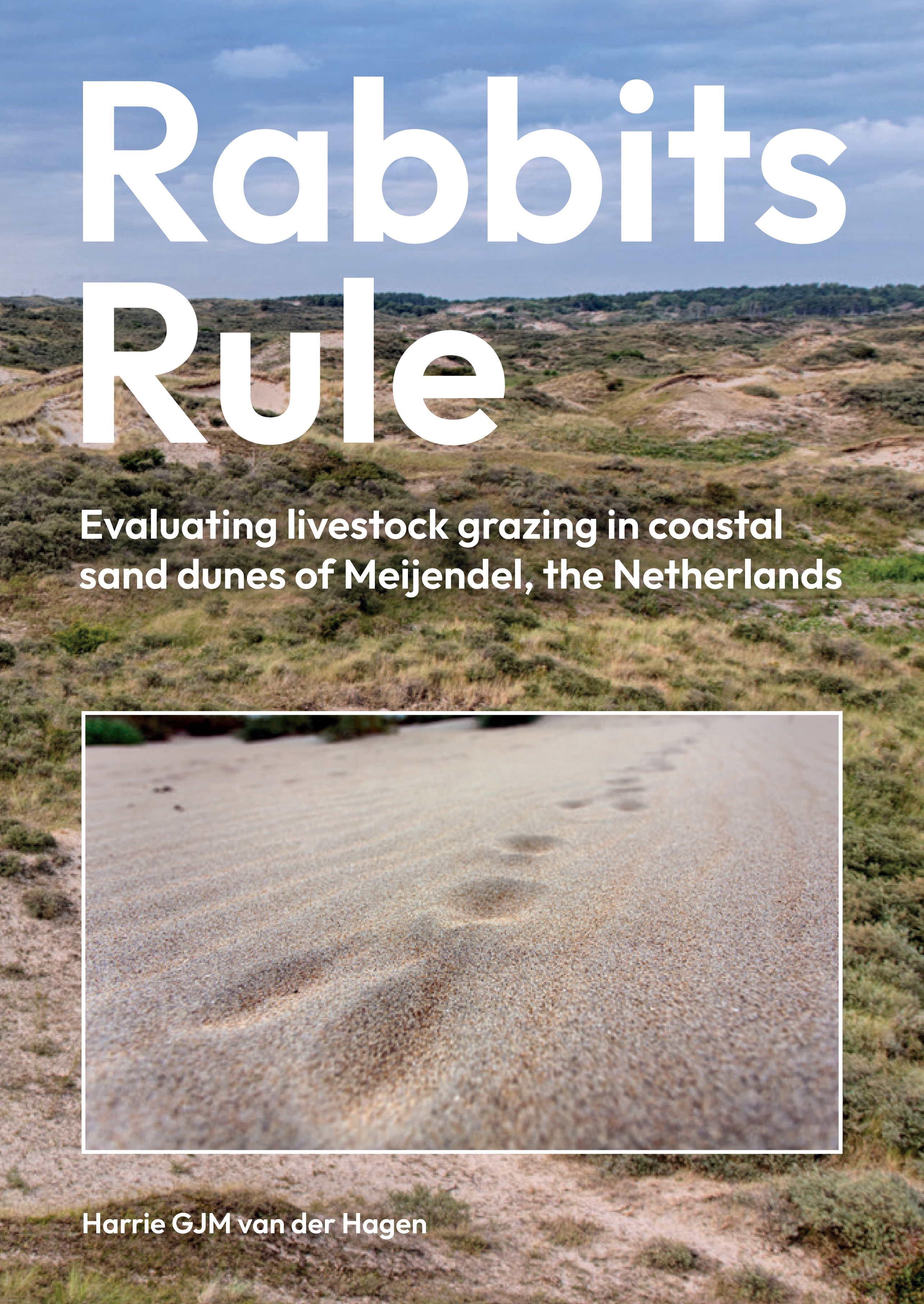

Rabbits Rule

Evaluating livestock grazing in coastal sand dunes of Meijendel, the Netherlands

Harrie GJM van der Hagen

Propositions

1. Livestock grazing in coastal dunes gets too much attention from nature conservation.
(this thesis)

2. Rabbits have a steering impact on the vegetation development of coastal dunes.
(this thesis)

3. The increase of plant biomass, as a result of climate change, is the biggest challenge for nature conservation.

4. Rigid contracts in nature management smother biodiversity.

5. The destiny of Dutch nature lies more in the hands of lawyers than of nature managers.

6. Not high values, but low prices dictate the design of our society.

Propositions belonging to the thesis, entitled

Rabbits Rule. Evaluating livestock grazing in coastal sand dunes of Meijendel, The Netherlands

Harrie G.J.M. van der Hagen
Wageningen, 11 October 2022

Rabbits Rule

Evaluating livestock grazing in coastal sand dunes of Meijendel, the Netherlands

Henricus G.J.M. van der Hagen

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Rabbits Rule

Evaluating livestock grazing in coastal sand dunes of Meijendel, the Netherlands

Henricus G.J.M. van der Hagen

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*For my father,
who gave me
freedom of choice*

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Contents

Chapter 1

General introduction

Harrie G.J.M. van der Hagen

Looking at the Netherlands from above, the country is a large delta, formed by several large European rivers, with a 350 kilometre coastal barrier bordering the North Sea. Coastal sand dunes are seen as the golden fringe of the European coasts. The long golden Dutch fringe is no exception and is divided into two phytogeographical regions by the lime content of the sand. The southern Rhenodunal district is rich in lime and the northern Wadden district poor in lime (Duistermaat 2020), with some local variations (e.g. Van Haperen 2009). Most coastal nature areas are protected by the Habitats Directive within the Natura 2000 legislation (Council of the European Communities 1992), and almost all habitats of the coastal dunes are protected. These habitats present a mosaic of bare sand, dune grasslands, shrubland and forests. For decades, the area covered by, and the quality of the dune habitats has been threatened. One example of priority habitats at risk are the 'Grey dunes', which are fixed, dry coastal dunes with herbaceous vegetation, and are designated as a priority habitat type (H2130). Grey dunes not only contain a great number of vascular plants (Dutch lime-rich coastal sand dunes harbour 66% of the Dutch flora: De Vries et al. 1994), but they are also rich in bryophytes and lichens (Schaminée et al. 1995, 1996, 1998; Stortelder et al. 1999). Rejuvenation via bare sand is important to maintain these biodiverse Grey dunes.

During the past five decades, the vegetation in Dutch coastal dunes has changed considerably. Large areas with patches of bare sand and open grasslands have been transformed into rather monotonous vegetation stands and a considerable loss of biodiversity could be observed (Ketner-Oostra and Sýkora 2004; Kooijman et al. 1998; Veer and Kooijman 1997). The monotonous grasslands consist of tall grasses (mainly *Calamagrostis epigejos* and Ammophila arenaria (syn. Calamagrostis arenaria) and the sedge Carex arenaria (e.g. Kooijman et al. 1998). The changes also include a continuing encroachment of grassland by shrubland mainly by *Hippophae rhamnoides*. The main driving factors were (i) the stabilisation of natural aeolian dynamics over many decades by planting Ammophila for artificial fore dune stabilisation, resulting in a high and stable "sand dike", (ii) still continuing high nitrogen deposition and (iii) two devastating epidemic diseases affecting the populations of the European rabbit (*Oryctolagus cuniculus*). As a consequence, the biodiversity-rich short dune grasslands have largely disappeared.

From 1985, livestock grazing was introduced in most of the protected areas along the coast as a management tool (Van Dijk 1992). This is a relatively cheap management measure and the number of grazers is easily controlled. Installing livestock grazing was designed to counteract the undesirable processes, as mentioned above, that caused the losses in biodiversity. Ensuring the presence of bare sand resulting from small and large scale blow-outs is important for the rejuvenation of the species-rich dune grasslands (Aggenbach et al. 2018). Introduction of livestock was expected to cause blow-outs that would stimulate the rejuvenation process. Another change was an end to the obligatory planting of Marram grass on any open sandy areas. This was stopped around 1990. From 2000, other management activities were introduced. Blow-outs were deliberately created to stimulate the rejuvenation process. Blow-out sizes ranged between 0,5 to 25 ha. Since 2010, at a few places along the coastline, breaks in the dunes were made and restored the natural connectivity between the sea/beach and the dunes; in 2015 in Meijendel. The nitrogen deposition in the dunes reached its peak around 1990 of 35-40 $kg.ha^{-1}.yr^{-1}$ (Hey & Snijder 1991) with encroachment by tall grasses as a consequence and a loss of the biodiversity-rich dune grasslands. The nitrogen deposition decreased considerably due to external measures taken by industry and agriculture more significantly after 2000. Unfortunately, the level is still above the Critical Deposition level of 10 $kg.ha^{-1}.yr^{-1}$ and this affects the health of species-rich dune grasslands (H2130B) (Kooijman et al. 2017; Kooijman et al. 2021; Bobbink 2021).

THE COASTAL SAND DUNES OF MEIJENDEL

The dune area of Meijendel, in the Dutch province of Zuid-Holland near The Hague (GPS 52° 07‘ N; 4° 20’ E), covers approximately 1,800 hectares: 6 km long and almost 3.5 km wide (Fig.1), and is part of the lime-rich Rhenodunal district. The area is currently managed by a not-for-profit company, Dunea. Dunea delivers drinking water to approximately 1.3 million people in the western part of the Netherlands. Statutorily, Dunea is also responsible for nature conservation, and it takes care of other functions like recreation, coastal defence (preventing flooding of the hinterland) and the cultural historic and archaeological values. Like other large dune areas along the Dutch coast, Meijendel is a Natura 2000 site. Dunea is the responsible body that has to comply with the European Habitats Directive. Compliancy means that the quantity of the different habitat types and their quality must be maintained in good condition. Due to several causes, as mentioned earlier, the quantity and especially the quality of the dune habitats are not and have not always been in good condition. In order to sustain and improve these measures, Dunea applies several management tools, like (local) mowing, sod-cutting in dry dunes (to artificially activate blow-outs) and wet dunes (dune slacks), eradication of invasive exotic species and livestock grazing.

Fig. 1. The Dutch coast and the location of Meijendel, the main subject of this thesis.

In Box 1, the ecological landscape zones of Meijendel with its plant communities and plant species are explained. It helps to understand the Meijendel dune landscape in the subsequent chapters of this thesis.

LIVESTOCK GRAZING AS A MANAGEMENT TOOL IN MEIJENDEL

Livestock grazing in coastal sand dunes is not a recent practice. Up to the 1960's, farmers used the dunes as pasture for their livestock. In the Meijendel area, the agricultural activities stopped around 1910 (Boerboom 1957), 36 years after the establishment of the local drinking water company Duinwaterleiding van 's-Gravenhage in 1874 that later developed into Dunea. The groundwater level in Meijendel has dropped considerably, mostly as a result of its water extraction activities, which made it uneconomic to maintain these agricultural activities. The first indications of agricultural decline are described by Vuyck (1898). The historic presence of livestock inspired nature managers to consider livestock grazing as a management tool to counteract encroachment by tall grasses and shrub (Van Dijk 1992). Apart from the introduced livestock, other grazers are present. Especially important is the European rabbit, which is key for maintaining short and biodiverse grasslands (Salman and Van der Meijden 1985; Wallage-Drees 1988). Due to the 1954 outbreak of myxomatosis and the 1989 outbreak of RVHD (Rabbit Viral Haemorrhagic Disease), rabbit numbers have significantly decreased (by 90-95%; Wallage-Drees 1988; Van der Bildt et al. 2006). Other grazers to consider are leaf and root lice, snails, beetles (larvae) and lepidopteran caterpillars (Van der Meijden 1992) and common voles (*Microtus arvalis*) (Bakker 2003).

Mowing is an alternative management tool to reduce biomass. But because of the topography of steep dunes (relief) and wetlands in Meijendel, mowing is impractical when applied over hundreds of hectares. It is mostly practiced in the relatively flat dune slacks.

PURPOSE OF THE STUDY: EVALUATING LIVESTOCK GRAZING IN MEIJENDEL

As large livestock strongly prefer graminoid species (Lamoot et al. 2005; Kohyani et al. 2011), these herbivores were thought to be potentially able to counteract the process of stabilisation and ecological succession towards monotonous stands of vegetation, dominated by tall grasses and a sedge species and counteract shrub and forest encroachment (Ten Haaf 1990; Van Dijk 1992; Kooijman & De Haan 1995; Provoost et al. 2011). Livestock grazing was expected to be able to restore the species-rich aspects of open and closed dry grasslands, to instigate blow-outs and reduce the area of shrubland/forests. In 1989, Fallow deer (Cervus dama) as a grazer was not considered. But in retrospective, introducing Fallow deer would have given other serious problems controlling their numbers by yearly culling of at least half of the population (FBE Noord-Holland 2020). Controlling domesticated livestock numbers is easier by controlling the presence of males.

In 1989, some staff members of the Duinwaterleiding van 's-Gravenhage (now Dunea), visited England and Wales to see results of long term livestock grazing in coastal sand dunes. Based on the findings, the general conclusion was that introduction of livestock in Meijendel was a good idea to counteract ecological succession of the vegetation. This thesis evaluates the impact of the introduced livestock. Late 1990, year-round grazing by Galloway cows and Nordic Fjord ponies was introduced. In 2005, the Fjord ponies were replaced by Konik horses. The livestock density was maintained at 0.06-0.07 LLU.ha^{-1}.year^{-1} (Large Livestock Units; 1:12-18 ha). This density was advised as the best option for the Meijendel situation (Ten Haaf 1990). Wallis de Vries et al. (1998) consider this density of a relative low level of impact. The scale that Wallis de Vries at al. (1998) use is a general one, but it does not take the variety of soil types (rich and poor) in the Netherlands in consideration. Because of the low amount of palatable biomass in coastal sand dunes, the LLU was adjusted down to provide for winter survival of the animals (e.g. Ten Haaf 1990; Ebrahimi 2007). The LLU in the Meijendel situation could still be considered relatively high, because, in some years, some animals of the herd only just survive the end of the winter.

Incentive

The practical incentive of this thesis was the upcoming evaluation of the introduction of livestock to Meijendel since 1990 as a replacement of rabbit grazing. Earlier reports were undertaken after five (Van der Hagen 1996) and ten years (Van der Hagen 2003) on botanical and faunal aspects of the introduction. The general conclusion of these reports was to maintain livestock grazing and even extend the area grazed, despite some negative impact on fauna (more specifically some breeding birds). The moment of the 20 year livestock evaluation was transformed into a PhD thesis. Another reason for the study was the massive amount of long term data available, which had been little used, to date. However, apart from the impact of livestock grazing, several other changes were present around 1990 to affect the vegetation development, like the end to mandatory marram planting, the peak in nitrogen deposition and the arrival of RVHD in 1989. It seems very likely that a number of factors will be responsible for changes in the vegetation cover. Therefore a number of questions arise. What is the impact of the changing numbers of rabbits, knowing that they are fully capable of restoring grass encroached grasslands into a short turf (personal communication Q.L. Slings)? What might be the impact of changes in nitrogen deposition and changing climate parameters? Notwithstanding these arguments, the basic question of this thesis remained as: does livestock grazing result in an increase in the surface of bare sand, in an increase of the biodiversity-rich short open an closed dune grasslands. Further, does it lead to a decrease in the area of shrubland and forest, and overall ensure that the Habitats Directive is fully met?

OUTLINE OF THIS THESIS

For this thesis, a unique and large amount of data from Meijendel was available, which had only been incidentally used for evaluation purposes. The main material came from four sets of high-resolution false color infrared (fc-ir) digital orthophotos. Additionally, data from permanent plots and exclosures offered a long term and reliable dataset as well as the national relevé database. This national database contains a massive amount of relevés of the so-called *Zeedorpenlandschap* (Doing 1988; Slings 1994), where human interference in the dunes has maintained the botanical quality of the dune grasslands. In combination with datasets from twice yearly rabbit counts (since 1984) and data on nitrogen deposition, the total available data should give some answers to the main hypothesis.

The main hypothesis of this study is that the introduction of livestock will lead to regressive succession by grazing and trampling, as expressed by an increase of bare sand, a decrease in the area of shrubland, and a subsequent increase of the area of dune grassland as well as an improvement of the quality of the dune grasslands. In brief, species-poor, grass-encroached stands should change into species-rich short dune grasslands. Livestock grazing is particularly expected to stop the increase, and even cause a decrease of shrubland and forest or, at least, open up the shrubland and forest to the benefit of species-rich dune grasslands.

Chapter 2 focusses on the changes in area of three crisp classes with hard boundaries, based on fc-ir orthophotos: bare sand, all grasslands as one class (in a fine grained fuzzy mosaic) and shrubland/forests. This chapter compares three livestock-grazed areas and three ungrazed controls within Meijendel. The hypothesis is that the introduction of livestock will lead to regressive succession expressed in an increase of bare sand, a decrease of the area of shrubland, and a subsequent increase of grassland.

Chapter 3 covers the division of the crisp grassland class, as mentioned in chapter 2 into five fuzzy grassland classes in the same three livestock-grazed areas and three ungrazed controls as in chapter 2. Dune grasslands appear in a very fine mosaic (fuzzy) with changes over distances of less than one meter. Livestock grazing is expected to counteract the grasslands encroached by tall grasses (one of the fuzzy classes) and improve the quantity (and indirectly the quality) of the four other fuzzy grassland types. The hypothesis is that the introduction of livestock will lead to an increase of open sandy and closed dune grasslands with higher botanical quality. This will also to a reduction of the vegetation type of tall grasses (grass encroached) due to the opening up of shrubland and forest. Changes in rabbit numbers and nitrogen deposition are also investigated for their potential role in the changes observed.

For chapter 2 and 3 the software program DICRANUM is used, which was designed for interpreting these crisp and especially fuzzy classes in dune ecosystems (Droesen 1998; Assendorp 2010).

Chapter 4 evaluates succession in 41 permanent plots mostly installed in the early 1950's (Boerboom 1960a). Classification groups phytosociological clusters into successional stages. The shifts in these successional stages are then calculated. The hypothesis is that the grazers slow down the dominant progressive succession towards thickets and forest, decrease tall grass and shrub encroachment and stimulate bare sand that then causes blow-outs.

Chapter 5 evaluates data on exclosures, which were installed in 1975 to monitor the impact of rabbits in Meijendel as they were considered to be important grazers. The development of these eight exclosures, each with a reference plot, is studied. The hypothesis is that rabbits are a crucial factor in preserving an open dune landscape with its variety of dune grasslands. In absence of rabbits, seedlings of shrubs can have an opportunity to establish and to encroach on grassland vegetation.

In **chapter 6**, the so-called Dutch *Zeedorpenlandschap* (the historically farmed dune landscape near seaside villages) is reviewed as being part of a dune ecosystem with a large human influence. The farming included livestock, the cultivation of farm products on small arable plots as well as shrub and tree cutting for fuel and for ovens of local bakeries. Up to 1960, these practices were wide spread in the lime-rich coastal sand dunes around these seaside villages. It is expressed in the occurrence of two special plant communities: the *Sileno-Tortuletum* and the *Anthyllido-Silenetum*, characterized by a number of plant species that have diminished in the past decades. The hypothesis is that due to other types of human activities (e.g. recreation), the typical plant communities of the *Zeedorpenlandschap* still survive despite the disappearance of the historical, small-scale land use, of which livestock grazing was one thread.

These five chapters will culminate in a syntheses of the results and a reflection on what these results mean for future management. Did livestock grazing as a management tool in lime-rich sand dunes fulfil the expectations anticipated in 1989? Or is livestock grazing only a part of the answer? Is the impact of rabbit grazing underestimated? From Salman and Van der Meijden (1985), we could conclude that the impact is comparable with grazing by livestock. On the other hand, are other factors partially responsible for the changes observed, such as the decrease in nitrogen deposition since around 1990? Changes in climate conditions have been seen to have an impact in the shift of species from south to north along the European coastlines, leading to a more Mediterranean climate in The Netherlands. Is there an influence from global warming also noticeable in Dutch coastal sand dunes?

Each of the chapters will give some of the answers to the general hypothesis evaluating livestock grazing. And not only livestock grazing. Other parameters to consider are the presence (or rather the absence) of rabbits, of stopping the mandatory marram planting, temporal changes in nitrogen deposition and general climate parameters and of the previous farmers' usage of the land. Integrating these answers will culminate in a better understanding of the life history of the dune grasslands and of the dune landscape as a whole over the past 50-70 years with drastic changes in environment and management.

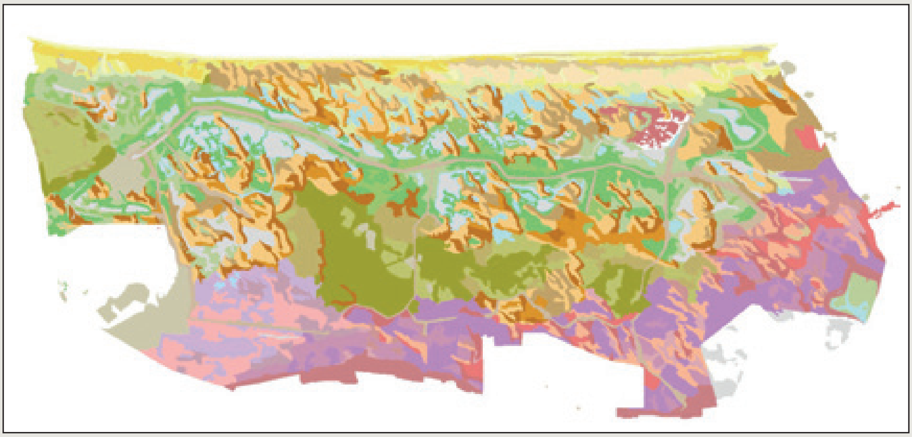
This thesis evaluates a huge dataset, that is unique for dunes. And it documents an example of a long-time co-evolution of nature and man to gain a better understanding and increased respect for our natural coastal heritage.

