van ook hier een heleboel namen op te noemen, heb ik besloten om activiteiten op te noemen. Voel je je aangesproken door iets wat je leest? Perfect! Dan is de kans groot dat ook ik een goed gevoel krijg als ik aan dat moment terugdenk.

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Ik kan het natuurlijk niet maken om helemaal geen namen te noemen ;-)

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Ruben Van De Walle
maart 2023

Curriculum Vitae

Personal data

Last name: Van De Walle
First name: Ruben
Date of birth: 23 April 1995
Place of birth: Ghent, Belgium
Nationality: Belgian

Scientific career

2018-2023: Joint PhD student supported by Ghent University and Université de Lille; Supervised by Prof. Dr. Dries Bonte (UGent), Prof. Dr. Martijn L. Vandegehuchte (NTNU) and Dr. François Massol (ULille)
International context (INTERREG 2 Seas - Endure)

Education

2016 – 2018: Master of biology, Ghent University
Major: Global Change Ecology — Minor: Research
*Thesis: I’m watching you: assessing foraging efficiency of lesser black-backed gulls (*Larus fuscus*)by means of direct observations at terrestrial feeding sites*

2013 – 2016: Bachelor Biologie, Ghent university

Academic experience

Supervising students

2021-2022: Master of Science in Statistical Data Analysis thesis: Ward Langeraert
With Prof. Dries Bonte and Prof. Dries Benoit
Joint species distribution modelling within a natural dune ecosystem using Bayesian inference

2019-2020: Master of Science in Biology thesis: Garben Logghe
With Prof. Dries Bonte and Prof. Martijn Vandegehuchte
Upscaling of pairwise trophic interactions to food web structure in marram grass dunes: an experimental approach.

Master of Science in Biology thesis: Noëmie Van den Bon
With Prof. Dries Bonte and Prof. Martijn Vandegehuchte
The importance of vegetation configuration in coastal dunes to preserve diversity of marram-associated invertebrates. Is habitat configuration a driver of diversity in dunes?

Master of Science in Marine and Lacustrine Science and Management: Reagan Okoth,
With Prof. Dries Bonte and Prof. Martijn Vandegehuchte

Quantifying Changing Ecosystem Services in Relation to Coastal Defense Planning along the North Sea

2018-2019: Master of Science in Biology thesis: Laurian Van Maldeghem
With Prof. Dries Bonte and Prof. Martijn Vandegehuchte
The invertebrate diversity of marram dunes. And how this is influenced by spatial configuration of marram grass and marram grass properties

Master of Science in Biology thesis: Gillis Sanctobin
With Prof. Dries Bonte and Prof. Martijn Vandegehuchte
How the spatial configuration of Ammophila arenaria *(marram grass) influences associated arthropod food webs*

Bachelor Biologie thesis: Cyr Mestdagh
With Prof. Martijn Vandegehuchte
Helmduin is helmduin, of toch niet? Door de ogen van bladluizen en cicaden

Teaching

2019-2021: Supervision of a research topic at the field week for the course "Field biological Research". Third year of Bachelor in Biology

2019-2021: Guiding day excursions to the coast & the Virion; guiding a two-day excursion visiting multiple sites. For the course "Biological Excursions". Second year of Bachelor in Biology.

Publications

Bonte D, Batsleer F, Provoost S, Reijers V, Vandegehuchte ML, **Van De Walle R**, Dan S, Matheve H, Rauwoens P, Strypsteen G, Suzuki T, Verwaest T, Hillaert J (2021) Biomorphogenic Feedbacks and the Spatial Organization of a Dominant Grass Steer Dune Development. Frontiers in Ecology and Evolution 9: 1–12. https://doi.org/10.3389/fevo.2021.761336

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Scientific presentations

2022: Building Coastal Resilience | Brugge
2021: VLIZ Marine Science Day | online
2019: Workshop Dynamisch Kustbeheer | Bergen, NL

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