BOX 1. ECOLOGICAL LANDSCAPE ZONES IN MEIJENDEL

To research and understand the impact of livestock grazing in the following chapters, the ecological landscape zones of Meijendel are explained. These zones (Van der Meulen et al. 1985) are based on two main landscape characteristics: terrain form of the landscape and vegetation cover by structural and floristic composition. It follows the ITC landscape guided approach (Faculty of Geo-Information Science and Earth Observation, Enschede; Zonneveld et al. 1979). The three main colours yellow (fore dune), brown (parabolic dunes) and purple (inner dunes) reflect the three main periods of in-blowing or through-blowing sand in the Meijendel landscape. The vegetation type often is an exponent of the terrain form. The light tones stand for low, open stands of vegetation, e.g. open grasslands with mosses and lichens. The dark tones represent tall vegetation, e.g. shrubland/forest. In between the parabolic system (brown) and the inner dune system (purple), the extensive dune valleys (green colours) are situated. Notice that the parabolic dunes, the extensive dune valleys and the inner dunes do not run parallel to the coast, only the fore dunes do. The species and plant communities mentioned below are described as typical of the priority habitats of the Habitats Directive.

Fore dunes

The fore dunes date from around the first part of the 19th century. They consist of parallel ridges that were, until recently, heavily planted with Marram grass (Ammophila arenaria) forming a 15-20 meters high sand dike. The fore dunes separate the dynamic processes of the sea and beach on the one hand, and the dunes on the other. A natural coastline has connectivity by notches through which sand is transported from the beach into the dunes. Here the habitat type of 'White dunes' (H2120) mainly occurs. In 2015, five notches were made in the sand dike in Meijendel over a length of 700 meters, giving a part of this section of the coastline a more natural appearance. It was executed without concessions to the anti-flooding safety.



Parabolic dunes

The parabolic dunes have a pronounced relief and are intermixed with (wet) dune valleys. Soils are generally rich in lime, up to 3% by weight. They consist of more or less U-shaped dunes with trailing arms aligned in the direction of the prevailing southwestern winds. They often have short steep (> 15°) slopes, which are alternately exposed in more or less northern and southern directions. The average height is 10-20 meters. In the dry areas, the vegetation is dependent on rainwater and is covered in a mosaic of sandy pioneer dune grassland species, predominantly on southern slopes (e.g. *Phleum arenarium, Saxifraga tridactylites*). The closed dune grasslands predominate on northern exposures (e.g. *Silene nutans, Gentiana cruciata*) in a mosaic with open sand (blow-outs). The 'Zeedorpen' plant communities are another special grassland type with species like *Orobanche purpurea, Orobanche picridis, Silene nutans* and *Silene otites*. All of these grasslands belong to the priority habitat 'Grey dunes' (H2130). Up to 1990, blow-outs were stopped by mandatory Marram grass planting; more recently blow-outs returned to the dune ecosystem. Also dwarf shrubs, like *Hippophae rhamnoides* (H2160) and Salix repens, and higher shrubs of *Euonymus europaeus* and *Crataegus monogyna* and trees like *Quercus robur* are present in the Parabolic dune zone.

Most depressions lie between 2 and 6 meters above sea level. These wet dune valleys (H2190) are covered with dune slack communities, rich in orchid species as well as *Parnassia palustris, Schoenus nigricans* and *Juncus anceps* and, recently, due to successful restoration projects, *Littorella uniflora* and *Centunculus minimus* (Van Heusden 2019). In this zone, the infiltration ponds for drinking water production are also situated (blue/grey colour).

Inner dunes

The inner dunes are the oldest of the "Younger Dunes", dating from about the 9th-13th century. The parabolic shapes have more or less disappeared. The height varies between five and 35 meters above sea level. The leaching of lime from the topsoil and wind exposure are the main causes for the relatively open character of these dunes, which is characterized by short grasses like *Corynephorus canescens*, mosses and lichens (priority habitat H2130B). One lichen species is exceptional. Meijendel is the only place in the Netherlands where *Usnea articulata*, together with *Evernia prunastri*, is found growing on the ground still (Boerboom 1960a). Up to 1990, in this zone, blow-outs were halted by mandatory Marram grass planting, stimulating an accelerated acidification of the soil. For the purpose of increased sand stabilisation, extensive amounts of varieties of *Populus* have also been planted in places. More recently blow-outs have started to return to the "Inner dunes". From erosion by rainwater, the top acidified soil layer has shifted down slopes locally, exposing the lime-rich sand. This sand is then sensitive to wind transport. This can generate rejuvenation of the lime richer dune grasslands, often in a mix with lime-poor grasslands. In the lower valleys, shrubland of *Crataegus* and associated species dominate in mosaics with small forests of Betula and *Quercus* (H2180).

Large dune valleys

Large blow-outs originally formed the large dune valleys. They vary in size from 25 ha for Harstenhoek; prior to the expansion of Scheveningen village the area was 45 ha; 30 ha in the case of Bierlap and Kijfhoek to around 100 ha for the dune valley Meijendel in the middle). In the 18th and 19th century, large parts of these valleys were flattened down to the average ground water table and fertilized with dung, to be used as arable land for crops and for meadows. These fields were surrounded by low sand dikes. In the time before barbed wire was invented, the prickly *Crataegus* was used to separate crops from pastures. The use of dung leached out the lime to a depth of 50 cm or more. Due to the industrial exploitation of the ground water for drinking water and the subsequent lowering of the ground water table, the farmers abandoned these lands. Nowadays, these extensive dune valleys bear summer-green forests of Betula and Quercus (H2180) and lichen-rich dune grassland on acid soils or grasslands with a coverage of *Carex arenaria* and *Calamagrostis epigejos*. In the south of Meijendel near Scheveningen around the Harstenhoek, the plant communities of the Zeedorpenlandschap were present and partially still do exist.

Chapter 2

Is livestock grazing a key factor for changing vegetation patterns in lime rich coastal dunes in The Netherlands?

Harrie G.J.M. van der Hagen, Dan Assendorp, Wim Calame, Frank van der Meulen, Karlè V. Sýkora, Joop H.J. Schaminée

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ABSTRACT

In 1990, livestock grazing was introduced in Meijendel, a 1,800 ha lime-rich coastal dune area, at a density of 0.06-0.07 LLU.ha^{-1}.year^{-1} (1:12-18 ha) to counteract encroachment of tall grasses and shrubland on dune grassland and increase the bare sand area. Monitoring was based on four digital orthophotos (1975-1990-2001-2009) with a high spatial resolution (pixel size 25x25 cm). The changes were tested using Generalized Estimating Equations. Habitat changes occurred, but contradicting our hypothesis, there was no significant impact from the grazing on bare sand, grassland or shrubland within 11 and 19 years post livestock introduction. (1) After several decennia of decreasing bare sand, there was a significant increase between 2001 and 2009, irrespective of livestock presence. (2) The changes in grasslands and shrublands are independent of the livestock, but dependent on distance to the coast. (3) Bare sand and shrub cover determine the space left for the dune grasslands. It appears other factors than livestock grazing must have induced the changes. Changes in climate conditions and nitrogen load might have stimulated bare sand. An interaction with the end of Marram planting in 1990 cannot be concluded from available data. The disease-led reduction of rabbit grazing from the mid-1950s led to an expansion of the dominant shrub *Hippophae rhamnoides*. However, *Hippophae* shrubland typically regresses to grasslands on its collapse after 25-40 years. Tree species like *Crataegus, Betula* and *Quercus* will gradually dominate the landscape for far longer. Active removal of these indigenous species is necessary to prevent future loss of dune grasslands.

KEYWORDS Coastal dunes, blowout, aerial photographs, livestock grazing, Oryctolagus cuniculus, Hippophae rhamnoides

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INTRODUCTION

Lime-rich coastal sand dunes in The Netherlands are species rich and harbour 66% of the Dutch flora (De Vries et al. 1994). Under the Natura 2000 legislation (Council of the European Communities 1992) almost all habitats of the coastal sand dunes are protected. These habitats are a mosaic of bare sand, dune grasslands, shrubland and forests. ‘Grey dunes’, i.e. fixed coastal dunes with herbaceous vegetation, are designated as a priority habitat type (H2130) by Natura 2000. Grey dunes not only contain a great number of vascular plants, but they are also rich in bryophytes, mosses and lichens (Schaminée et al. 1995, 1996, 1998,1999).

During the last five decades, the vegetation in Dutch coastal dunes has changed considerably. Patches with bare sand and open grasslands have changed into areas mainly dominated by tall grasses and sedges, shrubs and forest that has gradually led to a rather monotonous vegetation and a considerable loss of local biodiversity (Ketner-Oostra and Sýkora 2004; Kooijman et al. 1998; Veer and Kooijman 1997). These processes have been associated with several phenomena: (1) the outbreak of Myxomatosis and Viral Haemorrhagic Disease (RVHD) in populations of rabbits (Oryctolagus cuniculus), (2) routine planting of Marram grass (Ammophila arenaria) and shrubs and trees to stabilize dunes, (3) planting of shrub and tree species for mainly aesthetic reasons and wood production, (4) a high input of airborne nitrogen, (5) changes in land use, including abandonment of agricultural practices like livestock grazing and crop cultivation, (6) the impact of changes in climate conditions, (7) an on-going anthropogenization of the landscape (e.g. recreation), accompanying a rapid spread of introduced non-native species, and (8) autonomous succession (Provoost et al. 2011; Remke et al. 2009; Noordijk 2007; Jones et al. 2004; Eerens and Van Dam 2001; Drees and Olff 2001, Kooijman et al. 1998, Ten Harkel 1998; Ten Harkel and Van der Meulen 1996; Schaminée et al. 1995, 1996, 1998, 1999; Bakker et al.1974; Boerboom and Westhoff 1974; Ranwell 1960). As large herbivores were thought to counteract the process of stabilisation and monotonisation (Van Dijk 1992; Kooijman and De Haan 1995; Provoost et al. 2011) and the fact that large herbivores strongly prefer graminoid species (Lamoot et al. 2005) extensive grazing by domestic livestock has been introduced in many nature reserves in The Netherlands and elsewhere.

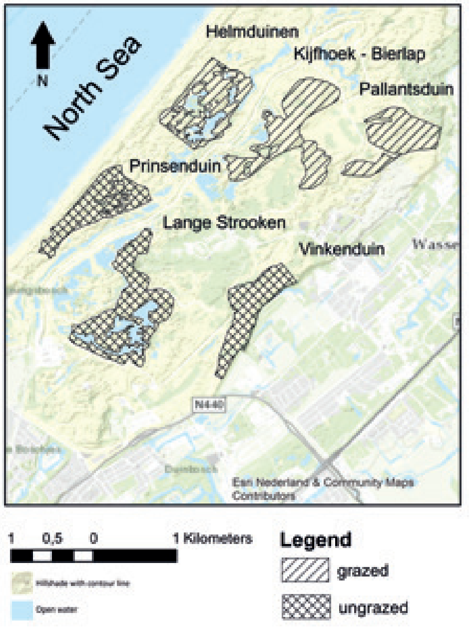

Fig. 1. The six study sites in Meijendel, The Netherlands with their area names. The three northern areas are grazed, from West to Central to East: Helmduinen, Kijfhoek/Bierlap, Pallantsduin. The three southern areas are ungrazed - from west to east: Prinsenduin, Lange Strooken, Vinkenduin. The West and Central areas are in the parabolic landscape zone; the East areas are in the inner dunes. The black outer line separates the sand dunes (with the six study sites) from the urban area with the main road system

In late 1990, year-round grazing by livestock was introduced in the coastal dunes of Meijendel near The Hague, The Netherlands (GPS 52° 7‘N; 4° 20’E). The livestock density was 0.06-0.07 LLU.ha^{-1}.year^{-1} (1:12-18 ha). Generally speaking, Wallis de Vries et al. (1998) consider this to be a relatively low level of impact. However, the level of LLU had been adjusted to the low level of palatable biomass in coastal sand dunes (e.g. Ebrahimi 2007) and expected winter survival of the animals. In some years, some animals of the herds barely survived winter, which meant a relatively high impact on this nutrient-poor environment. By trampling and grazing, the vegetation was expected to be damaged to a large degree, initiating blowouts. Grazing was expected to stop the increase, or even cause a decrease, of shrubs and trees or, at the least, open up the shrubland and forest to the benefit of species rich dune grasslands.

The hypothesis of this study is that the introduction of livestock will lead to regressive succession, as expressed in an increase of bare sand, a decrease in the area of shrubland, and a subsequent increase of dune grassland. This paper focusses on the changes in area cover of these three classes (bare sand, grassland and shrubland), by comparing three livestock-grazed areas and three ungrazed controls within the coastal dunes of Meijendel in The Netherlands.

Area of investigation

The dunes of Meijendel are a well-known and highly valued example of the lime-rich dune landscape of the Atlantic coast (Janssen and Schaminée 2003; Van der Meulen and Van der Maarel 1993). Meijendel covers an area of approximately 1,800 hectares (Van der Meulen et al. 1985). Van der Meulen et al. (1985) distinguished four landscape ecological zones running more or less parallel to the coast with increasing distance from the sea: (i) Fore Dunes; parallel dune ridges mainly with Marram grass, which was extensively planted for stabilisation purposes as a coastal defence measure, (ii) Parabolic Dunes; dunes with a pronounced relief (2-20 m) and small moist dune valleys in between, whose soils are rich in lime. The drier dunes are mosaics of bare sand, pioneer grasslands (southern exposures), closed grasslands (northern exposures) and shrubs of Sea Buckthorn (*Hippophae rhamnoides*) and other shrubs; it is the zone for artificial recharge for drinking water production (Fig. 1; open water), (iii) Large Dune valleys; decalcified grasslands and deciduous woodlands where tree species like *Betula, Crataegus* and *Quercus* dominate, which in the 19th century were partly flattened and used as arable land, and (iv) Inner Dunes; in general higher dunes (5-35 m) with less pronounced parabolic and rolling dunes. The topsoil is partly decalcified and supports dune grasslands with short grasses, mosses and lichens, open *Hippophae* shrubland and forest patches. Occasional sand blowouts generate a mosaic with grasslands richer in lime.

MATERIAL AND METHODS

Aerial images

Along the Dutch coast, sequential mapping of aerial photographs have shown drastic changes in vegetation cover (e.g. Van Dorp et al. 1985; Kruijsen et al. 1989; Van Til and Mourik 1999; Janssen 2004), but in complex systems like coastal sand dunes, manual and especially manual sequential mappings have their limitations (Janssen 2004; Assendorp 2010). Drawing lines between vegetation types in discrete landscapes with crisp (sharp) boundaries is relatively easy. But drawing lines in a landscape with fuzzy spatial transitions between vegetation types, such as coastal dunes where every metre can be different to the next, the interpretation of vegetation types is highly dependent on personal interpretation. Therefore, other remote techniques are required and used for vegetation mapping and land surveys (e.g. Campbell 2006; Groom et al. 2006; Potter 2013). Assendorp (2010) demonstrated that geometrically and radiometrically corrected orthophotos with a high spatial resolution largely overcomes the difficulties of manual mapping.

Four sets of high-resolution false colour infrared digital orthophotos of Meijendel were available with clear time intervals: 1975, 1990, 2001 and 2009. All four were taken in the same period of the year (end June/beginning July). The years 1975 and 1990 are ±330 2 mu scanned analogue images (34x34 cm), which have been geo-referenced and radiometrically corrected to one orthophoto. The years 2001 and 2009 were direct digital recordings and also radiometrically corrected. For the technical details of orthophoto production see Assendorp (2010). The feature space data were processed in ArcGis 10.3. The accuracy of the classification of scanned analogue false colour images of 1975 and 1990 and of the digital photos of 2001 and 2009 were 80-95% as demonstrated by Assendorp (2010). This percentage is generally accepted as appropriate for a vegetation structure map (Foody 2002; Assendorp 2010). All four sets of orthophoto images were resampled to a pixel size of 25x25 cm. At this resolution, bare sand and shrubland/trees are defined (crisp) objects and consist of multiple pixels in the image. Grasslands differ within a 25x25 cm pixel and have a reflection at the subpixel level (fuzzy). Bare sand has a specific reflection and is easily separated in the feature space (Assendorp 2010) and is defined as 100% coverage of blond windblown sand without any vegetation cover and no grey humic sand on the surface. Shrubland/trees, defined as 100% coverage of woody plants, are also easily distinguished from the rest in a traditional supervised image classification (Assendorp 2010). In the six selected areas, the shrubland category consists almost entirely of *Hippophae rhamnoides*. The grasslands are sharply clustered within one class.

Selection of research areas

As the focus of this research is on groundwater independent dunes, dune slacks and water bodies were left out and in the case of infiltration ponds given an extra margin of 10 metres around. Similarly, all human-disturbed open areas were left out. These include (i) areas with extraction wells for artificial recharge for drinking water production, (ii) intentionally denuded areas to stimulate blowouts, (iii) the foreshore and Fore Dunes as grazing is prohibited, (iv) parts of the Parabolic dunes which were intentionally planted with shrubs and trees, and (v) the larger dune valleys as these valleys are an unnatural feature, and have no ungrazed counterpart. Up to 1990, all over Meijendel except for the Fore Dunes compulsory plantings of Marram grass was equally applied.

From West to the Central and the East, the test grazing areas are represented by the Helmduinen (43 ha), Kijfhoek/Bierlap (65 ha) and Pallantsduin (43 ha), whereas Prinsenduin (43 ha), Lange Strooken (65 ha) and Vinkenduin (43 ha) represent the ungrazed control areas (Fig. 1); in total 302 ha. The study areas are positioned within the areas of the (ii) Parabolic Dunes and the (iv) Inner Dunes (Van der Meulen et al. 1985).

In late 1990, year-round grazing with Galloway cattle and Norwegian Fjord horses was started, just after the 1990 orthophotos were taken. It is assumed that the impact of rabbit grazing on the three vegetation classes is equal. The rabbit populations fluctuate over the years because of variations in the impact of epidemic diseases (Myxomatosis from around 1954 and RVHD in 1989, just before the introduction of the livestock). Rabbits are counted, but the transects cross over the areas of this research.

Statistical analysis and confounding factors

With late 1990 as the starting point of grazing, the changes of the crisp vegetation classes in hectares between 1975 and 1990 as well as between the test starting date of 1990 and 2001 and equally between the test starting date of 1990 and 2009 have each been calculated per research area in order to view time-dependent impact of grazing on the outcome, while acknowledging the changes in impact by starting levels. The interval between 1975 and 1990 is considered as a period without large herbivore grazing. By subtracting the outcome per plot at the various times from status at the start, data are transferred into change values: the change in amount of hectares covered by the various vegetation types per time interval (before and after start of grazing) per period. Two main sets of data were obtained: one with grazing and the other without (control). Subsequently the values were tested as to what extent grazing affected the relative distribution of the three types of vegetation using Generalized Estimating Equations (GEE) analysis with dummy variables (Kleinbaum et al. 1998). As potentially confounding factors, the starting values (at t=0) and the relative locations in the dune area (1=West; 2=Central; 3=East; Fig. 1) were taken into account as variables. The regression equation (equation 1) used was:

$$y = (a_1 x_1) + (a_2 x_2) + (a_3 x_3) + a_4 \qquad \text{Equation 1}$$

in which:

y = change in hectares per time interval
x_1 = dummy variable, taking the values 0 for not grazed control area and 1 for grazed area
x_2 = time interval
$x_3 = (x_1) \times (x_2)$
$a_{1\text{-}4}$ = coefficients.

In a second stepwise regression analysis confusing was checked by the introduction of location: West, East and Central, all coded by a discrete character, and starting value at 1975 to detect potential impact by this factor on the outcome. In the latter analysis, variation in the change of hectares was associated with variation of the above factors, together with dummy coding (0: ungrazed versus 1: grazed).

Fitting of the equation model was evaluated by Wald Chi-square test. GEE analyses were done using STATA, version 12 (StataCorp, College Station, Texas, US). Graphic representation was performed via GraphPad Prism, version 6 (LaJolla, CA, USA). Throughout the study, using two-sided testing, P values of 0.05 or lower were considered to be of statistical significance.

Apart from the statistical analysis on the changes, the weighted average of the three crisp classes of the three grazed and three ungrazed controls is calculated and fitted to figures in MS Office Excel 2010.

RESULTS

Impact by livestock

For the period of fifteen years before (1975-1990), and respectively eleven (1990-2001) and nineteen (1990-2009) years after the start of livestock grazing, the changes in relation to the start of livestock grazing (1990) are presented (Fig. 2a, b, c) as well as the weighted average of the three areas of grazed versus ungrazed (Fig. 3a, b). The changes in hectares of bare sand, grassland and shrubland between grazed and ungrazed areas are - in contrast with the hypothesis - not different (Fig. 2a, b, c; Table 1). A similar conclusion was reached for the mean proportion of the three structural types (bare sand, grassland and shrub; Fig. 3a, b). A decline of bare sand up to 2001 and an increase of shrubland up to 1990, as direct outcomes of progressive succession, is clearly visible in both the grazed and ungrazed control areas.

The results for each crisp class is described in different sections. The classes of bare sand and shrubland are described first, because bare sand and shrub development seem to determine the space left for the dune grasslands.

Changes in bare sand

Between 1975-1990 and 1990-2001, there is a steady decrease in the area of bare sand. In the period 2001-2009, an increase in bare sand is visible, though not significant (Fig. 2a; Table 1). Before the introduction of livestock, between 1975 and 1990 aerial photographs show that bare sand mainly evolves into grasslands, but no significant differences could be observed between the grazed and ungrazed areas because in the pre-1990 time frame they were both ungrazed. From 1990 onwards, we expected clear differences due to grazing. Surprisingly, there is no difference between the grazed and the ungrazed areas, and -surprisingly- the change in the ungrazed areas is more pronounced, but statistically not different.

Between 2001 and 2009, there is a clear increase of bare sand both in the grazed and ungrazed sites with no significant difference ($p>0.05$; Table 1). Time ($p<0.04$) and location ($p<0.01$) explains the differences in the changes in area of bare sand, irrespective of grazing. There is an overall reduction in the bare sand areas between 1975 and 2009, while the reduction in the central dune area is more pronounced than in the west and the east dune areas. Again, there is no significant effect because of livestock grazing.

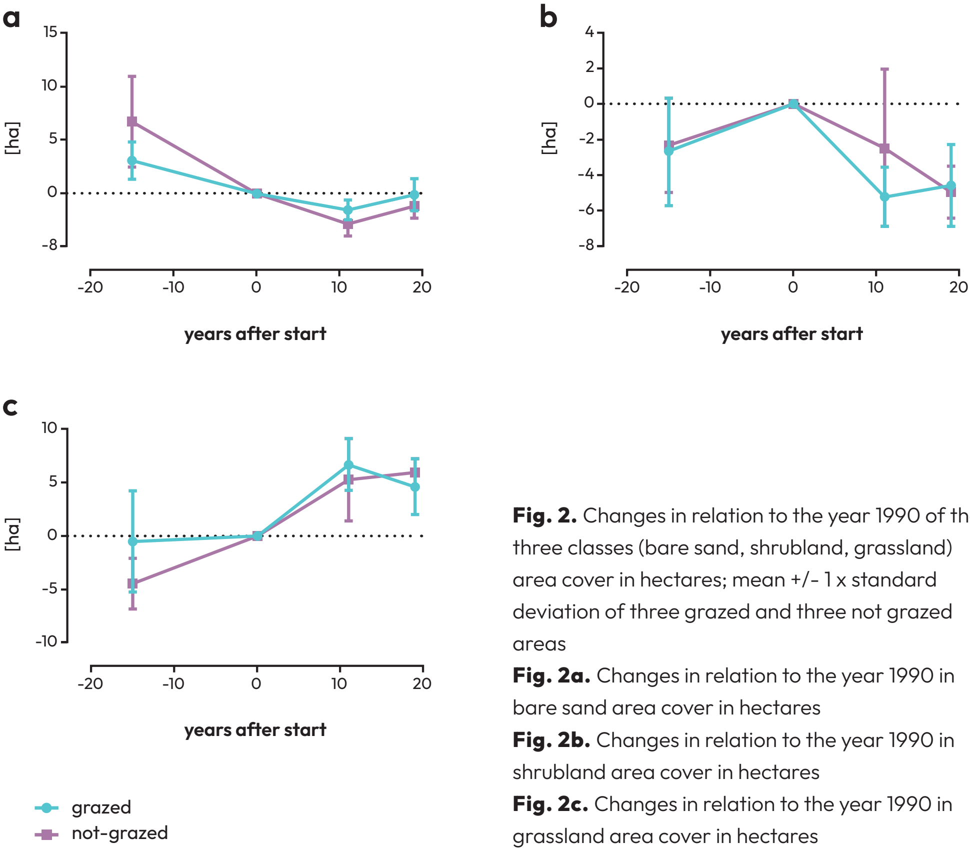

Fig. 2. Changes in relation to the year 1990 of the three classes (bare sand, shrubland, grassland) area cover in hectares; mean +/- 1 x standard deviation of three grazed and three not grazed areas

Fig. 2a. Changes in relation to the year 1990 in bare sand area cover in hectares

Fig. 2b. Changes in relation to the year 1990 in shrubland area cover in hectares

Fig. 2c. Changes in relation to the year 1990 in grassland area cover in hectares

Within the studied time interval of 34 years, the coverage of bare sand varied between 2.7% and 21.5% (Fig. 3a, b; online appendix Table 1a, b). The grazed and ungrazed areas show similar trends in bare sand cover. In 1975, the weighted average proportion of bare sand was 14.5% in the pre-1990 grazed area and 21.5% in the control. In 1990, it had decreased to 8.9% and 8.4% in the post 1990 grazed versus the control area. The lowest percentage was reached in 2001 with 5.8% and 2.7% after which it increased to 8.3% and 6.2%, respectively.

Changes in shrubland

Between 1975 and 1990 prior to the start of the grazing, shrubland increased by an average of three hectares in both grazed and ungrazed sites (Fig. 2b; Table 1). This is according to the expectations, because all sites were ungrazed before 1990. Between 1990 and 2001, the average change was a decrease of about 4 hectares, again in both grazed and ungrazed areas. In between 2001 and 2009 however, there is almost no change in the extent of shrubland. Again, location ($p<0.01$) is the parameter explaining the changes in

Table 1. Statistical matrices of the Generalized Estimating Equations analysis and the following stepwise regression analysis checking confounding factors. The number of observations is 12.

	F-VALUE	R²	T-VALUE	P-VALUE	SIGNIFICANCE
BARE SAND					
	$F_{(2,9)}$=4.73	0.51			
Grazing			1.84	0.099	n.s.
Time			2.47	0.036	*
SHRUBLAND					
	$F_{(1,10)}$=10.46	0.51			
Location			3.23	0.009	**
GRASSLAND					
	$F_{(2,10)}$=6.29	0.39			
Location			-2.51	0.031	*

* = significance <0.05
** = significance <0.01
n.s. = not significant

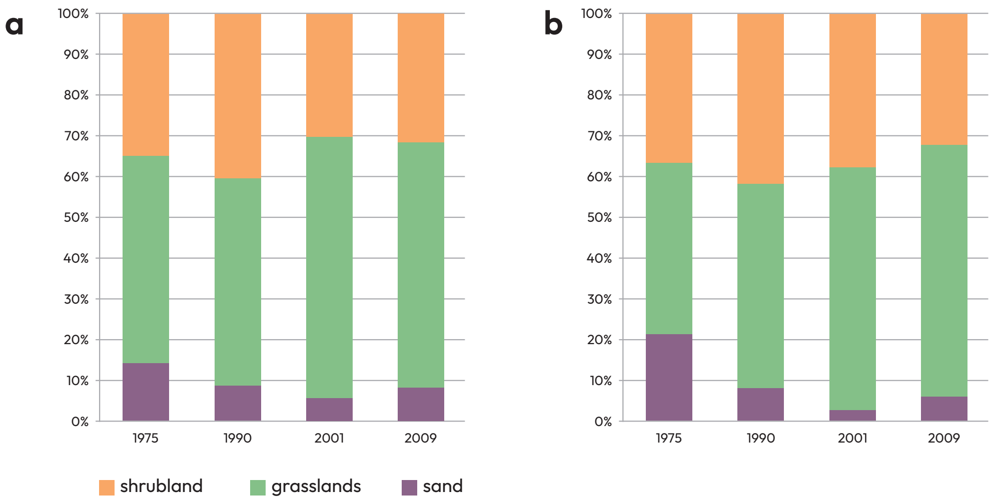

Fig. 3. Weighted average of pixel number of the three crisp classes in the four years; 1990 is the year of introduction of livestock just after the orthophoto flight .The percentages are given in an online appendix Table 1

Fig. 3a. Weighted average of the three grazed areas

Fig. 3b. Weighted average of the three ungrazed areas shrubland between the grazed and the ungrazed areas. In the west part of the dunes, the decrease in shrub area is significantly (p<0.01) higher than in the central area with the central being significantly (p<0.01; Table 1) higher than in the east. A clear west to east effect in the reduction in shrubs is demonstrated. In the ungrazed situation of Lange Strooken and Vinkenduin the decline starts in 2001; in the other four areas the decrease started already in 1990. Aerial photographs show an overall regressive succession as when *Hippophae* shrubs start to die, the shrubs open up and gradually shift to grassland.

In all years and areas, the proportion of shrub varied between 30 to 42% of the area (Fig. 3a, b; online appendix Table 1a, b). In all six areas, the dominant shrub is *Hippophae rhamnoides*. The main changes in coverage are mainly caused by the growth and decline of this species. Between 1975 and 1990, the proportions of shrub increased from 35.2 to 40.7% (grazed) and from 37 to 41.9% (ungrazed). Aerial photographs show an expansion of closed thickets of *Hippophae* shrubs. From 1990 to 2001, this tendency is followed by a decline from 40.7 to 30.5% (grazed) and from 41.9 to 37.8% (ungrazed). From 2001 to 2009, in the grazed area, shrubland increases slightly from 30.5 to 32.0%, whereas in the ungrazed areas the shrubland further decreases from 37.8 to 32.2%).

Changes in grasslands

In the ungrazed areas, the average change between 1975 and 1990 amounts to 5 hectares (bare sand changes mainly into grasslands); in the grazed area, almost no changes are observed (Fig. 2c; Table 1). From 1990 to 2001, there is an increase of about 5 hectares in both the grazed and ungrazed areas. Between 2001 and 2009, the extent of grasslands stabilize but there is a difference by location. The further east, there is a reduced change (p<0.04) to grassland.

The loss of grasslands by the increasing share of bare sand in the period 2001-2009 is explained by a larger decrease in shrubland. Grazing pressure and time variables do not explain the model variables.

In the mosaics of bare sand and shrubland, the dune grassland in all the years of observation and in all areas forms the largest portion of the three crisp classes, illustrating the relative openness of the coastal dune landscape. The dune grassland varies between 41 and 64% of the area (Fig. 3a, b; online appendix Table 1a, b). Between 1975 and 1990, the extent of grassland in the grazed area remains the same, while in the ungrazed areas the grassland proportion increased from 41.5 to 49.7%, but the changes are different. Between 1990 and 2001, both grazed and ungrazed areas of grassland show an increase of 13.3 and 9.8%, respectively. In the 2001-2009 period, the grassland slightly decreased with 4% in the grazed area. In the ungrazed situation, the grassland increased slightly by 2.1%.

In overall conclusion, the extent of grasslands is determined by the space left over from the changes in the development of both bare sand and shrubland.

DISCUSSION

We analysed the effect of the introduction of livestock grazing on changes in the presence and changes in cover extent of the crisp classes of bare sand, grassland and shrubland in the coastal dunes of Meijendel. We hypothesized that due to grazing and trampling caused by the livestock, and the rejuvenating effects of blowouts, the areas of bare sand, and grassland would increase, while simultaneously shrub encroachment at least would be stopped, and even reduced.

Regressive succession occurred, but contrary to our hypotheses, no significant impact of the introduced livestock could be demonstrated in the observed changes of the extent of bare sand, grassland and shrubland with the grazing intensity applied. In the ungrazed areas, similar changes occurred as in the grazed. The question arises which factors could explain this unexpected outcome.

Bare sand

Which factors can explain the decrease in bare sand up to 2001 and its subsequent increase in all six areas irrespective of livestock grazing?

Bare sand in coastal dunes is normally present as blowouts and in paths. The decrease of bare sand from 1975 until 1990 can be linked to the compulsory planting of Marram grass all over Meijendel as in other dune areas (e.g. Van Dorp et al. 1985; Van Til 1999). Annually, in Meijendel up to 1.2 million Marram tufts were planted and in many places this was repeated, stimulating a shift towards stabilisation (Van der Meulen and Jungerius 1989; Mensing 2002). In 2001, bare sand mainly consisted of small spots and long paths, as well in the grazed Helmduinen (Fig. 4a) as in the ungrazed Prinsenduin (Fig. 5a). The paths originate from monitoring volunteers, rangers and (illegal) visitors, all taking the same routes over and over again. Though expected, introducing livestock in 1990 did not result in an extra increase of bare sand in the grazed areas. Grazed and ungrazed areas have a similar decrease (Fig. 2a) and shift (Fig. 4a, 5a).

Between 2001 and 2009, there is a substantial and comparable increase of bare sand in the grazed Helmduinen (Fig. 4b) as well as in the ungrazed Prinsenduin (Fig 5b). In 2009, the paths are still there, but the larger part of the new bare sand is formed by blowouts with areas much broader than paths. These new blowouts are mainly found on slopes with a southwest orientation with climate extremes in spring and summer. Former Marram grass planters confirm that the areas, which were regularly involved in Marram planting, opened up again as part of a natural process irrespective of livestock grazing.

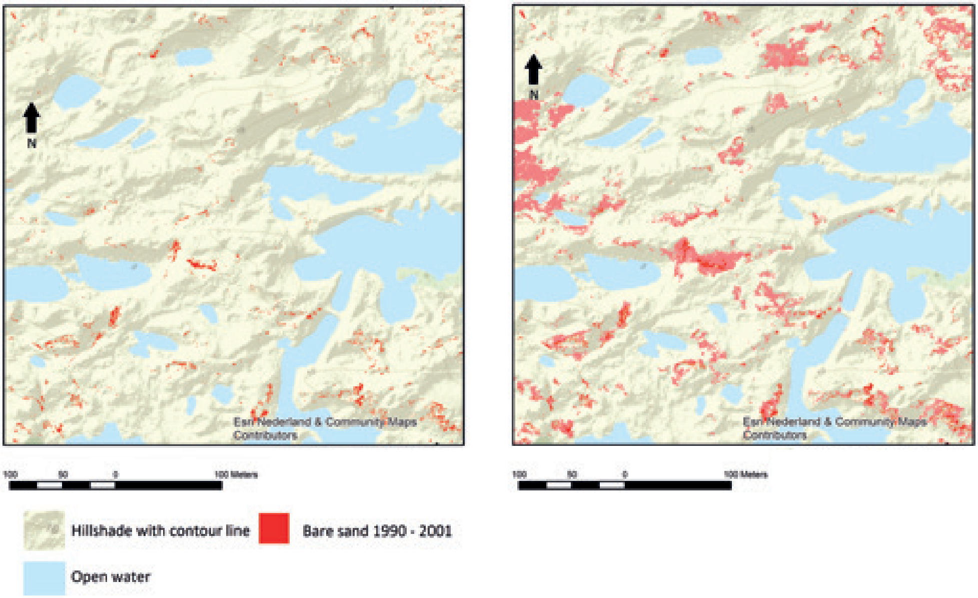

Fig. 4. Major part of the grazed Helmduinen area showing the 25x25 cm pixels where the land cover changed into bare sand
Fig. 4a. The changes into bare sand from 1990 to 2001 (red). They are predominantly linear structures in reality observed as paths
Fig. 4b. The changes from 1990 to 2001 (red) combined with the changes from 2001 to 2009 (pink). The substantial increase in the 2001-2009 period is clearly visible, predominantly surface structures in the field observed as blowouts

Whether the Marram planting hampered the 1990-2001 development of blowouts is impossible to conclude from our data.

Since 1990, the airborne nitrogen load in the dunes has almost halved (Noordijk 2007) and this is likely to have consequences on the increase of bare sand. Primary succession on bare sand starts with algal crusts (Van den Ancker et al. 1985; Pluis and De Winder 1989). Cyanobacteria are the initial colonizers mostly members of the genera *Microcoleus, Oscillatoria* and *Tychonema*, in more stable conditions, to be followed by the dominating green algae *Klebsormidium flaccidum*. These organisms all depend on airborne nitrogen (Pluis and De Winder 1989) and a substantial reduction must have had its implications on the colonization, growth and cohesion of these algal crusts.

A temperature jump in the average mean from 9.2 °C to 10.5 °C, starting in 1988 (KNMI 2013), and just before the introduction of livestock, is likely to have caused more droughts in the coastal sand dunes stimulating blowouts, irrespective of livestock grazing. Several

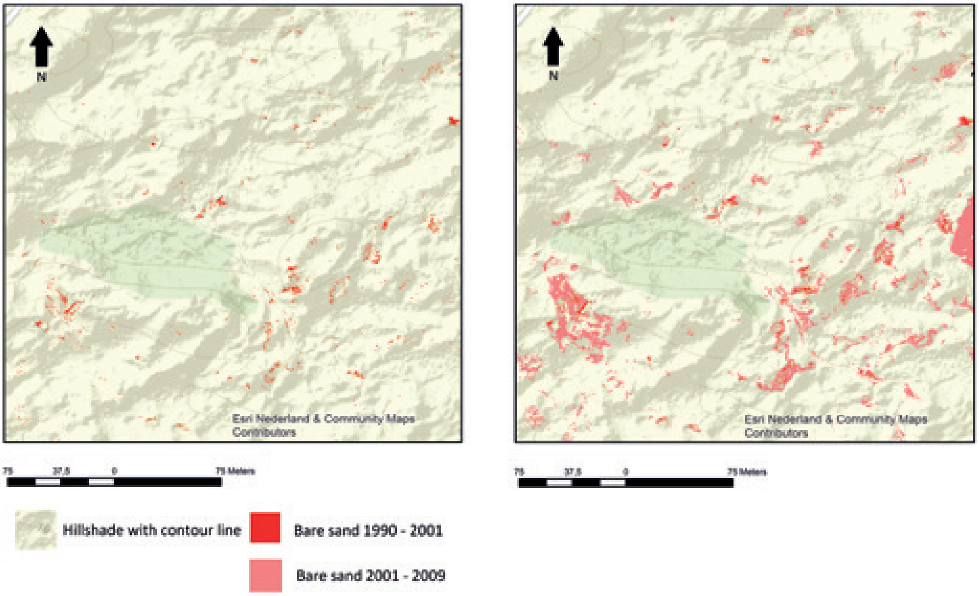

Fig. 5. Major part of the ungrazed Prinsenduin area showing the 25x25 cm pixels where the land cover changed into bare sand
Fig. 5a. The changes into bare sand from 1990 to 2001 (red). They are predominantly linear structures in reality observed as paths
Fig. 5b. The changes from 1990 to 2001 (red) combined with the changes from 2001 to 2009 (pink). The substantial increase in the 2001-2009 period is clearly visible, predominantly surface structures in the field observed as blowouts

spring droughts and dry winter winds from the East in the period 2001-2009 are also likely to have stimulated sand blowouts. Model calculations based on changing climate conditions confirm this theory (Witte et al. 2008, 2012).

On the other hand, changes in climate conditions also led to more intense summer rains and a longer growth period that stimulates an increased and more palatable biomass production over a longer period during a year. Civerolo et al. (2008) found an interaction between a higher nitrogen input and climate change because of higher summer rainfall, making it difficult to pinpoint the changes in our data to any one factor.

This research shows that the location (west, central, east) does not explain the shifts in area of bare sand over time, though the wind intensity is presumed to have a greater effect in the western part of the dunes (Arens et al. 2013). Depending on the presence of organic matter, dune sand is more sensitive to erosion by wind or by water. Yellow lime-rich sand, mainly in the western part of the dune, is without cohesion and is more easily transported away by wind. Further east, grey lime-poor top soils contains more organic matter. This sand resists wind erosion, but because of its water repellency, the top layer can be easily washed downslope and this happens especially with heavy rainfall after a period of dry weather. Once the top layer is eroded, wind erosion picks up the underlying yellow sand leading to blowouts (Jungerius and Van der Meulen 1988). Between 2001 and 2009, it is believed that both processes lead to a substantial and comparable increase of bare sand.

Apart from changing nitrogen loads and changing climate factors, very slow increasing numbers of rabbits since the outbreak of RVHD in 1989 might lead to more collapsing warrens in all areas resulting in more points where wind erosion processes could take hold.

Shrubland

Rabbit grazing is likely to have an great impact on the shifts in shrubland. Rabbits not only graze the grasslands, have warrens, which can collapse that opens up the land to wind erosion, but especially favour nutrient rich seedlings of shrub and tree species (Jungerius and Van der Meulen 1988; Drees and Olff 2001; Van Tongeren 2006). The increase of shrubland can be explained by sudden and steep decreases in rabbit densities due to two rabbit diseases, which became epidemic in Meijendel. These are Myxomatosis from around 1954 and RVHD from around 1989 (Drees and Olff 2001; Scheffer 2012). Myxomatosis is considered by site managers to be responsible for shrubland increase between 1975 and 1990 and for its unexpected decrease between 1990 and 2001 (Fig. 3a, b). *Hippophae rhamnoides* can grow in nutrient poor and sandy pioneer conditions due to bacterial nodules on its roots (Oremus 1982). In the absence of rabbit grazing in the years directly after 1954, many seedlings or young sprouts of shrub species, including *Hippophae,* survived. The young plants invaded the surrounding area through clonal spreading, forming male and female monocultures of *Hippophae* shrubs. The life span of this shrub is about 25-40 years (Zoon 1995). The degeneration process is initiated by nematodes causing malfunctioning of the root nodules (Oremus 1982; Maas et al. 1983; Zoon 1995), finally resulting in dieback of the plants (Westhoff and Van Oosten 1991). The massive expansion from 1954 would therefore logically lead to a massive decrease starting around 1985 (Fig. 2b; 3a, b). *Hippophae* shrubs typically return to grasslands (regressive succession: this study; see also Provoost et al. 2011; Cornelissen et al. 2014), but the fine scale analysis of 25x25 cm field size pixels reveals the degenerating process at an earlier stage and better than manual mapping. On the other hand, new blowouts can generate new opportunities for *Hippophae* especially in a low density of rabbits due to both diseases being still epidemic. Provoost et al. (2011) report that livestock grazing in *Calamagrostis epigejos* dominated grasslands also led to a renewal of *Hippophae* shrubs, but in the Meijendel situation, the decreases outweigh (local) increases. This degenerating process has also been noticed in other dune areas

(Aggenbach et al. 2017). The process is the same in all six areas, but the changes in the extent of shrubland are related to the location and the area seems to be smallest in the eastern areas. *Hippophae rhamnoides* as a pioneer species, has a preference for lime rich sands, which are devoid of nematodes feeding on its root nodules. The chances of finding these favoured conditions diminish from west to east, leading to reduced *Hippophae* populations.

The shrub *Crataegus monogyna* and tree species *Betula pendula*, *B. pubescens* and *Quercus robur* also demonstrate similar rabbit-related expansions in Meijendel. In the mid 1970's, tree ring research in Meijendel was done on *Crataegus* within a sea-to-inland transect (three kilometres west-east). About 80-85% of all *Crataegus* specimens originated from the first few years after the outbreak of myxomatosis in 1954 (Salman and Van der Meijden 1985). Due to the life span of *Crataegus* (200 years or more), this species might eventually dominate the dunes in future decades before a massive collapse in 150 years time. A relatively sudden decline of Betula pubescens in the dune valley Bierlap (30 ha) in Meijendel was considered to be related to a lowering of the water table due to the extraction of groundwater. This was not the case (Van der Meulen and Wanders 1985). Sequential vegetation mapping showed the real cause of its expansion and decline (Maasdam 1988). Aerial photographs of 1938 showed that *Betula* invaded most of the valley from west to east after the abandonment by the farmers around 1890. Later years (1962, 1975, 1980) showed that the degeneration of *Betula* forest also went from west to east through the valley. Most of the *Betula* trees had disappeared by 1985 (Maasdam 1988). Based on the nutrient poor soil of the Bierlap valley, these *Betula* trees had a life span of about 70-90 years (see Fitter and Peat 1994; Beck et al. 2016). *Prunus spinosa* in the riverine sand dunes of Junner Koeland (The Netherlands) shows the same life span process of increase after myxomatosis and its latter collapse (pers. comm. J. Bokdam; M. Gleichmann).

Dune grasslands

In traditional progressive succession schemes, grasslands are the outcome of stabilized sand overgrown by vascular plants and mosses after a period of algal crusts. This process takes several decennia (Mensing 2002; Arens et al. 2007, 2009). These grasslands are gradually invaded by shrub species, which expand, and with progressive succession end up as dune forest, reducing the grassland area. In Meijendel, the shrub encroachment is related to the sudden collapse of the rabbit population due to diseases, starting with the 1954 myxomatosis, offering sudden opportunities for seedlings and young sprouts of *Hippphae rhamnoides* and other shrub and tree species. Over a period of 35 years, *Hippophae* shrub increased at the expense of the grassland area. Due to aging, the shrub collapses and grasslands re-emerge (regressive succession). Because of the now acidified soil, the species composition will differ in the grassland compared to before the *Hippophae* expansion.

On the other hand, because of the increase of bare sand since 2001, the extent of the grasslands decrease in all research areas irrespective of livestock grazing. This means that it is plausible that -at least in the Meijendel situation- the changes in the extent of space for the grasslands is dictated by the increase and decrease of bare sand and of shrubland; grasslands fill in any left-over space. The regressive succession from *Hippophae* shrubland into grassland has also been noticed in other areas (Aggenbach et al. 2017) and is likely to be a regular phenomenon along the lime-rich coastal sand dunes. But this also means that apart from bare sand taking a part of the total grassland share, the cutting of indigenous long living shrubs and trees (like *Crataegus* and *Quercus*) is unavoidable to maintain a large amount of the EC priority (Council of the European Communities 1992) grasslands habitat.

ONLINE APPENDIX TABLES

Table 1. Weighted average of pixel number (#) and share (%) of the three crisp classes in the four years; 1990 is the year of introduction of livestock just after the orthophoto flight

Table 1a. Weighted average of the three grazed areas

	1975		1990		2001		2009	
	#	%	#	%	#	%	#	%
shrub	118543	35.2	136865	40.7	102516	30.5	107421	32.0
grassland	169210	50.3	169494	50.4	214530	63.7	200969	59.7
bare sand	48721	14.5	30116	8.9	19429	5.8	28086	8.3

Table 1b. Weighted average of the three not grazed areas

	1975		1990		2001		2009	
	#	%	#	%	#	%	#	%
shrub	123952	37.0	140472	41.9	126752	37.8	108101	32.2
grassland	139349	41.5	166628	49.7	199677	59.5	206591	61.6
bare sand	72096	21.5	28297	8.4	8970	2.7	20705	6.2

Chapter 3

The impact of livestock grazing on dry coastal dune grasslands in Meijendel, The Netherlands

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ABSTRACT

In 1990, livestock grazing was introduced in Meijendel, a 1,800 ha lime-rich coastal dune area, at a density of 0.06-0.07 LLU.ha^{-1}.year^{-1} (1:12-18 ha) to counteract encroachment of tall grasses and shrub on dune grassland and increase the bare sand area. The research is based on four digital orthophotos (1975, 1990, 2001, and 2009) with a high spatial resolution (pixel size 25x25 cm). The changes in the grassland classes were tested using Generalized Estimating Equations. Changes occurred, but contradicting our hypothesis, there was no significant impact derived from the livestock on all four fuzzy grassland classes within 11 and 19 years after the livestock introduction. (1) Positive and negative impacts on the grassland class were found in relation to rabbit density. (2) In some cases, changes in the aerial nitrogen deposition could explain the changes seen in grassland class condition. It appears that other factors than livestock grazing must have induced the changes observed. The high or low density of rabbits is one crucial factor, which was caused by disease and led to a significant reduction in rabbit grazing from the mid-1950s (myxomatosis) and from 1989 (RVHD). Due to the post-1990 decrease in aerial nitrogen deposition in the direction of a non-critical level in the lime rich dunes, this factor has had a reduced impact on the grassland ecosystem. From the literature, some other factors in changes in climate conditions are likely to have had an impact, (e.g. blow-outs and auto-cyclic events). But this needs more study. Three complicating factors in the overall analysis are that the start of livestock grazing was almost simultaneous with the disease-led reduction of rabbits (RVHD), the reduction of aerial nitrogen deposition and changes in climate conditions.

KEYWORDS Coastal dunes, Aerial photographs, Livestock grazing, Rabbit, Oryctolagus cuniculus L., vegetation development

Syntaxonomic nomenclature is according to Schaminée et al. (1996; 1998; 2010), Stortelder et al. (1999), and Kopecký and Hejný (1974). Taxonomy of vascular plants is according to Van der Meijden (2005), mosses according to Siebel and During (2006) and lichens according to Van Herk and Aptroot (2004).

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INTRODUCTION

Lime-rich coastal sand dunes in The Netherlands are species-rich and harbour 66% of the Dutch flora (De Vries et al. 1994). Under the Natura 2000 legislation (Council of the European Communities 1992) almost all habitats of the coastal sand dunes are protected. These habitats are a mosaic of bare sand, dune grasslands, shrubland and forests. ‘Grey dunes’, i.e. fixed coastal dunes with herbaceous vegetation, are designated as a priority habitat type (H2130) by Natura 2000 and are hotspots of plant biodiversity in dry coastal sand dunes (Kuiters et al. 2009) as rich in vascular plants as in bryophytes, mosses and lichens (Schaminée et al. 1995, 1996, 1998; Stortelder et al. 1999).

During the last five decades, the vegetation in Dutch coastal dunes has changed considerably. Patches with bare sand and open grasslands have changed into areas mainly dominated by tall grasses and sedges, shrubs and forest that has gradually led to a rather monotonous vegetation and a considerable loss of local biodiversity (Ketner-Oostra and Sýkora 2004; Kooijman et al. 1998; Veer and Kooijman 1997). These processes have been associated with several phenomena: (1) the outbreak of Myxomatosis and Rabbit Viral Haemorrhagic Disease (RVHD) in populations of rabbits (*Oryctolagus cuniculus*), (2) routine, government-led planting of Marram grass (*Ammophila arenaria*), shrubs and trees to stabilize dunes, (3) planting of shrub and tree species for mainly aesthetic reasons and wood production, (4) a high input of airborne nitrogen, (5) changes in land use, including abandonment of agricultural practices like livestock grazing and crop cultivation, (6) the impact of changes in climate conditions, (7) the growing human impact on the landscape (e.g. recreation), accompanied by a rapid spread of introduced non-native species (e.g. *Prunus serotina, Senecio inequidens*), and (8) autonomous succession (Provoost et al. 2011; Remke et al. 2009; Noordijk 2007; Jones et al. 2004; Eerens and Van Dam 2001; Drees and Olff 2001, Kooijman et al. 1998, Ten Harkel 1998; Ten Harkel and Van der Meulen 1996; Schaminée et al. 1995, 1996, 1998; Stortelder et al. 1999; Bakker et al.1974; Boerboom and Westhoff 1974; Ranwell 1960). As large herbivores were thought to counteract the process of stabilisation and monotonisation by grasses (Van Dijk 1992; Kooijman and De Haan 1995; Provoost et al. 2011) and large herbivores strongly prefer graminoid species (Lamoot et al. 2005) extensive grazing by domestic livestock was introduced in many nature reserves in The Netherlands and elsewhere.

In late 1990, year-round grazing by livestock was introduced in the coastal dunes of Meijendel close to The Hague, The Netherlands (GPS 52° 7‘N; 4° 20’E). The livestock is a mix of horses and cattle, with some species-specific impact on the dune ecosystem (Lamoot et al. 2005). The livestock density was 0.06-0.07 Large Livestock Units.ha^{-1}.year^{-1} (1:12-18 ha). According to Wallis de Vries et al. (1998) this density normally has a low level of impact on the biodiversity of natural areas. However, the level of LLU had been adjusted downwards, considering the low level of palatable biomass in coastal sand dunes (e.g. Ebrahimi 2007). Despite a predictable loss of weight during winter, a healthy survival of the animals was expected. In one year out of the 19 years of livestock grazing, a few animals did barely survive winter. This grazing impact indicator may show that, in the nutrient-poor coastal sand dunes, a relatively low LLU could still have an impact on reducing grass encroachment. By grazing and trampling, the vegetation dominated by tall grasses and sedges was expected to diminish or even to disappear to the benefit of more species-rich dune grasslands. Damaging due to tram-

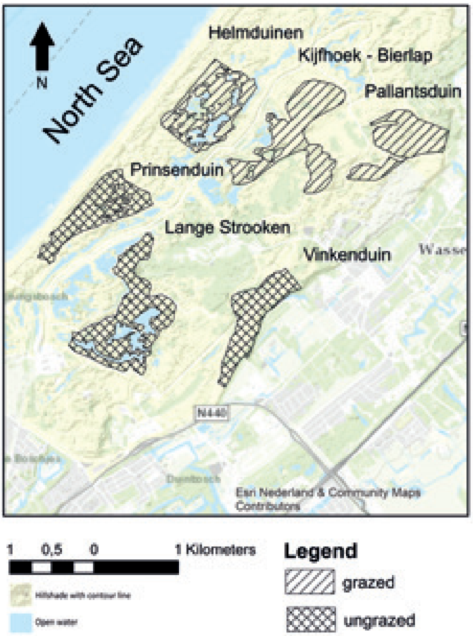


Fig. 1. The six study sites in Meijendel, The Netherlands with their area names. The three northern areas are grazed, from West to Central to East: Helmduinen, Kijfhoek/Bierlap, Pallantsduin. The three southern areas are ungrazed - from west to east: Prinsenduin, Lange Strooken, Vinkenduin. The West and Central areas are in the parabolic landscape zone; the East areas are in the inner dunes

pling was also expected to develop into sand blow-outs and hereby initiate open sandy dune grasslands. Grazing was also expected to stop the increase, and possibly cause a desirable decrease of shrubland and forest area by opening up the whole area to the benefit of species-rich dune grasslands.

The aim of this study is to evaluate effects of grazing by livestock on different grassland types of the dry dune with fuzzy image interpretation techniques, by comparing the changes in grazed areas with control areas in the same landscape ecological zones (Van der Meulen et al. 1985). The hypothesis of this study is that the presence/absence of livestock will lead to a sharp reduction of the grass-encroached vegetation type (associated with tall grasses and sedges) and an increase of relatively open sandy dune grasslands and closed species-rich dune grasslands partly, due to the opening up of shrubland. This study focusses on the changes in areas covered with five grassland types, by comparing three livestock-grazed areas and three ungrazed controls within the coastal dunes of Meijendel, The Netherlands.

Area of investigation

The dunes of Meijendel are a well-known and highly valued example of the lime-rich dune landscape of the Atlantic coast (Janssen and Schaminée 2003; Van der Meulen and Van der Maarel 1993). Meijendel covers an area of approximately 1,800 hectares (Van der Meulen et al. 1985). Van der Meulen et al. (1985) distinguished four landscape ecological zones running more or less parallel to the coast with increasing distance from the sea: (i) Fore Dunes; parallel sandy dune ridges mainly with Marram grass, which was extensively planted for stabilisation purposes as a coastal defence measure, (ii) Parabolic Dunes; lime-rich dunes with a pronounced relief (2-20 m) and small moist dune valleys in between. The drier dunes are covered with mosaics of bare sand, pioneer grasslands (predominantly southern exposures), closed grasslands (predominantly northern exposures) and shrublands of Sea Buckthorn (*Hippophae rhamnoides*) and other woody species; it is also the zone utilised for artificial groundwater recharge for drinking water production (Fig. 1; open water), (iii) Large Dune valleys; decalcified grasslands and deciduous woodlands where tree species like *Betula*, *Crataegus* and *Quercus* dominate, which in the 19th century were partly flattened and used as arable land, and (iv) Inner Dunes; in general higher dunes (5-35 m) with less pronounced parabolic and rolling dunes. The topsoil is partly decalcified and supports dune grasslands with short grasses, mosses and lichens, open *Hippophae* shrubland and forest patches. Occasional sand blow-outs generate a mosaic with grasslands richer in lime.

MATERIAL & METHODS

Aerial images

Along the Dutch coast, sequential mapping of aerial photographs has shown drastic changes in vegetation cover (e.g. Van Dorp et al. 1985; Kruijsen et al 1989; Van Til and Mourik 1999; Janssen 2004), but in complex systems like coastal sand dunes, manual and especially manual sequential mappings have their limitations (Janssen 2004; Assendorp 2010). Drawing lines between vegetation types in discrete landscapes with crisp (sharp) boundaries is relatively easy. But in a landscape with fuzzy spatial transitions between vegetation types, such as coastal dunes where every metre can be different to the next, the interpretation of vegetation types is dependent on personal interpretation (Janssen 2004). Therefore, other remote techniques are required and used for vegetation mapping and land surveys (e.g. Campbell 2006; Groom et al. 2006; Potter 2013). Droesen (1998) and Assendorp (2010) demonstrated that geometrically and radiometrically corrected orthophotos with a high spatial resolution, largely overcome the difficulties of manual mapping.

Four sets of high-resolution false colour infrared digital orthophotos of Meijendel were available with clear time intervals: 1975, 1990, 2001 and 2009. All four were taken in the same period of the year (end June/beginning July). The years 1975 and 1990 are ±330 2 µm scanned analogue images (34x34 cm), which have been geo-referenced and radiometrically corrected to one orthophoto. The years 2001 and 2009 were direct digital recordings and also radiometrically corrected. For the technical details of orthophoto production see Assendorp (2010). The spatial data were processed in ArcGis 10.3. The accuracy of the classification of scanned analogue false colour images of 1975 and 1990 and of the digital photos of 2001 and 2009 were 80-95% as demonstrated by Assendorp (2010). This percentage is generally accepted as appropriate for a vegetation structure map (Foody 2002; Assendorp 2010). All four sets of orthophoto images were resampled to pixels with a resolution of 25x25 cm in the field. At this resolution, the objects (blowouts, scrubs and trees) consist of multiple pixels in the image. The grassland area is a continuous cover. Within the 25 cm resolution, the reflection has a fuzzy character at the sub- and superpixel level.

Based on the reflection characteristics in the feature space, the dune grasslands, as one crisp class by Van der Hagen et al. (2020), can be separated in five continues classes, which also have a continuous (fuzzy) character in the spatial dimension (Assendorp 2010). For each fuzzy grassland class, each pixel has a membership value assigned, summarized to 5 20% classes (0-20% share; 21-40%; etc.). The crisp classes have a membership value of 100%. The seven classes (five fuzzy and two crisp classes), its abiotic and biotic characterization, the processes involved and characteristic communities or species are described in Table 1 (Assendorp 2010, adapted after Assendorp and Van der Meulen 1994). For this study, fuzzy class 3 and 5 from Table 1 are combined into one class, because of the overlap in the feature space in the 2001 aerial images. As for fuzzy class 4 (high grass/moss with litter), in the false colour images it is not possible to distinguish the different grass encroaching plant species *Calamagrostis epigejos, Carex arenaria* and *Ammophila arenaria*.

Table 2 gives the producer's and user's accuracy of the crisp (cc1; cc7) and five fuzzy classes (fc2-fc6). The accuracies of the fuzzy classes are sometimes substantially lower than the accuracy of the crisp classes, but are good or compliant to regular standards regarding other studies (Assendorp 2010; Groom et al. 2006; Acosta et al. 2005; Bock et al. 2005). Note that for fc2 in 2001 and 2009, the accuracy is low.

Selection of research areas

As the focus of this research is on groundwater independent dunes, dune slacks and water bodies were left out of the analysis and in the case of infiltration ponds, an extra margin of 10 metres around the ponds was excluded. Similarly, all human-disturbed open areas were left out. These include (i) areas with extraction wells for artificial recharge for drinking water production, (ii) intentionally denuded areas to stimulate blow-outs, (iii) the foreshore and Fore Dunes where grazing is prohibited, (iv) parts of the Parabolic dunes which were intentionally planted with shrubs and trees, and (v) the larger dune valleys as these valleys are an unnatural feature, and have no ungrazed counterpart. Up to 1990, over all of the Meijendel dunes, except for the Fore Dunes, compulsory plantings of Marram grass was applied by the government for protection of the land from the sea.

From West to the Central and the East, the test grazing areas are represented by the Helmduinen (43 ha), Kijfhoek/Bierlap (65 ha) and Pallantsduin (43 ha), whereas Prinsenduin (43 ha), Lange Strooken (65 ha) and Vinkenduin (43 ha) represent the ungrazed control areas (Fig. 1); in total 302 ha. The study areas are positioned within the areas of the (ii) Parabolic Dunes and the (iv) Inner Dunes (Van der Meulen et al. 1985).

In late 1990, year-round grazing with Galloway cattle and Norwegian Fjord horses was started, just after the 1990 orthophoto was taken. It was assumed that the impact of rabbit grazing on the three vegetation classes inside the six areas is equal. The rabbit population fluctuates over the years, because of variations in the impact of epidemic diseases (Myxomatosis from around 1954 and RVHD-1 from 1989, just before the introduction of the livestock). Rabbits are counted; the transects overlap large parts of the area of this research.

Statistical analysis and confounding factors

With late 1990 as the starting point of grazing, the changes in the fuzzy vegetation classes in hectares between 1975 and 1990 as well as between the test starting date of

Table 1. Description of the crisp and fuzzy vegetation classes (Assendorp 2010; Table 4.4, adapted after Assendorp & Van der Meulen 1994). The plant communities follow Schaminée et al. 1996; Stortelder et al. 1999)

CLASS	NAME	ABIOTIC AND BIOTIC CHARACTERIZATION	PROCESS (AND CHARACTERISTIC PLANT COMMUNITY/ SPECIES)	
Crisp class 1 (cc 1)	Bare sand	A 100% cover of blond aeolian dune sand with no vegetation cover and no grey sand at the surface	Active blow-out or sand paths	
Fuzzy class 2 (fc 2)	Thin grass/ herb cover with blond sand	A mixture of dominating blond sand (with negligible amount of organic matter) and pioneer plants (annuals mainly) with grasses of the clonal solitary type; tussock forming grass types can be present.	Lightly overblown with blond sand (e.g. Phleo-Tortuletum).	
Fuzzy class 3 (fc 3)	Intermediate herb/moss cover with grey sand	This type is defined by a mixture of a substantial part of grey humic sand and vegetation. Moss species dominate the plant coverage with additionally annuals and biennials and solitary and tussock grasses.	Lightly overblown with grey sand (e.g. Violo-Coryneophoretum).	
Fuzzy class 4 (fc 4)	High grass/ moss cover with litter	Defined with a lush vegetation of grasses with a certain amount of litter, dead ectorganic matter. Mainly grasses and perennial of clonal herbs cover the soil completely. Woody plants can occur on the subpixel level.	Grass encroachment	
Fuzzy class 5 (fc 5)	High moss cover	Dominated or totally covered by mosses and some lichens with some annual and biennial herbs; grasses are nearly absent.	Moss dominated Campylopus introflexus.	
Fuzzy class 6 (fc 6)	High moss and low grass cover	A mixture of mosses, herbs and grasses. Herbs and grasses are small (grazed) and woody plants can occur on the subpixel level with a developed soil profile.	Herb and moss rich dune grasslands grazed by rabbits: rabbit meadows. (e.g. Taraxaco-Galietum).	
Crisp class 7 (cc 7)	Shrubs and trees	A 100% cover of woody plants with an individual size of the plants lager than the image resolution. Presented as a crisp class it is internally heterogeneous in structure and species distribution.	Relative stable, homogeneous shrubland and heterogeneous forests (this research: mainly Hippophae shrubland).	

Table 2. Producers / users accuracy (%) of the two crisp (sand; shrubland) and five fuzzy grassland classes in the aerial photographs (non-stratified) of the four years in Meijendel. For the series of 2001 and 2009 the validation step with values from field data is included (Assendorp 2010: chapter 3) and the overall accuracy is subsequently higher

	1975	1990	2001	2009
cc1	76 / 53	77 / 100	72 / 89	68 / 100
fc2	60 / 42	65 / 54	27 / 54	33 / 43
fc3	73 / 64	75 / 55	58 / 42	79 / 68
fc4	69 / 36	73 / 31	65 / 54	68 / 45
fc5	69 / 25	66 / 29	39 / 16	68 / 22
fc6	64 / 30	67 / 30	67 57	66 / 68
cc7	58 / 98	54 / 100	89 / 98	89 / 99
Overall	62	61	76	79

1990 and 2001 and equally between the test starting date of 1990 and 2009 have each been calculated per research area in order to investigate the time-dependent impact of grazing on the outcome, while acknowledging the impact at the starting level. The interval between 1975 and 1990 is a period without large herbivore grazing. By subtracting the outcome per plot at the various times from that at the start, data are transferred into change values: the change in number of hectares covered by the various vegetation types per time interval (before and after start of grazing) per period. Two main sets of data were obtained: one with grazing and the other without (control). Subsequently the values were tested as to what extent grazing affected the relative distribution of the three types of vegetation using Generalized Estimating Equations (GEE) analysis with dummy variables (Kleinbaum et al. 1998). The analysis was performed in a stepwise fashion during which at each step, the variable with the highest non-significant outcome was removed. Subsequently the procedure was repeated until all remaining variables showed a significant association with the dependent variable (change in respective fuzzy vegetation class). The variation in the change of hectares per fuzzy class was associated with variation of various confounding factors, together with the presence or absence of grazing. Note that the livestock is a presence/absence parameter, while most other factors are variable amounts. Grazing is coded as dummy (0: ungrazed versus 1: grazed), time interval and the change in hectares over time (dummy x time). Potential confounding factors were (a) the starting values (at t=0 (in the year 1990)), (b) the relative locations in the dune area (1=West; 2=Central; 3=East; Fig. 1), (c) the rabbit numbers in the years of this research (1990, 2001, 2009) from standardized monitoring routes in grazed areas (average maximum counts of 6 routes) and ungrazed areas (of 2 routes), and (d) the total nitrogen deposition and NO_x and NH_3 as separately measured by the National Institute for Public Health and the Environment (RIVM). The RIVM data on total nitrogen deposition, NO_x and NH_3 are the nationwide average results, but are perfectly applicable for the Meijendel dunes. The regression equation (Equation 1) used was:

$$y = (a_1 x_1) + (a_2 x_2) + (a_3 x_3) + a_4 \qquad \text{Equation 1}$$

in which:
y = change in hectares per time interval
x_1 = dummy variable, taking the values 0 for ungrazed control area and 1 for grazed area
x_2 = time in years
$x_3 = (x_1) \times (x_2)$
$a_{1\text{-}4}$ = coefficients in the model.

Evaluation of the fit of the equation model was evaluated by Wald Chi-square test. GEE analyses were done using STATA, version 12 (StataCorp, College Station, Texas, US). Graphic representation was performed via GraphPad Prism, version 6 (LaJolla, CA, USA). Throughout the study, using two-sided testing, P values of 0.05 or lower were considered to demonstrate statistical significance.

For the GEE model, calculations are performed on the numbers of rabbits in specific years of this research. Rabbits are counted along monitoring transects in the light bundle of a car during twilight eight times in spring and eight times in autumn. These transects are up to two kilometres long and lie partly in the research areas as given in Fig. 1. Still, these relative rabbit numbers are a good indicative trend on the number of rabbits in Meijendel as a whole and in grazed and ungrazed parts of Meijendel specifically.

RESULTS

Changes in the fuzzy grassland classes

The six areas, three grazed since 1990 and three ungrazed, show more or less the same shifts in the overall grassland and in three of the four fuzzy dune grasslands classes (Fig. 2a, b, c, e). Only the changes in the grass encroached fc4, are different in the grazed versus the ungrazed areas (Fig. 2d). Table 3 gives the changes in hectares of the overall grassland class. In general, the same increase/decrease changes occur in grazed versus ungrazed, with two exceptions: Pallantsduin (1975-1990) and Prinsenduin (2001-2009). The statistical matrix of the GEE analysis is given in Table 4; only the significant factors (< 0.05) are given.

Changes in overall grassland classes

Fig. 2a shows the change in the overall grasslands with no difference between grazed and ungrazed, as concluded in Van der Hagen et al. (2020). Livestock presence did not explain the changes seen. We added new data series to the GEE model as possible confounding factors. The higher the NO_x deposition, as part of the total nitrogen deposition, the higher is the change in the amount of the overall grassland class ($p = 0.005$). The time factor also explains part of the changes ($p = 0.003$): the longer the period of time passed, the higher the impact of changes. In the changes to the percentage share of the overall grasslands, neither livestock nor rabbits play a significant role ($p>0.05$).

In general, Table 3 (based on Appendix 1) shows comparable changes in the amount of hectares of total dune grassland class, overall about 4.1 ha (0.3-9.9 ha). The share of changes can vary considerably from 1.2 to 55% (Table 3). Specifically, changes in fuzzy class fc3+5 (grey sand grasslands & moss dominated grasslands) and fc6 (rabbit meadows) contribute to the changes observed (Appendix 1). In the period 1990-2001, in all six areas there is an increase in the area of the dune grasslands. There are three deviations (Table 3). (1) Pallantsduin, grazed after 1990, differs from both other post-1990 grazed areas. The area of grasslands increases by 5.9 ha (30.7%). (2) In the three ungrazed areas, including 1975-1990, there is always an increase of the grasslands by 4-5 ha up to 9.9 ha.

Table 3. Increase or decrease of area of the dune grasslands (in ha) as one crisp class in the three grazed and three ungrazed research plots. Note that the 1975-1990 all six areas are ungrazed

		1975 > 1990	1990 > 2001		2001 > 2009
Helmduinen	Ungrazed	Decrease 25.1 > 24.8 -0.3 (1.2%)	Increase 24.8 > 30.1 +5.3 (21.4%)	Grazed	Decrease 30.1 > 27.9 -2.2 (7.3%)
Kijfhoek-Bierlap	Ungrazed	Decrease 32.8 > 30.3 -2.5 (7.6%)	Increase 30.3 > 39.4 +9.1 (30.0%)	Grazed	Decrease 39.4 > 36.9 -2.5 (6.3%)
Pallantsduin	Ungrazed	Increase 19.2 > 25.1 +5.9 (30.7%)	Increase 25.1 > 29.5 +4.4 (17.5%)	Grazed	Decrease 29.5 > 26.9 -2.6 (8.8%)
Prinsenduin	Ungrazed	Increase 21.2 > 24.5 +3.3 (15.5%)	Increase 24.5 > 34.4 +9.9 (40.4%)	Ungrazed	Decrease 34.4 > 29.0 -5.4 (15.7%)
Lange Strooken	Ungrazed	Increase 28.3 > 31.6 +3.3 (11.7%)	Increase 31.6 > 35.9 +4.3 (13.6%)	Ungrazed	Increase 35.9 > 37.8 +1.9 (5.3%)
Vinkenduin	Ungrazed	Increase 13.3 > 20.6 +7.3 (54.9%)	Increase 20.6 > 22.7 +2.1 (10.2%)	Ungrazed	Increase 22.7 > 23.7 +1.0 (4.4%)

Table 4. Statistical matrix of the Generalized Estimating Equations (GEE) analysis and the following stepwise regression analysis checking confounding factors of the overall grassland class (total) and the fuzzy (grassland) classes fc2-fc6. The number of observations is 12. Note that livestock never explains the changes seen

	TOTAL	FC2	FC3 + FC5	FC4	FC6
F	12.68	11.08	19.84	11.01	10.45
p	0.001	0.001	0	0.001	0.005
R^2	0.63	0.6	0.73	0.59	0.40
adj. R^2	0.58	0.54	0.69	0.54	0.36

NOx	0.005				
Time	0.003				
Start		-0.007			
Interaction			0.0009		
NH_3				-0.003	
rabbits		0.018	-0.0009	-0.001	0.005

Prinsenduin is the exception with a decrease of 5.4 ha of grasslands in the period 2001-2009. (3) In the period 2001-2009, there is a consistent decrease of the total grassland class in the grazed areas by 2.5 ha (7.5% on average).

Thin grass/herb cover with blond sand: fc2

The fc2 class, with plant communities on blond sand like *Phleo-Tortuletum*, slightly decreases in the first and second period (1975-1990 and 1990-2001; Fig. 2b). In the period of 2001-2009, this class increases, with one exception (Lange Strooken; Appendix 1). The outcome of the GEE model is that rabbits have a significant positive effect on the changes observed ($p = 0.018$). Livestock has no role in these changes. In 1990 ($t=0$) there is a difference in the amount of presence in grazed versus ungrazed areas. The higher the presence in 1990, the lower the increase.

Intermediate herb/moss cover with grey sand + high moss cover: fc3+5

In 2001, eleven years after the introduction of livestock, there is a substantial increase of the herb/moss cover with grey sand & moss-dominated fuzzy classes (Fig. 2c, Appendix 1). This occurs as well in the grazed as in the ungrazed areas; livestock grazing has no influence on this process (Table 4). In the period 2001-2009, the fuzzy classes fc3+5 generally decreases again and it falls back to its size in 1975 (Central areas Kijfhoek/Bierlap and Lange Strooken) or 1990 (the four others). The GEE model shows that rabbits have a negative impact (p = -0.0009). The more rabbits present, the less the cover of this fuzzy class fc3+5. Fig. 2c also shows that the changes in the grazed areas is systematically higher than in the ungrazed areas. There is no impact on the results because of the starting point 1990 (t=0).

High grass/moss cover with litter: fc4

Grass encroached dune grasslands with a high amount of dead organic matter (litter) are a constant and substantial part of the grassland ecosystem in all six areas despite the introduction of livestock (Appendix 1). In the false colour photo images it is not possible to distinguish between the different grass encroaching species: *Calamagrostis epigejos*, *Carex arenaria* and *Ammophila arenaria*. The hypothesis was that livestock grazing would decrease fc4. In all six areas, this fuzzy class has increased its presence in the period 1990-2001 either in livestock grazed or ungrazed areas (Fig. 2d), though the increase is larger in the ungrazed Prinsenduin (Appendix I). In the last period 2001-2009, in the grazed areas fc4 decreases whilst in the ungrazed areas, on the average fc4 persists (Fig. 2d). More into detail, fc4 increases substantially in the ungrazed Lange Strooken and slightly decreases in ungrazed Prinsenduin (Appendix 1). The outcome of the GEE model shows that there is a significant negative correlation between the presence of rabbits and this fuzzy class fc4 (p = -0.001), as well as for the NH_3 deposition (p = -0.003). Both factors, separately as well as together correlate with the changes observed.

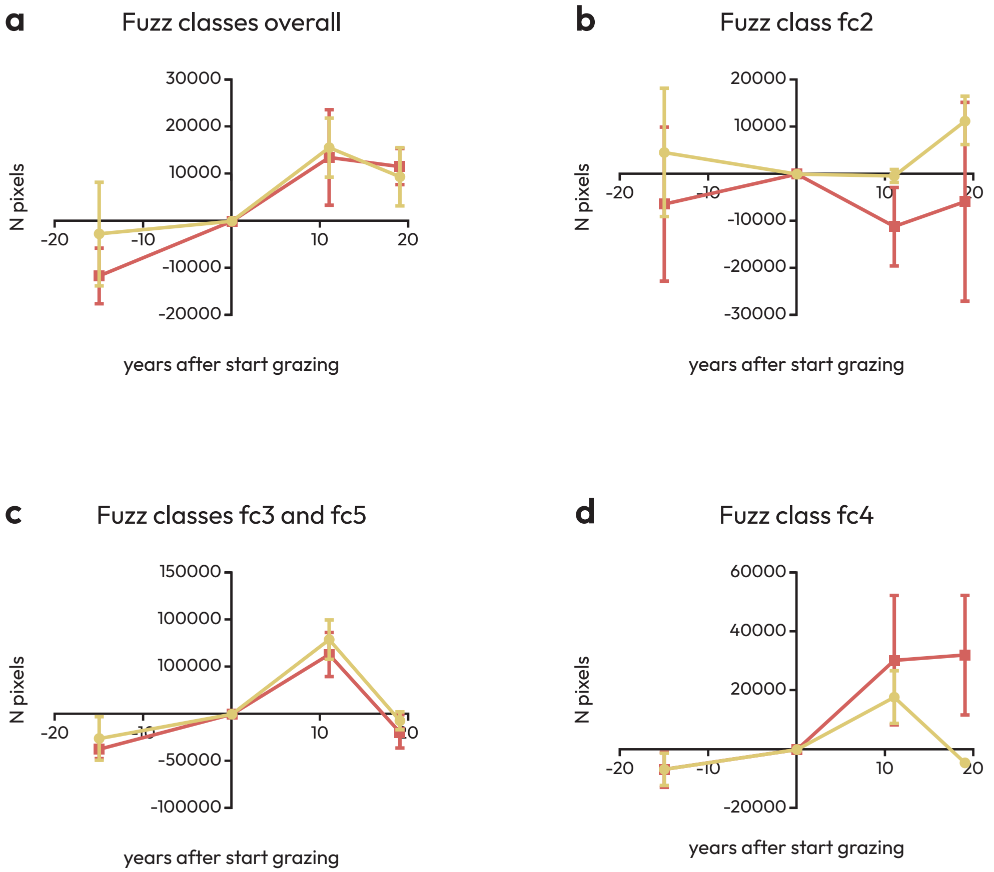
High moss and low grass cover (rabbit meadows): fc6

The hypothesis was that this fuzzy class (e.g. *Taraxaco-Galietum*; Table 1) would improve due to the livestock replacing rabbit grazing. In all six areas, there is a decrease in the period 1975-1990 (all ungrazed; Fig. 2e) except for Prinsenduin (Appendix 1). Also in the period 1990-2001 (Fig. 2e), there is a considerable decrease of fc6 in all six areas, whether in livestock grazed or ungrazed areas. In the period 2001-2009, there is a similar increase of fc6 in all six areas (Fig. 2e). After 2001, this results in a considerable increase. Nineteen years after the introduction of livestock the share of fc6 is even larger than in all preceding years (Appendix 1) with no difference between livestock grazed and ungrazed areas. The outcome of the GEE model shows that the only significantly correlating factor for the changes seen, is the presence (absence) of rabbits (p = 0.005). If the rabbits increase, this grassland type, rich in small palatable grasses and herbs, increases as well. Livestock is not a significant factor.

DISCUSSION

Changes in the dune grasslands, grazed versus ungrazed

Towards the end of 1990, livestock grazing started. Van der Hagen et al. (2020) showed that the changes across the three crisp classes: bare sand, dune grasslands (Fig. 2a) and



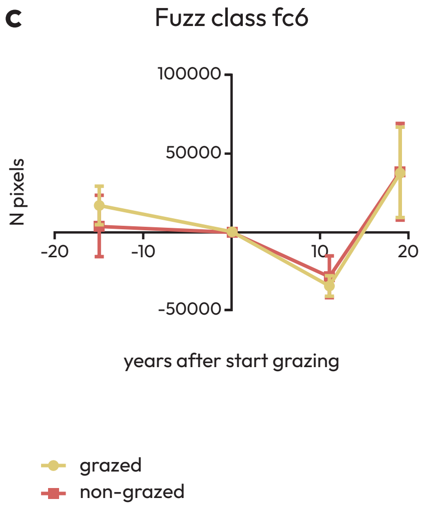


Fig. 2. Changes in hectares in relation to the year 1990 of the fuzzy classes (overall, fc 2, fc3 & fc5, fc4, fc6) area cover in hectares; mean +/- 1 x standard deviation of three grazed and three ungrazed areas. (a) Changes in the years from t=0 (1990) in the overall fuzzy class of the grasslands. (b) Changes in the years from t=0 (1990) in the fuzzy class fc2. (c) Changes in the years from t=0 (1990) in the fuzzy class fc3&5. (d) Changes in the years from t=0 (1990) in the fuzzy class fc4. (e) Changes in the years from t=0 (1990) in the fuzzy class fc6

Fig.2a. Changes in relation to the year 1990 of the fuzzy classes overall

Fig. 2b. Changes in relation to the year 1990 of class fc2

Fig. 2c. Changes in relation to the year 1990 of class fc3 & class fc5

Fig. 2d. Changes in relation to the year 1990 of class fc4

Fig. 2e Changes in relation to the year 1990 of class fc6 shrubland in the three grazed and the three ungrazed areas are statistically not different. Based on the statistics of our data, livestock grazing did not seem responsible for the changes observed in the three crisp classes ($p > 0.05$). For the evaluation of four fuzzy grassland classes (fc2, fc 3+5, fc4, fc6), rabbit numbers and nitrogen deposition rates were included as possible confounding factors. These two factors might also explain the changes in the total grasslands classes (Fig. 2a) as well as in the four fuzzy classes individually (Fig. 2b-e). The statistical matrix of the GEE analysis is given in Table 4.

Dune grasslands are a shorter or longer lasting succession phase in the dune ecosystem ‘squeezed’ in between the changes from bare sand up to the development of shrubland and/or forest (Assendorp 2010). We found that the changes in the four fuzzy grassland classes are independent of the introduction of livestock. In the GEE model, livestock presence does not explain the changes in none of the four fuzzy classes. In all four fuzzy classes, the high or low presence of rabbits partly explains the changes observed, consistent with Moulton et al. (2019). Sometimes nitrogen deposition can play a role.

Changes in overall grassland class

In the period 1990-2001, there is an increase in all six areas of dune grasslands (Table 3) whether grazed or ungrazed. As a result of the 1954 outbreak of myxomatosis, about 90-95% of the rabbit population died (Drees and Olff 2001). The large scale reduction by rabbits of the highly palatable young shoots of trees and shrubs stopped (e.g. *Crataegus*: Van Groenendael et al. 1982; Salman and Van der Meijden 1985). The myxomatosis outbreak led to a window of opportunity for trees and shrubs. Apart from the consumption of palatable shoots, rabbits are in this way capable of holding back the expansion of shrubland (Smit and Ruifrok 2009). The 1990-2001 expansion of grasslands is due to the collapse of *Hippophae* shrubland, which were at the end of their lifespan of around 40 years after the Myxomatosis outbreak in 1954 (Van der Hagen et al. 2020). Due to the acidification of the topsoil during the lifespan of *Hippophae* and the entry of light-sensitive grasses (Van der Hagen et al. 2020), the fuzzy class fc3+5 and the grass-encroached fuzzy class fc4 expanded as part of the total grassland class.

In the period 2001-2009, in all three livestock grazed areas, the amount of grassland decreases, as well as in the ungrazed Prinsenduin (Table 3). Rabbits are not a factor in the changes seen in the crisp overall grassland class. Rabbits have their specific influence in parts of the grassland ecosystem. More specifically, they have a positive correlation in fc2 and fc6 and a negative correlation in fc3+5 and fc4 (see below).

For the three livestock grazed areas, NO_x and time are factors to consider (Table 4). In general, in the pre-industrial period the amount of nitrogen deposition was around 6-8 $kg.ha^{-1}.yr^{-1}$ (Remke et al. 2009; Dorland et al. 2011) and in dunes at even lower levels of

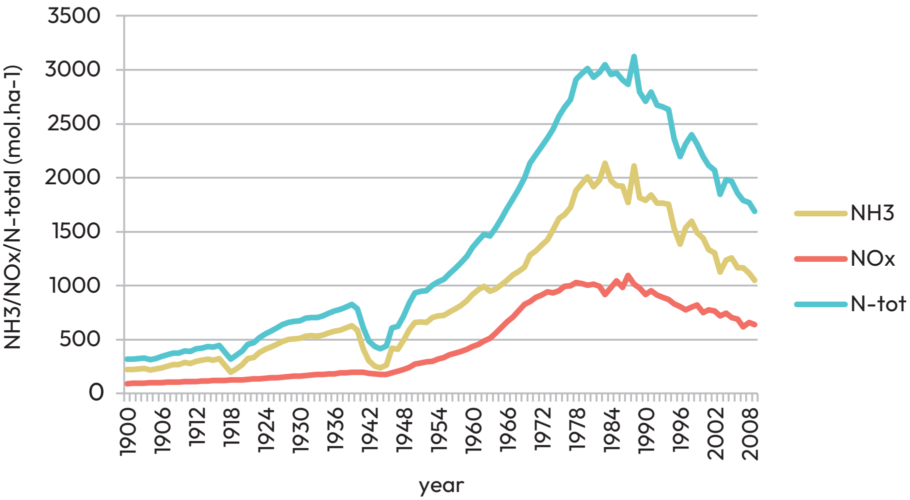


Fig. 3. Development of the nitrogen deposition in mol.ha^{-1}.yr^{-1} in the Netherlands from the year 1900 up to 2009. Notice a dip during the First and Second World Wars and the peak around 1990

around 2 kg.ha^{-1}.yr^{-1} (Fowler et al. 2004; Kooijman et al. 2017) with a slow increase from 1900 up to 1960. After 1960, the nitrogen deposition accelerated with its peak around 1990 of around 35-40 kg. ha^{1}.yr^{-1} (Hey & Snijder 1991). This coincided with the collapse of the rabbit population in Meijendel due to RVHD in 1989. Due to industrial control measures taken, the nitrogen deposition slowly decreased to around 15 kg. ha^{-1}.yr^{-1} (Fig. 3) (Noordijk 2007, RIVM dataset; Kooijman et al. 2017), but this amount is still higher than the critical load of 10 kg. ha^{-1}.yr^{-1} that is acceptable for the fc3 component of the fc3+5 fuzzy class (*Violo-Corynephoretum*), which is the most critical dune grassland in the Meijendel ecosystem (Bobbink et al. 2010). This fuzzy class fc3+5 overall increased in the period 1990-2001, pushing the grassland area as a whole to its maximum extent over the 1975-2009 period. However, the growth was not all positive and the fuzzy class fc3+5 area reduced in 2009 to its 1990 level (except Lange Strooken) reducing the whole crisp grassland class to a lower level of presence. Nitrogen deposition from NO_x correlates positively with the changes in the crisp grassland class (Table 4), but despite the correlation between NO_x and the changes observed, we have no consistent explanation for all these changes.

Thin grass/herb cover with blond sand: fc2

The plant communities linked with this fuzzy class (e.g. *Phleo-Tortuletum*) thrive under a thin cover of lime-rich blond sand. Since 2003, the lime-rich part of the coastal dunes of the Netherlands had a significant increase of blow-outs from an average of 26 up to 82 blow-outs per km^2 in the province of Zuid-Holland, of which Meijendel is an important part. For the whole of the Dutch coast the average is 1.9 blow-out per km^2 (Aggenbach et al. 2018). A combination of factors are likely to be responsible: higher maximum heights of the dune system, more profitable orientation to the coastline, more rainfall and wet days, higher lime content in the sand, more rabbits and a reducing nitrogen deposition nearing the critical load (situation 2014) (Aggenbach et al. 2018). In the pre-1990 situation, a continuous stabilisation of bare sand by Marram grass was a common feature in coastal dunes (Jungerius and Van der Meulen 1997; Van der Hagen et al. 2020). The increase of fc2 between 2001 and 2009 is due to the natural reactivation of blow-outs, which started in this period (Aggenbach et al. 2018), leading to deposition of thin layers of blond lime-rich sand where species of the *Phleo-Tortuletum* (see Table 1) thrived. It is logical that this was seen to occur in all six areas, since the return of blow-outs is irrespective of livestock grazing (Van der Hagen et al. 2020). The exception is Prinsenduin, where there was a large blow-out in 1983 and a highly effective afforestation process due to invading *Populus canescens* as root-shoot shrub. This species extends its root system by meters yearly mainly into open dune grassland like the class fc2.

Although in 1989 RVHD further reduced rabbit numbers considerably, rabbits were also seen to play an important and indirect role in the increase in blow-outs resulting in a positive correlation of rabbits and fc2 in the GEE model. Aggenbach et al. (2018) show a parallel development of rabbit numbers and the changes in aeolian processes, which was also the case at the end of the 1970's and beginning of 1980's (Jungerius and Van der Meulen 1997).

In between 2001 and 2009 several climate extremes occurred which did not happen in the period of 1975-2001 (with the exception of 1976 with its extreme long summer drought). In 2003, 2006 and 2007 there were heat waves resulting in severe drought. Wind power by itself seems of no significance (Aggenbach et al. 2018), but the stormy winters of 2005 and 2007 might have promoted sand movement in already existing blow-outs. In 1990, at the start of livestock grazing, the amount of existing fc2 is negative correlated with the change. This might mean that there is a maximum area of blow-outs resulting in a maximum of fc2 in the ecosystem. The more fc2 at the start, the less the growth can extend to that maximum. Also wet days are significantly correlated with blow-out initiation due to water erosion on (steep) slopes. Only in the case of heavy overgrazing, livestock grazing stimulates the start of blow-outs (Aggenbach et al. 2018).

But there are indications that climate induced blow-out formation may be repetitive over time and blow-out occurrence maxima are auto-cyclic events. González-Villanueva et al. (2013) mention a repetitive fixation and remobilization of the dunes of the Targa region in Spain. Also Gares and Nordstrom (1995) present data on the cyclic evolution of blow-outs along the New Jersey coasts, mentioning a four-stage pattern from formation to closure over 20 years. Sawakuchi et al. (2008) link the autonomous formation of blow-outs inducing wind extremes along the Brazilian coast. Blow-out formation is generally associated with increased wind speeds caused by the onset of cold fronts. For North-western Europe, the return of negative phases of both the North Atlantic Oscillation, the Arctic oscillation and the East Atlantic Mode can be responsible for cold fronts. A study by Van Rooijen et al. (2022) suggests, that the occurrence of open grassland vegetation in the dunes of Meijendel, based on NDVI (Normalized Difference Vegetation Index)-observations over 13 years, coincide with sea level fluctuations of the North sea. Seip & Grøn (2019) found an auto-cyclical pattern of ocean and sea oscillations of ca. 21 years. This is consistent with the sea level cycle (20-24 years) observed along the Dutch coast, which may be a factor of significance in promoting circumstances for increased aeolian activity. If these factors are indeed the key in promoting favourable conditions for open sand and open grassland vegetation, these factors will have an important interaction with the success (or lack of success) of measures taken to promote open vegetation, such as the introduction of livestock or artificial blow-out initiation. The success rates of these measures may be increased by incorporating these more-or-less predictable factors in dune management schemes, and at least to consider when to initiate a management measure.

Intermediate herb/moss cover with grey sand + high moss cover: fc3+5

Two processes interact here. First, due to rabbit grazing, the correlating factor in the GEE model, grass-encroached grasslands (fc4) change into moss-dominated grasslands (fc3+5). The mosses are already present in between the moist grass tussocks (e.g. in between the tufts of *Calamagrostis epigejos*). Second, the expansion of *Hippophae* from 1954 onwards due to myxomatosis leads to increased cover of *Hippophae*. Around 1990, towards the end of its lifespan of 35-45 years, the shrubs open up and subsequently collapse from the centre (Van der Hagen et al. 2020). This collapse of shrubland leads to two grassland types: open grassland communities with grey sand (fc3+5) and grass encroachment with litter (fc4) more specifically grass encroachment by *Calamagrostis epigejos* with litter. This process occurs in 1990-2001 period, irrespective of livestock. The organic matter content in the soil of *Hippophae* shrubs is low (Oremus and Otten 1981), but the soil is more acidic in the top layer. Fc3+5 is prevailing in the more acidified parts of the dune, but is also present in the originally lime-rich western part of the dune system, and specifically when *Hippophae* shrub is opening up. Another factor stimulating acidification in the western part is the pre-1990 Marram grass stabilisation activities that serves to prevent any blow-outs. Only in a few cases *Hippophae* shrubland does change into taller shrubs such as communities of the *Rhamno-Crataegetum* (Van der Hagen et al. 2020).

In the period between 2001-2009, the fuzzy class fc3+5 generally falls back to the 1975 or 1990 situation, but with the *Hippophae* shrubland being partly collapsed, the grey sand

and moss dominated communities of fc3+5 stay a dominant feature in the grassland ecosystem (Appendix 1). In the eastern part of the dune area with overall topsoil acidified soils, a substantial part of fc3+5 might consist of moss carpets of *Campylopus introflexus*, which is an already existing and persistent species there (Van der Meulen et al. 1985). The significant negative correlation between fc3+5 and rabbits can be explained as follows. Part of the food of rabbits consists of plant roots, whose removal causes some openness in the deeper lime-rich parts of the soil. Given time, this leads to small blowouts and a shift in fuzzy class type. As a direct effect of rabbits, fc2 and fc6 might also increase as they also profit from the collapse of *Hippophae* shrubland. After the re-entry of Red Fox (*Vulpes vulpes*) in the mid 1970's, rabbits shifted their burrows from open grasslands to the safety of the *Hippophae* shrubland (Dekker et al. 2022). After the collapse of the *Hippophae* shrub, rabbits were therefore forced to leave the area. Large clusters of burrows with open sand are exposed to the wind, which might lead to bare sand, and around it, the fc2 grassland class. Also due to the burrow making, these acidified top-soils turn lime-rich, which are suitable for as well fc2 as fc6 grassland classes. Both factors are likely to lead to a reduction of fc3+5 and specifically an increase of fc6 (oral comm. Q.L. Slings).

The fact that area of fc3+5 is consistently higher in the grazed areas (Fig. 2c) means that the changes are positive in the livestock grazed areas, which might be a result of livestock grazing (facilitation of rabbits being the major factor in the changes observed), but this is not confirmed by the GEE model. Maybe it is not the grazing directly, but disturbance by livestock of the fc3+5 grassland class that plays a role.

High grass/moss cover with litter: fc4

There is a parallel development of fc4 in the first period 1975-1990, a situation with all six areas ungrazed by livestock. After the 1990 introduction of livestock, the share of fc4 increases as well in the livestock ungrazed as livestock grazed areas (Fig. 2d). This does not seem logical (Kohyani et al. 2011), but is argued for two reasons. In the first place, as mentioned in the paragraph above, the on-going collapse of *Hippophae* shrubland leads to an increase of grass-encroached grasslands with litter (fc4) inside the remnants of this shrubland. On the other hand, rabbits are capable of grazing these grass-encroaching grasslands. The rabbits were drastically reduced by RVHD-1 around 1989, just before the introduction of the livestock. Around 2002, rabbit numbers increased again with a lower increase in the livestock ungrazed areas (Fig. 4), with a subsequent effect on grasslands in the grazed and ungrazed areas. This study covers the period 1975-2009; after 2009 the rabbit numbers increased to a higher number in the ungrazed area than in the grazed area (not in Fig. 4). This study shows that there is a negative relationship between the numbers of rabbits and grass encroachment. This means that with higher numbers of rabbits, the extent of the grass-encroached fc4 area is reduced. So, rabbits have a functional role in counteracting grass encroachment. They are capable of reducing the extent of grass-encroached vegetation and change it into a vegetation type with herbs and mosses and lichens on grey sand (fc2). In due course, increased rabbit burrows and root digging and scrapes by rabbits are likely to change the system into a lime-rich top layer, promoting fc2 and fc6.

In the period 2001-2009, the average share of grass-encroached grassland (fc4) remains high in the three livestock ungrazed areas, whilst in the three livestock grazed areas, fc4 reduces considerably. The first assumption is that livestock must be the cause behind this difference (Kohyani et al. 2011). Close examination of the results reveals a different explanation. The anomaly can be seen in the period 2001-2009 when even the ungrazed Prinsenduin shows a decrease of grassland area similarly to the three grazed areas and unlike the two ungrazed areas (Table 3; Appendix I). This table shows that in the Prinsenduin the amount of the grass-encroached grassland fc4 is reduced just as in the livestock grazed areas. To the contrary, in Lange Strooken the amount of fc4 increases due to afforestation by invading *Populus canescens* as root shoot shrubs (see also fc2). This means that another factor than livestock must explain the changes observed. Increasing rabbit numbers, especially in the grazed (Fig. 4) and in the western areas with more palatable food for rabbits is likely to explain this dissimilarity. Ongoing research on rabbit vitality in relation with viral diseases due to food quality is hopefully providing some answers (Dekker et al. 2022).

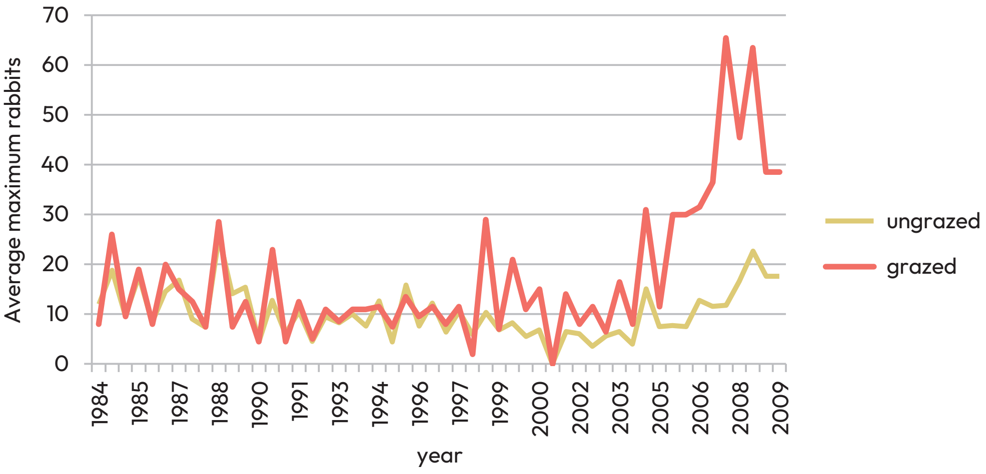


Fig. 4. Average maximum counts of rabbit numbers in spring and autumn alternately per year in livestock grazed (6) and ungrazed (2) routes in Meijendel 1984-2009. Spring 2001 had no data due to Foot and Mouth Disease; all grazed areas were closed. Data Dunea

The changes observed also have a significant negative correlation with NH_3 changes; the higher the NH_3 deposition, the lower the changes in fc4 and the other way around, the lower the NH_3 deposition rate, the greater the increase in fc4. A reduction of NH_3 since 1990 should have the same type of effect on all six areas, but they do not react in the same way. This difference between the grazed and ungrazed areas is not easy to explain, given all the studies on nitrogen deposition and grass encroachment (e.g. Kooijman et al. 2009; Kooijman et al. 2017). We have no sound explanation for this correlation, or for the combination of the impact of rabbits and NH_3 deposition.

High moss and low grass cover (rabbit meadows): fc6

From 1975 up to 2001, the decrease of fc6 in each sampled area is in line with a general decline of this grassland type in all lime-rich dune areas along the Dutch coast. There are changes into grass encroached grasslands (fc4) and in larger quantities into fc3+5, which originated from the general collapse in *Hippophae* shrubland. In the first period 1975-1990 this change is logical, because all six areas are ungrazed by livestock. In the period of 1975-1990, there is one exception: Prinsenduin (Appendix I): where there are fc6 increases. In this pre-RVHD period, rabbits appear to have had a larger influence in Prinsenduin, followed by a steep decline in rabbit populations in 2001 that took the fc6 increases back to a comparable level as in the other areas. After 2001, the situation in Prinsenduin returned to the 1990 situation and to the same extent as in the other ungrazed areas (Lange Strooken and Vinkenduin).

In the period 1990-2001, the dramatic decline of fc6 is present in all six areas, irrespective of livestock grazed or ungrazed (Appendix 1). Two factors might explain that decline. It might be a lag effect of the nitrogen deposition and a rather slow reestablishment of rabbits after the 1989 RVHD-1 catastrophe.

Initially, the rabbits have difficulties regaining their highly palatable grasslands fc6 (also known as rabbit meadows) from grass-encroached fc4. Around 2002, as the impact of RVHD-1 has reduced, the rabbit population started to grow again (Fig. 4). Due to rabbit activities of grazing, root digging and making scrapes, the fuzzy class fc6 returned. From 2001 to 2009, fc6 shows a large increase in all six areas and this fuzzy class returns to an even larger area than in 1975. It appears that the higher the number of rabbits, the larger the presence of fc6. In lime-rich dunes there has been no extra accumulation of nitrogen in the organic profile due to nitrogen deposition (Aggenbach et al. 2017) and due to the fixation of phosphates as calcium phosphates. In addition, there has also been a reduction of the nitrogen deposition down to the critical deposition level of these dune grasslands. It is considered that the system shifts back to open species rich grassland communities (fc6) with the presence of enough rabbits. Livestock has no significant correlation with the changes seen, but it does not mean that there is no impact.

Fuzzy class interpretation

The semi-automatic interpretation of fine scale false color aerial photography was in the 1990's a relative new technique. The development of DICRANUM (Assendorp 2010) for coastal sand dunes has a (high) producers and users accuracy compared with the classical interpretations done for vegetation mapping (Table 2; Assendorp 2010; Janssen 2004). Only the series of fc2 in 2001 and 2009 and of fc5 in 2001 have a low producers/users accuracy. In the last case, for this study fc3 and fc5 (always a very small presence in the Meijendel dunes) was combined to form fc3+5. As for fc2, the difference between the years 1975 and 1990 on the one hand and 2001 and 2009 on the other is a difference between flying techniques. The first series were hard copy slides processed to one orthophoto; the last series were direct digitally flown photographs. In the last case, the differentiation between strictly bare sand and fc2 is less easy to be made sharply. The conclusions on fc2 in the flights of 2001 and 2009 are less clear than of the other fuzzy and the crisp classes, but in line with Van der Hagen (2020) as a consequence of more blow-outs.

Complicating factor

1990 was a crucial year with all the changes taking place. It was not only the year of the introduction of livestock in Meijendel. It was also the year after the 1989 outbreak of RVHD, as well as being close to the peak of the nitrogen deposition. These factor are likely to be intertwined. The GEE model explains the impact of different factors to different fuzzy classes, but livestock presence is in not any of the changing classes a significant factor. This does not mean, that there is no relation between these three factors or that grazing has no impact at all (Lamoot et al. 2005; Kooijman et al. 2017).

CONCLUSIONS

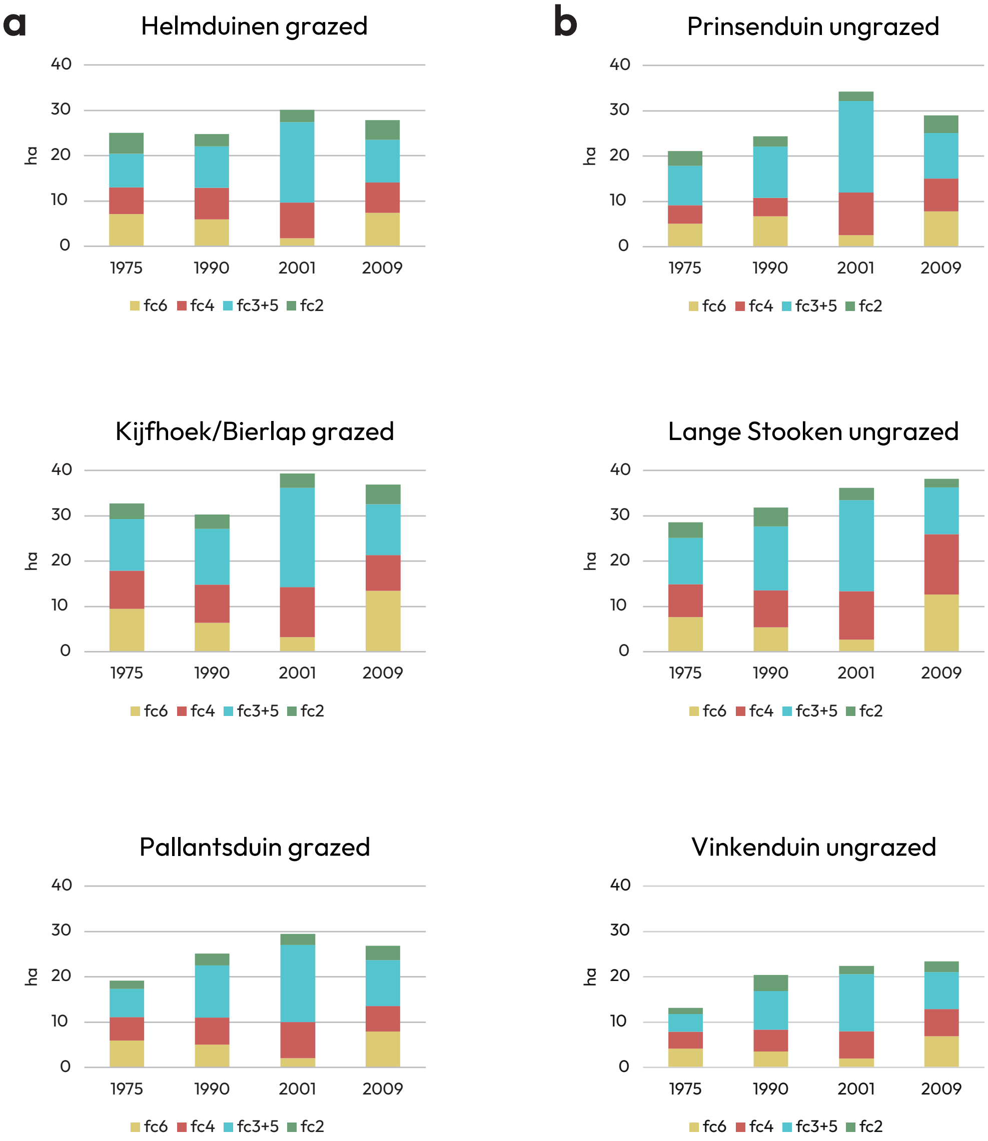
In none of the grassland fuzzy classes does the presence of livestock (at a density of 0.06-0.07 LLU.ha^{-1}.year^{-1}), explain the changes seen from 1990 onwards. However, changes in the number of rabbits and in nitrogen deposition levels (whether NO_x or NH_3) correlate with the changes in the fuzzy classes in the lime-rich dunes of Meijendel. Rabbits are selective in their use of the dune grasslands, but have a high impact when present, especially in high numbers (Moulton et al. 2019). Fuzzy types of 'Thin grass/herb cover with blond sand (fc2)' and 'High moss and low grass cover (rabbit meadows) (fc6)' both increase when rabbit numbers increase. Fuzzy type 'Intermediate herb/moss cover with grey sand (fc3+5)' and 'High grass/moss cover with litter (fc4)' decrease when rabbit numbers go up. In the case of NO_x, the higher the deposition levels, the greater the change in the amount of the overall grassland class is, and specifically the fc3+5 class. The higher the NH_3 deposition, the lower level of change in the 'Grass encroached fuzzy class fc4'. Sound explanations for these interactions are not easy to give, because nitrogen deposition has an equal impact over Meijendel as a whole, but may be having a different impact closer to the sea compared to the east part of the dune with more topsoil acidity.

The hypothesis of this study was that the introduction of livestock would lead to a sharp reduction in the vegetation type of tall grasses and sedges (fc4), an increase of relative open sandy dune grasslands (e.g. fc2) and dune grasslands (fc6) after livestock effected an opening up of shrubland. Concerning the livestock densities applied, this hypothesis must be rejected. Other densities might lead to different results.

Rabbits are crucial actors across the whole coastal sand dune ecosystem and these grazers react to the four fuzzy classes in a specific way with a high correlation to the GEE model. Also the interaction of rabbits, directly or indirectly, is closely related to the development of the shrubland of *Hippophae* (Van der Hagen et al. 2020). For this fuzzy class interpretation, we added rabbit numbers and nitrogen deposition as extra factors to explain the changes. Adding climate parameters to the GEE model, more correlations may be found between the changes of these four fuzzy classes and possible climatic factors. Natural processes like sand dynamics in combination with changing climate conditions (Aggenbach et al. 2018; Van der Hagen et al. 2020) are likely factors in provoking some of the other changes observed, overruling any impact from livestock grazing, which may still be present, but is not proven with the data presented.

ONLINE APPENDIX TABLES

Share in m² of four fuzzy grassland classes in the four years (1975-1990-2001-2009) of the six research plots, (A) three grazed, and (B) three not-grazed. The total research area is 43 ha for Helmduinen, Pallantsduin, Prinsenduin and Vinkenduin, and is 65 ha for Kijfhoek/Bierlap and Lange Strooken



Chapter 4

Assessing the impact of livestock grazing using permanent plot data from the coastal dunes of Meijendel, The Netherlands

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ABSTRACT

The vegetation of coastal sand dunes is characterized by a high species diversity and comprises some of the rarest vegetation types in Europe. Dune grasslands include particularly species-rich plant communities and are a priority habitat under the Natura 2000 legislation. At the end of 1990, livestock (Galloway cows and Nordic Fjord horses) was introduced in Meijendel to change the monotony of the vegetation and counteract grass and shrub encroachment as well as stimulate areas of bare sand (the last to be achieved through trampling by the animals). Previously, in the 1950's, 41 permanent plots had been set up to study vegetation succession in the dry dunes of Meijendel, the Netherlands. This long-term research, repeated every four years on average, was set up to evaluate the impact of artificial recharge for drinking water production and the development of grasslands and forests in the area. Up to 1990 there was more or less an equilibrium between progressive and regressive succession, but after 1990 there was a clear shift towards progressive succession. The pronounced shifts in succession are, however, not related to the later introduction of livestock. The 1954 myxomatosis outbreak, and probably also the 1989 RVHD-1 outbreak seem the most plausible cause, apart from or together with other factors, like changes in nitrogen deposition and climate condition parameters.

KEYWORDS Coastal dunes, livestock, European rabbit, Oryctolagus cuniculus L., vegetation development

Syntaxonomic nomenclature is according to Schaminée et al. (1996; 1998; 2010), Stortelder et al. (1999), and Kopecký and Hejný (1974). Taxonomy of vascular plants is according to Van der Meijden (2005), mosses according to Siebel and During (2006) and lichens according to Van Herk and Aptroot (2004).

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We thank Dunea for financing this study, and Georgette Leltz in particular for stimulating innovative research answering a practical question on grazing by livestock. We thank Jan Boerboom particularly for starting the permanent plot research in Meijendel; because of his insight in vegetation research an evaluation of livestock grazing on succession by permanent plots was possible. Dunea is also acknowledged for their consistent financial support of monitoring of these series of permanent plots in a four yearly sequence; in the Netherlands this represents a highly valuable and unique series of vegetation data.

INTRODUCTION

The vegetation of coastal sand dunes is characterized by a high species diversity and comprises some of the rarest vegetation types in Europe. Dune grasslands are particularly species-rich (Kuiters et al. 2009) and represent a priority habitat under the Natura 2000 legislation (Council of the European Communities 1992). Much effort is now being put into the protection of species diversity, as biodiversity has declined dramatically since industrialization in the 19th century, changing land-use and intensification of agriculture (Westhoff 1952; Schaminée and Weeda 2009; Piersma and Olff 2010).

For centuries, humans only used coastal sand dunes for small-scale agriculture and animal husbandry. Shrubs and trees were cut and used for fire wood. Livestock, however, was removed at the end of the 19th century from most areas of the dunes (Vera et al. 2006). As rabbit (*Oryctolagus cuniculus L.*) numbers had declined strongly, due to epidemic diseases, livestock was introduced (again) to counteract tall grasses, shrubland and forest encroachment, and to restore a higher biodiversity with an emphasis on grasslands. The rabbit disease outbreaks include myxomatosis in 1954 (Drees and Olff 2001) and Rabbit Viral Haemorrhagic Disease (RVHD-1) in 1989 (Scheffer 2012), reducing the rabbit population by 90-95%. After a slight recovery, RVHD-2 again reduced the numbers of rabbits in 2015 (Montizaan and IJzer 2016).

Boerboom (1960a) published a vegetation map of 1,900 ha of Meijendel, which showed a landscape with a mosaic of grasslands, some shrubland and a few afforested areas. In the early 1950s, dozens of permanent plots were laid out to study vegetation succession. Soon after finalizing the vegetation map, a system of artificial recharge of ground water started, with about 100 ha of infiltration ponds, changing the hydrological situation of

Meijendel considerably. Some of the permanent plots reflect the consequences of this activity on the vegetation.

The introduction of livestock in autumn 1990 at 0.06-0.07 Large Livestock Units (LLU) ha^{-1} year^{-1} (1: 12-15 ratio) aimed to stimulate and maintain new areas of bare sand, enlarge the grassland area and reduce the shrubland and forest area. The hypothesis was that livestock slows down progressive succession towards tall shrubland and forest, decreases grass and shrub encroachment and stimulates patches of bare sand by trampling and damaging the vegetation. The overall and desired impact would be an increase in species-rich dune grasslands (Hoffmann 2002; Provoost et al. 2004).

METHODS

Meijendel and permanent plots

In 1952 and 1953, permanent plots were laid out in the coastal dunes in the northern part of Meijendel (Fig. 1; 52°7'N; 4°20'E). In later years, some additional permanent plots were installed. The permanent plots are scattered over the area in a west-east transect in the northern part of Meijendel (Fig. 1). The plots are positioned in the ecological zones of the parabolic dunes (Helmduinen; west part of Meijendel), and in extensive dune valleys (Kijfhoek, Bierlap, east part of Meijendel) (Van der Meulen et al. 1985). The landscape zone of the parabolic dunes have a pronounced relief (2-20 m) and enclose a number of moist dune valleys (Fig. 1). The soil is generally rich in lime. The dry areas are covered with a mosaic of pioneer dune grasslands (southern exposures), closed dune grasslands (northern exposures) and stands of dwarf shrub species, like *Hippophae rhamnoides L.* The extensive dune valleys contain lime-poor grasslands and deciduous forest with *Betula*, *Crataegus* and *Quercus* dominating, on partly flattened and former arable land (Van der Meulen et al. 1985). The distribution of the permanent plots were not randomly chosen. They were partly laid out in rare vegetation types (in the early 1950s), such as the *Anthyllido-Silenetum* (Schaminée et al. 1998) in the parabolic dune ecological zone. At that time, the dune forest ecology of Alno-Padion communities was also a topic of keen interest among dune ecologists. The Meijendel plots participate in the Dutch 'Network Ecological Monitoring'(Smits et al. 2002).

Plot selection and analysis

The focus of our study is on the vegetation development of the dry part of the dune ecosystem. Based on the plant communities of the dry ecosystem (Schaminée et al. 1996; 1998), only the 41 permanent plots of the dry dunes are evaluated for this study. As all 41 plots are situated in the grazed area, a comparison with the ungrazed plots was not possible. At the start, the plots were selected according to the principle of internal homogeneity as defined by the Zurich-Montpellier method (Braun Blanquet 1951, 1979). In time,

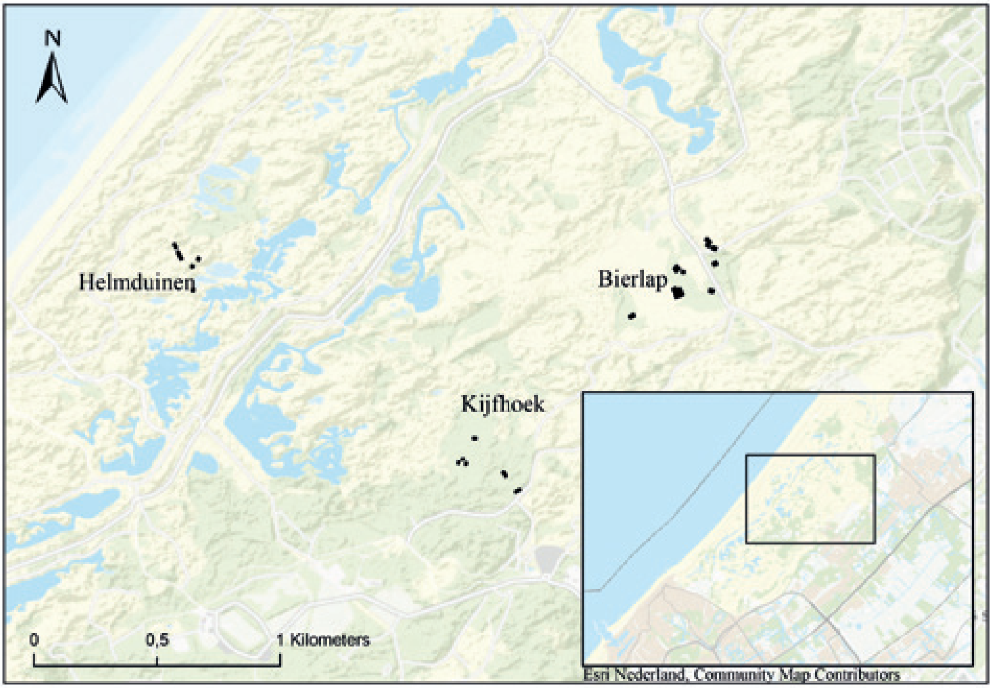


Fig. 1. Distribution of the selected permanent plots in Helmduinen, Kijfhoek and Bierlap in Meijendel. Upper left corner: North Sea, right side: inner dune edge near Wassenaar. Blue areas: infiltration ponds for artificial recharge, light blue: dune slacks. Bottom righthand corner: cutout of Meijendel, surrounded by the cities of The Hague and Wassenaar.

they developed into more heterogeneous plots comprising several vegetation types. In the beginning, the plots were monitored every year, according to the Braun-Banquet approach (Braun-Blanquet 1951; Westhoff and Van der Maarel 1973; Schaminée et al. 1995). In the 1970s, this sequence was scaled down to once every four years on average. Over time, different abundance scales were used to describe the vegetation (e.g. Braun-Blanquet, Doing, Segal, Londo; see Schaminée et al. 1995). These scales were transformed to one ordinal scale, by using the database management system TURBOVEG (Hennekens and Schaminée 2001).

After classification with TWINSPAN (Hill and Šmilauer 2005; version 2014), 32 clusters were distinguished (Table 1). These clusters are assigned to formal syntaxa according to the Dutch national vegetation classification system (Schaminée et al. 1995; 1996; 1998; Stortelder et al. 1999), based on the preponderant syntaxonomic species groups. Every year without a relevé, the same cluster name is prolonged until the next relevé is made with possible changes to a different cluster. These 32 phytosociological clusters were

Table 1. Assignment of phytosociological clusters into successional stages 1 to 9. 1: pioneer grasslands of lime rich soils; 2: dune grasslands of lime rich soils; 3: exclusive dune grasslands of the Zeedorpenlandschap type (Van der Hagen et al. 2022a); 4: dune grasslands of acidic topsoils; 5: grassland with tall shrubland elements; 6: semi-closed shrubland with grassland elements; 7: tall shrubland with elements of low shrubland; 8: tall shrubland with forest elements; 9: closed forest with tall shrubland elements.

SUCCESSION STAGE	CLUSTER NAME VEGETATION TYPE
1	Tortulo-Koelerion/Polygalo-Koelerion
1	Phleo-Tortuletum/Festuco-Galietum
1	Phleo-Tortuletum/Violo-Corynephoretum
1	Cladonio-Koelerietalia/Violo-Corynephoretum
2	Taraxaco-Galietum veri
2	Taraxaco-Galietum veri/Anthylllido-Silenetum
2	Taraxaco-Galietum very with Anthyllildo-Silenetum elements
3	Anthyllido-Silenetum
4	Festuca ovina-[Koelerio-Corynephoretea]
4	Agrostis capillaris-[Plantagini-Festucion]
5	Taraxaco-Galietum/Rhamno-Crataegetum
5	Festuco-Galietum/Rhamno-Crataegetum with Potentilla reptans, Viola canina
5	Festuco-Galietum/Rhamno-Crataegetum with Agrostis capillaris
5	Festuco-Galietum/Rhamno-Crataegetum with Asparagus officinalis, Hypericum perforatum
5	Festuco-Galietum/Taraxaco-Galietum/Rhamno-Crataegetum
6	Rhamno-Crataegetum/Festuco-Galietum with Agrostis capillaris
6	Rhamno-Crataegetum/Festuco-Galietum with Agrostis stolonifera
6	Hippophao-Ligustretum/Festuco-Galietum
6	Rhamno-Crataegetum/Polygalo-Koelerion
6	Hippophao-Ligustretum/Festuco-Galietum/Echio-Verbascetum
7	Hippophao-Ligustretum
7	Rhamno-Crataegetum with Hippophae dominance
7	Rhamno-Crataegetum with Sambucus nigra
7	Hippophao-Ligustretum/ Rhamno-Crataegetum
7	Rhamno-Crataegetum with Ligustrum vulgare, Rosa canina
8	Rhamno-Crataegetum/Populus tremula-[Alno-Padion] with Agrostis capillaris
8	Betula spec.-[Alno-Padion] = Rhamno-Crataegetum/Betula pubescens-[Alno-Padion]
8	Rhamno-Crataegetum/Quercus robur-[Alno-Padion]
8	Rhamno-Crataegetum/Populus tremula-[Alno-Padion]
8	Rhamno-Crataegetum/Betula pubescens-[Alno-Padion]
9	Quercus robur-[Alno-Padion]/Rhamno-Crataegetum
9	Quercus robur- Rhamno-Crataegetum

Table 2. The percentage of permanent plots in the different successional stages in four different years: the start of the permanent plot studies (1953), just before introducing livestock (1989), just after introducing livestock (1992) and the last plot study (2012). The vegetation type mentioned in this table is the dominant vegetation type during the succession stage (see table 1).

SUCCESSION STAGE	VEGETATION TYPE	1953	1989	1992	2012
1	Phleo-Tortuletum	19	16	0	4
2	Taraxaco-Galietum	23	4	5	8
3	Anthyllido-Silenetum	4	4	5	0
4	Festuca-Agrostis basal communities	0	16	0	0
5	Festuco-Galietum with shrubland elements	8	16	20	0
6	Rhamno-Crataegetum with grassland elements	12	0	0	0
7	Rhamno-Crataegetum with elements of low shrublands	8	12	20	38
8	Rhamno-Crataegetum with forest elements	27	32	45	38
9	Quercus robur/Rhamno-Crataegetum	0	0	5	12

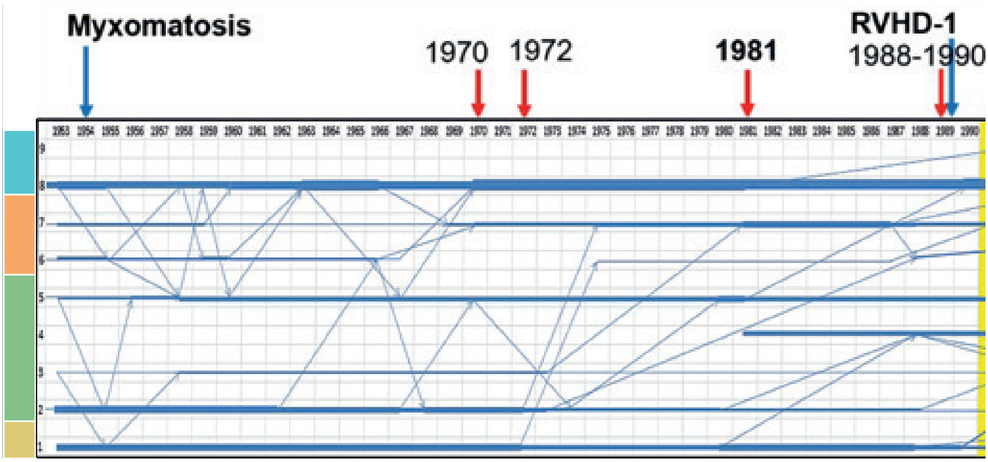
grouped into nine successional stages, from pioneer grasslands to forest types, which on their turn were summarized in four successional stages (Table 1): open dune grasslands (stage 1), closed types of grasslands, including the *Anthyllido-Silenetum* grasslands of the *Zeedorpenlandschap* (Doing 1995) (stage 2, 3, 4, 5), low and tall semi-open shrubland in mosaic with grassland (stage 6, 7), and tall shrubland and forests (stage 8, 9) (Table 2). The shifts per year in each permanent plot were counted and put into a diagram (Fig. 2).

RESULTS

Shifts in successional stages

In 1953, seven out of nine successional stages were present with a dominance of tall shrubland of *Rhamno-Crataegetum* with forest elements (8), *Taraxaco-Galietum*, a dune grassland of lime rich soils (2), and the pioneer grassland *Phleo-Tortuletum* (1). Additionally, in 1953, the rare and species-rich *Anthyllido-Silenetum* (3) was present in some permanent plots. At the start in 1953, two successional stages were absent. These were the Festuca-Agrostis basal community characterized by an acidic topsoil (4), and the *Quercus robur* forests with tall shrubland elements (9) (Table 2).

In 2012, the last year of the relevés, the permanent plots presented only five out of nine successional stages, with a focus at both ends of the succession (Table 2). On the one hand, the open and closed dune grasslands *Phleo-Tortuletum* and *Taraxaco-Galietum* (1, 2)



were still present in the plots, but much less than in 1953. On the other hand, the *Quercus* forest with tall shrubland elements (9) appear since 2004. Over time, the *Rhamno-Crataegetum* with elements of low shrubland (7), and the tall shrubland of *Rhamno-Crataegetum* with forest elements (8) have become prominent, having its peak in 1992 (Table 2). The intermediate stages of succession, including the rare *Anthyllido-Silenetum*, have disappeared in the plots (Fig. 2).

Overall, between 1953 and 2012 many changes occurred (Fig. 2; Table 2), predominantly leading to both extremes of successional stages.

Progressive versus regressive succession

In the pre-1990 period without livestock grazing, there was a balance between progressive and regressive succession. Since 1990, with livestock grazing, progressive succession dominates (Table 3). In more detail, the data show that from 1952 until 1970/1972, there are progressive and regressive changes between all successional stages. After 1970/1972, progressive succession starts to dominate with an emphasis on tall shrubland of the *Rhamno-Crataegetum* (Fig. 2) and this is more prominent since 2004. In between 1995 and 2004, closed forests with *Quercus robur* with tall shrubland (9) appear in the permanent plots, also becoming more prominent after 2004.

The lime-rich dune grasslands of the *Taraxaco-Galietum* (2) have a substantial presence in the permanent plots. They start decreasing after 1972, wihth after 1981 a further decrease. After 1988, almost nothing is left (Fig. 2; Table 2). There is a small return of the *Taraxaco-Galietum* after 2004 and up to 2012, but at a much lower level than its original level in 1952. Most of the lime-rich dune grasslands (1, 2) shift towards the *Rhamno-Cra-*

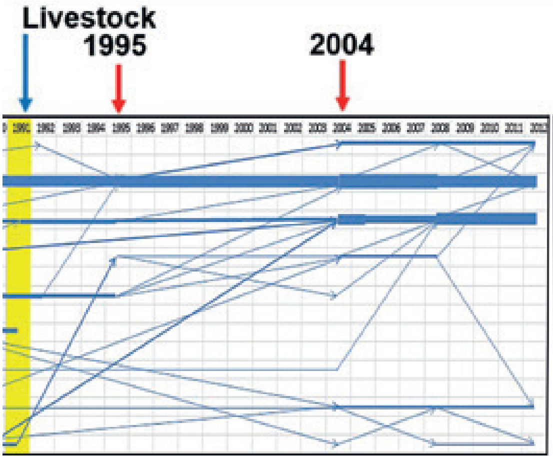


Fig. 2. Changes in nine successional stages (Table 2) from 1953 to 2012 based on 32 clusters of syntaxonomic species groups (Table 1) of the 41 permanent plots (Lammers 2015). The line thickness corresponds with the number of permanent plots in these successional stages; the changes from one to another successional stage is indicated with thin arrows. The thick red arrows indicate prominent shifts in succession. Thick bleu arrows indicate the rabbit diseases and the livestock introduction. The red block indicates the loss of large parts of the grasslands in the permanent plots.

taegetum with grassland elements (6) or with elements of low shrubland (7) (Fig. 2). In 1981, grasslands of the Festuca-Agrostis basal community (4) with acidic topsoils appear.

In the post-1990 period, only a few regressive shifts take place (10%: Table 3). The tendency is very prominent towards the *Rhamno-Crataegetum* communities (7, 8), and since 2004 *Quercus robur* is also present. In 1998, the Festuca-Agrostis basal community (4) partly shift into lime-rich grasslands (1, 2). Soon after the 1990 introduction of livestock, the sandy pioneer grasslands of the *Phleo-Tortuletum* (1) disappeared and reappeared after 2004 (Fig. 2). The rare *Anthyllido-Silenetum* (3) endured from 1953 up to 2004, with a small peak between 1958 to 1973. In 2004, it disappeared abruptly, and has not returned. The *Anthyllido-Silenetum* changed into a shrubland type.

DISCUSSION

Noteworthy changes occurred in the years 1970, 1972, 1981, 1988, 1989, 1990, 1995 and 2004 (Fig. 2). The hypothesis was that in 1990, introduced livestock would slow down progressive succession towards tall shrubland and forest, and would decrease grass and shrub encroachment. The livestock was expected to stimulate the development of patch-

Table 3. Relative changes (%) in progressive and regressive succession in the pre-1990 and post-1990 period. 1990 is the start of livestock grazing.

TIME PERIOD	REGRESSIVE SUCCESSION STATE	PROGRESSIVE SUCCESSION STATE
1952-1990	49	51
1991-2012	10	90

es of bare sand by damaging the vegetation. The overall impact was expected to have been an increase in the area of species-rich dune grasslands (Hoffmann 2002; Provoost et al. 2004). The opposite is the case; progressive succession dominates and only in a short period after 2004, the open and sandy grassland community of the *Phleo-Tortuletum* reappears.

Grazers: livestock and rabbits

In none of the years does the vegetation composition seem to be related to the introduction of livestock. The 1990 relevés were made just before the introduction of livestock. Up to the 1990s, there had been an equilibrium of progressive and regressive succession (51% progressive shifts versus 49% regressive). Since 1970/1972, and more explicitly since 1990, the shift moves to the outer ends of the successional stages of the dune ecosystem with significant changes of a 90% progressive shifts versus a 10% regressive shifts. Shrubs and trees in vegetation types of the *Rhamno-Crataegetum* with grassland (6), shrubland (7) and forest (8) elements became more common in the permanent plots, with a few remaining grassland plots of the *Phleo-Tortuletum* and *Taraxaco-Galietum*. As there seems no relation to livestock grazing, the changes observed must have another cause.

In contrast to the impact of rabbits, the grazing pressure of 0.06-0.07 LLU ha^{-1} $year^{-1}$ by livestock may have been too low to graze off most of the seedlings of shrubs (Ranwell 1960; Olff and Boersma 1998). Unlike rabbits, livestock are generalist grazers, not differentiating between grass, herbs, and young shrubs (Bokdam 2003). And, livestock concentrate their feeding on grasslands, not specifically on nutrient-rich seedlings, like rabbits do (Lamoot et al. 2005; Bakker 2003; Bakker et al. 2009; Smit and Ruifrok 2009; Runhaar et al. 2015).

The role of rabbits

In 1954, the devastating rabbit disease myxomatosis took place, killing most of the rabbits (Drees and Olff 2001). At first, the myxomatosis seems to have hardly any effect with respect to progressive succession in the permanent plots. It actually took some lag time to reveal the massive consequences of the loss of the rabbits. Around 1970/1972, it becomes visible when progressive succession starts to appear with shifts from the open grasslands towards the tall(er) shrubland of the *Rhamno-Crataegetum* (Fig. 2: 6 and 7). This happened because rabbits were not present as specialist grazers on the highly nutritious seedlings reported on *Crataegus monogyna* by Van Groenendael et al. (1982), Salman and Van der Meijden (1985) and Bakker (2003). In the low presence of rabbits, these seedlings are able to mature even in the presence of livestock, or when surrounded by poisonous plants like *Jacobaea vulgaris*, or when under thorny shrubs (Vera et al. 2006). Thorny and long-lasting shrubs, like *Crataegus*, dominate gradually and nurse seedlings of *Quercus robur* and *Betula* species (Vera et al. 2006). This is the start of a *Rhamno-Cratae-*

getum with forest elements that gradually changes into a forest with *Quercus robur*. These vegetation types are relatively unattractive to livestock, but also prevent a recovery of a large rabbit population. And since the return of the red fox (*Vulpes vulpes*) around 1975 (Mulder 2002), rabbits have shifted their burrows from grasslands into *Hippophae* shrubland to avoid predation.

In Van der Hagen et al. (2020a), it was illustrated that the shrubland of *Hippophae rhamnoides* (Table 1: *Hippophao-Ligustretum* plant community in clusters 6 and 7) increased from 1975 up to 1990. After 1990, large parts of the *Hippophae* shrubland collapsed and changed back to grasslands. This is explained by the physiological lifespan of *Hippophae* of around 40 years (Van der Hagen et al. 2020a). In this set of permanent plots however, the shrubland shifted mainly into tall shrubs (e.g. *Crataegus monogyna*; Van der Hagen et al. 2020b) from 1972 up to 2012 (Table 2: 6, 7, 8), finally shifting towards forests with *Quercus robur* (Table 2: 9).

In 1989, just before the introduction of livestock, another devastating rabbit disease RVHD-1 killed 90-95% of the revived rabbit population (Scheffer 2012). Again, the effect of the devastating reduction of rabbits due to RVHD-1 were not instantly visible in the plots; it takes about 15 years to manifest itself in around 2004. Whether the impact of the 1989 RVHD-1 was aggravating the 1954 myxomatosis impact is not possible to distinguish. Probably the effects of myxomatosis in 1954 are still the dominating factor.

Grasslands

In 2012, grasslands are almost absent in the permanent plots. Only the *Taraxaco-Galietum* perseveres. The grassland with the highest biodiversity, the *Anthyllido-Silenetum*, disappeared from the permanent plots in 2004. This vegetation type is linked to direct or indirect human activities in the dunes like livestock grazing (Slings 1994; Van der Hagen et al. 2022a). In both time spans before and after the introduction of livestock, the (direct) effects of the rabbit diseases are more likely to contribute to the development of tall shrubland and forests. The hypothesis on livestock stimulating bare sand could not be tested in the permanent plots, because there are no ungrazed controls located next to the permanent plots. But the fact that the open *Phleo-Tortuletum* returned in the permanent plots, even in the grasslands with acidic topsoils in 2004 and from 2008 onwards, is in line with the reality of an independently caused and general increase in the number of blowouts from 2001 onwards (Aggenbach et al. 2018; Van der Hagen et al. 2020a).

Critical notes

The permanent plots were not randomly chosen in the 1950's. Due to specific interests in the grassland *Anthyllido-Silenetum* and on succession in forest ecosystems, these two types were overrepresented in the permanent plots. Nevertheless, the processes seen

(Fig. 2) are in line with Van der Hagen et al. (2020a, 2020b) showing changes in the area of forests in 1,900 ha of Meijendel in the years 1938, 1966, 1983 and 2014 (see Van der Hagen et al. 2020b). On the other hand, regressive succession has manifested itself after an increase of blowouts with bare sand since 2001 (Aggenbach et al 2018; Van der Hagen et al. 2020a). The impact of these changes can also be seen in the re-occurrence of the *Phleo-Tortuletum* in a few permanent plots. Overall, the tendency to regressive and progressive succession processes squeeze the grasslands between both ends of the succession spectrum.

Because all permanent plots are in the livestock grazed areas, we cannot be sure of the effects of the livestock. But, it can be noted that at many other moments in time there are shifts (Figure 2), which are not connected with livestock presence at all.

A third point is using permanent plots data sets for succession analysis. Chytrý et al. (2014) state it as a ‘risky business’. The use of permanent plots for succession analysis is only legitimate when this type of research is confirmed by complementary research, which is the case (Van der Hagen et al. 2020a, 2020b; Van der Hagen et al. 2022a).

There are numerous other factors affecting vegetation changes in the dune landscape that might interfere with the developments in the permanent plots. One is the nitrogen deposition, with its peak around 1990, that might have an effect on progressive succession (Noordijk 2007; Kooijman et al. 2009). Although the lime-rich dunes of Meijendel are largely buffered against nitrogen deposition (Aggenbach et al. 2017), raised nitrogen levels can still have an effect on progressive vegetation succession (Kooijman et al. 1998). The same can be said for changes in climate conditions, irrespective of human interference.

In consideration of the priority of species-rich grasslands habitat in the Natura 2000 legislation, and the visible and progressive succession since 1990, active management by felling is unavoidable to reduce the amount of tall shrublands (Van der Hagen et al. 2020b) and give more space to the priority habitats of the grasslands.

CONCLUSION

The general hypothesis was that large grazers would slow down the dominant progressive succession towards tall shrubland and forest, would decrease grass and shrub encroachment and would stimulate bare sand by their trampling, damage the vegetation cover. In this study, we did not find evidence that the introduction of livestock slowed down succession from open grasslands into shrubland or forest. In contrast to our expectations, progressive succession seems increasingly dominant after the introduction of livestock. The post 1972 or 1990 balance between progressive and regressive successions becomes dominated by a shift to progressive succession. It is considered that the 1954 outbreak of myxomatosis and the 1989 outbreak of RVHD-1 is more likely to explain the observed shift in progressive succession. All in all, rabbits seem to be the crucial factor in these changes (Van der Hagen et al. 2020a, 2020b).

Livestock might replace the rabbit as a grazer, but will not replace the rabbits on the impact of the meticulous consumption of seedlings of shrub and tree species. Livestock does not specifically feed on seedlings as rabbits do.

The shift in the permanent plots towards the more open and sandy community of the *Phleo-Tortuletum* after 2004 might be the impact of an independent process of increased blowouts since 2001 (Aggenbach et al. 2018; Van der Hagen et al. 2020a). Irrespective of livestock grazing, blowouts re-emerge after 2001, possibly also stimulating the re-emerging of the *Phleo-Tortuletum* in the permanent plots.

The nature conservation target, as stated by Dunea as the nature manager of Meijendel, is to create more species-rich grasslands in the context of EU Natura 2000 priority habitat. The grazing regime by livestock with 0.06-0.07 LLU ha^{-1} year^{-1}, as applied in Meijendel, with the numbers adapted to winter survival, seems ineffective (Van der Hagen 2020a). Overall, succession is strongly influenced by rabbits and their diet (Drees 1988) including the consumption of the seedlings of shrub and tree species (Van der Hagen et al. 2020a, 2020b). A multiple activity program is therefore necessary to have the desired impact. The consequence of the lack of rabbits should result in an active program of chopping trees and shrubs to compensate for their absence. This will enlarge the grassland compound of the dune ecosystem. An additional possibility is introduction of RVHD-vaccinated rabbits from areas, which still have high numbers or are being shot for damage control.

Chapter 5

Forty years of rabbit influence on vegetation development in the coastal dunes of Meijendel, the Netherlands

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ABSTRACT

In 1975, eight exclosures were set up in the coastal dunes of Meijendel to study the effects of grazing by rabbits, each accompanied by a reference plot of the same size. In 1990, livestock was introduced in the area. The exclusion of rabbits resulted in most cases in the establishment of long-living shrub and tree species (*Crataegus monogyna* and *Quercus robur* in particular) and dense dune grassland vegetation. There is one exception: in one location, in the exclosures as well as its reference plot, *Hippophae rhamnoides* invaded. However, there is a difference between the exclosure and its reference. In the exclosure, the long-living shrub species *Crataegus monogyna* became co-dominant. On the other hand, in the reference plot two plant species indicating disturbance established (*Cynoglossum officinale* and *Jacobaea vulgaris*), probably due to the livestock intrusion opening up the *Hippophae* shrub and trampling the soil. In most of the exclosures, species richness is lower compared to the references. In the two exclosures with a southern exposition, the species richness was higher inside the exclosure than in the reference, mainly due to a higher number of lichen species.

The exclusion of rabbits lead to the establishment of trees and shrubs, but there is a difference in the impact between short (e.g. *Hippophae rhamnoides*) and long-living shrub species. The long-living shrub and tree species, like *Crataegus monogyna* and *Quercus robur*, dominate the exclosures. With the lack of rabbits, because of the impact of epidemic diseases, these long-living shrub species have ample opportunities to sprout and grow up into high shrubland or forest, finally dominating the landscape over a period of a century or more. A short living species like *Hippophae rhamnoides* expanded shortly after the myxomatosis outbreak and collapsed after around 40 years and the system mainly fell back to a grassland (Van der Hagen et al. 2022a). This means that long-lasting tree and shrub species like *Crataegus monogyna* and *Quercus robur*, with a lifespan of more than 150 years, may gradually lead to afforestation of the dune landscape. As rabbit populations are continually threatened by viral outbreaks, survival of young sprouts will manifest on a regular basis. The desired landscape is an open mosaic of bare sand and dry dune grasslands (a Natura 2000 priority habitat) with a low percentage of shrubland and forest. The consequence is that measures should be taken: removal of the major part of the long-living individuals resulting from earlier viral outbreaks, especially in the still relative open parts of the dunes.

KEYWORDS Exclosure, grazing, rabbit, livestock, phytosociological shift, species shift, disturbance

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NOMENCLATURE

Vascular plants are according to Van der Meijden (2005), mosses according to Siebel & During (2006) and lichens according to Van Herk & Aptroot (2004). Phytosociological nomenclature is according to Schaminée et al. (1996; 2010) and Stortelder et al. (1999).

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INTRODUCTION

In 1975, eight exclosures were installed with rabbit proof fence in the Meijendel (52°7'N; 4°20'E) dune area near The Hague, the Netherlands (Fig.1). The Meijendel site manager of the drinking water company Dunea (then Duinwaterleiding van 's-Gravenhage) wanted to investigate the effects of the absence of rabbits (*Oryctolagus cuniculus*) on dune vegetation development. The rabbits were expected to maintain the openness of the dune landscape in the form of dune grasslands. Proving this important function would provide arguments for a ban on rabbit hunting.

The exclosures are 5x5 m except one (10x4 m). Next to each exclosure, a reference plot of the same size was marked out. From seven location (No. 80 – 86) the development was analyzed and is presented. Unfortunately, one exclosure (No. 79) was accessible for rabbits during an unknown period, and for that reason was not taken into account within this analysis. To counteract grass and shrub encroachment in the larger Meijendel area, livestock was introduced at the end of 1990 partly to replace the lack of rabbit grazing, due to the (still) epidemic 1954 myxomatosis (Van Koersveld 1955; Pluis 1986) and the 1989 Rabbit Viral Haemorrhagic Disease (RVHD). Because of the presence of livestock, a fence with barbed wire one meter around the exclosure was placed to keep the livestock out of the exclosure. This lead to a situation in which the exclosure was not grazed by rabbits since 1975 and not by livestock and rabbits since end 1990; the reference plots were grazed by rabbits all along and since the end 1990 also by livestock.

The research questions for this study are: (1) what is the effect of grazing by rabbits (and later by livestock and rabbits) on vegetation structure and species number? (2) are rabbits crucial in preventing shrub and forest development? (3) is there a difference in the effect of grazing on short (around several decennia) and long-living (more than a hundred years) species of shrubs and trees? (4) will the difference between short and long-living shrub species have consequences for nature conservation in this Natura 2000 area?

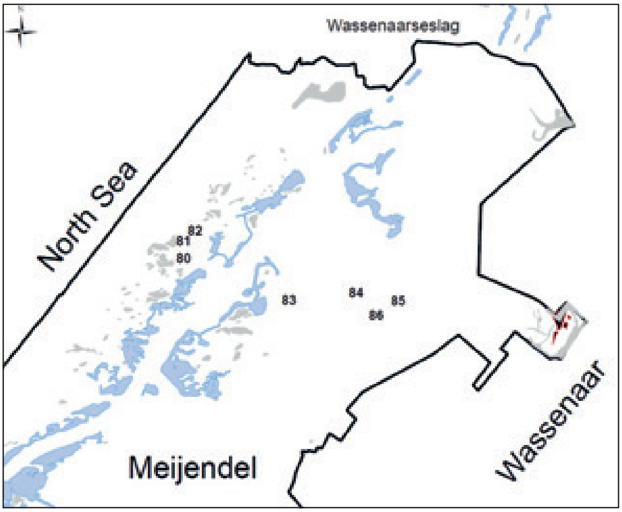


Fig. 1. Locations of the exclosure and reference plots within the outline boundaries of Meijendel (west-east distance 3 km). Blue shades: infiltration ponds; grey shades: dune slacks. 80, 81= Phleo-Tortuletem; 82= Anthyllido-Silenetum; 83= Hippophao-Ligustretum; 84, 85, 86= Basal Community Calamagrostis epigejos [Cladonio-Koelerietalia], 84 with Crataegus monogyna, 85 with Populus tremula, 86 with Quercus robur.

We hypothesize that rabbits are a crucial factor in preserving an open dune landscape with its variety of dune grasslands. In absence of rabbits, seedlings of shrub species may have the opportunity to establish and to encroach grassland vegetation for a certain extend of time dependent on the shrub's persistence.

MATERIAL & METHODS

Meijendel is part of the lime rich coastal sand dunes of the Netherlands (Van der Meulen et al. 1985). The area is about 2,100 hectares (6 x 3.5 km). The locations with an exclosures and reference plot (Fig. 1) are positioned in two out of the four landscape ecological zones in Meijendel, all running more or less parallel to the coastline (Van der Meulen et al. 1985). There are no locations in the first zone, which is a 250-350 meter strip of dune functioning as a sand dike protecting the hinterland for flooding. Location numbers 80, 81, 82, 83 are present in the zone of the predominantly dry parabolic dunes. These have a pronounced relief (2-20 m) and small moist dune valleys in between and are covered by mosaics of bare sand, pioneer grasslands (southern exposed; *Phleo-Tortuletum, Hippophao-Ligustretum*), closed grasslands (northern exposed; *Taraxaco-Galietum, Anthyllido-Silenetum*) and dwarf shrub species, like *Salix repens*. Further away from the coastline, the size of the parabolic dunes increase. Location numbers 84, 85, 86 lie in the third zone of the extensive dune valley Bierlap, 2.2 km inland. This valley is a flattened pre-1880 arable land with topsoil-decalcified dune grasslands (Basal Community Calamagrostis epigejos [*Cladonio-Koelerietalia*]) and deciduous forests with *Crataegus monogyna, Betula pendula, Populus tremula* and *Quercus robur*. There are no locations in the fourth zone, which are in general higher inner dunes (5-35 m) with less pronounced large parabolic and rolling dunes with a partly decalcified topsoil supporting dune grasslands with short grasses, mosses and lichens, open *Hippophae* shrubland and forest patches.

All exclosures and their references are 5x5 m except for location 82 for unknown reasons. The size of the exclosure on the northern slope is 4x10 m and its reference is 6.5x10 m. In 1975, all exclosures and their references were occupied by dune grassland. More in detail, the seven locations have the following characteristics (Table 1):

(1) Two locations with a southern exposition: No. 80 and 81. These are bearing a dune grassland of the *Phleo-Tortuletum* (Schaminée et al. 1996). This relative open plant community is characterized by moss and lichen species, which survive summer drought and typical spring annuals surviving as seed during these summer droughts. Topsoil summer temperatures can reach up to 60°C (Brandt 1974). The soil profile is thin with limited organic matter and in sandy situations with a 2 mm algal crust (Pluis & De Winder 1989). In 1960, the locations was a predominantly covered by *Phleo-Tortuletum* (Boerboom 1960; map legend 8). As the vegetation in 1990 and 2015 still consisted of a *Phleo-Tortuletum*, it can plausibly be assumed that the same was the case in 1975.

(2) One location with a northern exposition: No. 82. Because of this exposition it was covered by closed dune grassland in 1975. The vegetation map of Boerboom (1960; map legend 9) indicates the vegetation to be assigned to the species rich *Anthyllido-Silenetum*. The northern exposition, high lime content in and immediately under the organic layer, disturbance by livestock and human activities, higher soil moisture because of the northern exposition and consequently more nutrients sustain this vegetation type for a long time (e.g. Slings 1994; Dobkin et al. 1998; Mooij et al. in prep.).

(3) One location on the top of an undulating elevated dune ridge: No. 83. In 1975 this location most likely comprised a *Taraxaco-Galietum veri.* On the vegetation map of Boerboom (1960; map legend 8), it was a mosaic of *Phleo-Tortuletum* with *Taraxaco-Galietum, Violo-Corynephoretum* and elements of the *Elymo-Ammophiletum*.

(4) Three location on a topsoil-decalcified dune valley floor: No. 84, 85 and 86. In 1975 this pre-1880 farmland of the Bierlap valley was covered by dune grasslands and deciduous forests. Boerboom & Westhoff (1974) and Boerboom (1958) describe the vegetation as a dense turf of *Calamagrostis epigejos* with codominance of *Carex arenaria* (Boerboom 1960; map legend number 3). This can be classified as a Basal Community Calamagrostis epigejos [*Cladonio-Koelerietalia*] (Schaminée et al. 1996).

In July 2015, relevés were made of the seven exclosures and references according Braun-Blanquet method, using the extended Braun-Blanquet scale (Schaminée et al. 1995).

Table 1. Differences in general features of the relevés between the exclosure and reference plots based on the relevés made in July 2015; remarkable differences between exclosure and reference are in bold.

Abbreviations of the syntaxa:
P.T. = Phleo-Tortuletum
A.S. = Anthyllido-Silenetum
H.L. = Hippophao-Ligustretum
BC-C = Basal Community Calamagrostis epigejos [Cladonio-Koelerietalia]

Lollipop images according to Dansereau 1951).

	P.T.		**A.S.**	
	EXCL.	**REF.**	**EXCL.**	**REF.**
Plot number	80 & 81	80 & 81	82	82
Plot size	5x5	5x5	4x10	6.5x10
Lollipop images				
Number of sites	2	2	1	1
General features				
COVER (%)				
Total	91.5	45	90	50
Tree	-	-	-	-
Shrub	8.5	23	70	3
Herb	55.0	11.5	30	45
Moss	65	27.5	0	30
HEIGHT				
(High) shrub (m)	0.8	0.5	1.5	0.8
Low shrub (m)	0.2	0	0.5	0
(High) herb (cm)	20	15	30	10
Low herb (cm)	7.5	7.5	5	5
AVERAGE NUMBER				
Species	27.0	20.5	37	49
Tree/shrub species	1.5	1	6	2

	H.L.		BC-C	
	EXCL.	**REF.**	**EXCL.**	**REF.**
	83	83	84, 85 & 86	84 ,85 & 86
	5x5	5x5	5x5	5x5
				
	1	1	3	3
	95	90	95	85
	-	-	50	3
	70	70	23.3	3.7
	40	50	40	30
	40	20	20.7	61.7
	3	2	3	1.3
	1,5	1.5	0.5	0
	40	30	50	26.7
	10	10	20	6.7
	14	15	14.3	20.7
	3	2	4.7	3.0

RESULTS

There are no relevé data available from the 1975 situation. The vegetation differences and differences in the number of species found, are between the exclosure and its reference in the year 2015 after 40 years of development.

Locations 80 and 81: open dune grassland – open dune grassland with small shrubs

The vegetation of these southern exposed exclosures has developed into a closed grassland community with some shrubs and >90% plant cover. The references have a total cover of 45% (Table 1). The cover of the shrub layer in the references is higher though than in the exclosures: 23% versus 8.5%. The shrub cover in the reference of location 80 is 45% due to lateral ingrowth of *Hippophae rhamnoides* after 1990 (Fig. 2a). This is very high compared with reference of location 81 with only 1% shrub cover, which is much lower than in both exclosures (7% and 10%; online appendix Table 1a). The cover of the herb layer (high grasses cover) is higher in the exclosures (55% versus 11.5%; Table 1). The cover of the moss layer is higher in the exclosure compared to the reference (65% versus 27.5%).

The average number of species in the exclosure is higher than in the reference (27 versus 20.5; Table 1). Especially exclosure 81 with 33 species marks this difference (online appendix Table 1a). A noteworthy difference between the exclosure and reference plots is the number of lichen species and cover of lichens. Inside the exclosure there are 6 species with a total cover of 26% and in the references it is 2 species with a cover of 2.5%.

Location 82: closed dune grassland – shrubland

In 1990, already about 40-50% of the exclosure was dominated by low shrubs (Fig. 2b). They became dominant in 2015 (Fig. 2b). In 2015, the exclosure has been largely overgrown by shrub species, mainly *Crataegus monogyna* and developed into a *Rhamno-Crataegetum* (Stortelder et al. 1999). This expresses itself in the difference in the cover of total, shrub and herb layer of the exclosure versus the reference (90% versus 50%; 70% versus 3%; 30% versus 45%) and its height (1.5 m versus 0.8 m; 0.5 m versus absent; 30 cm versus 10 cm) (Table 1; Fig 2b). In 2015 the whole reference and the small grassland component of the exclosure can still be characterized as *Anthyllido-Silenetum*.

The species number and the cover of shrubs in the shrub layer are higher in the exclosure (6 versus 2; 70% versus 3%). The total number and the number of species in the herb layer are lower inside the exclosure (37 versus 49; 31 versus 47 species). Four Viola species are present in the reference, whilst the exclosure had none in 2015. The species composition of the reference comprises several characteristic species of the *Phleo-Tortuletum* (Table 2; online appendix Table1b). *Cirsium vulgare* expresses a ruderal aspect indicating a higher nutrient level in the exclosure (Table 2).

Location 83: grassland – Hippophae shrubland

In 1990, lateral ingrowth of *Hippophae rhamnoides* has occurred in both the exclosure and reference plot (Fig 2c). Also in 1990 derived from the photograph (fig. 2c), the cover of *Hippophae* was 30-40% in both the exclosure and reference plot. In 2015, both exclosure and reference belong to the *Hippophao-Ligustretum* and the exclosure is making a shift towards a *Rhamno-Crataegetum* community (Stortelder et al. 1999), because of the dominant presence of *Crataegus monogyna*. The exclosure has a 40% cover of *Crataegus* and the reference 4%. Furthermore, there are almost no differences between the exclosure and the reference as to cover and height of the total, shrub and herb layer and the species number. The only exception is the presence of *Cynoglossum officinale* and *Jacobaea vulgaris* in the grazed reference plot (Table 2; online appendix Table 1c) indicating disturbance of the soil.

Locations 84, 85, 86: decalcified dune grassland – forest

In 1990, the vegetation in locations 84 and 86 (Fig. 2d) seems comparable to the 1975 situation with small or no impact of rabbits; the dominating grasses *Calamagrostis epigejos* and *Carex arenaria* are not very palatable to rabbits. Location 85 is an exception. In 1990, Populus tremula dominates as trees in the exclosure plot (Fig. 2d); the reference has some low poplar stems and the grassy vegetation is a short turf presumably due to the presence of rabbits.

In 2015 the situation has changed considerably (Fig. 2d). The differences between the exclosure and reference became rather extreme in all three instead of only one (location 85 in 1990). The number of shrub and tree species between the exclosures and the reference is slightly different: 4.7 versus 3.0, but the difference between the cover and the height of the shrub/tree layer of the exclosures and reference is substantial: average cover 50% versus 3%; average height 8 m versus 2 m (Table 1; online appendix Table 1d). Consequently, the cover and height of the shrub layer differs (23.3% versus 3.7%; 3 m versus 1.3 m). There is no big difference in the cover of the herb layer but the average height of the herb layer and low herb layer differs between the exclosure and the reference (50 cm versus 26.7 cm; 20 cm versus 6.7 cm). The average moss cover of the exclosures is 20.7% while in the references it is 61.7%. The references have a higher number of species than the exclosure: 20.6 versus 14.3.

DISCUSSION

Our results show that the 1975 exclosure experiment has a major impact on the development of the vegetation structure. In all exclosures, shrub and forest species have established while this is not the case in most references. This confirms the impact of rabbits as a controlling factor in the establishment of seedlings of shrub and tree species.

Table 2. Differences in species occurrence between the exclosure and reference plots based on the relevés made in July 2015.

Abbreviations of syntaxa:
P.T. = Phleo-Tortuletum
A.S. = Anthyllido-Silenetum
H.L. = Hippophao-Ligustretum
BC-C = Basal Community Calamagrostis epigejos [Cladonio-Koelerietalia].

Abbreviations of taxa:
C. fol. = Cladonia foliacea
C. rang = C. rangiformis
C. cocc = C. coccifera
C. fimb = C. fimbriata
C.mono = Crataegus monogyna
L.vulga = Ligustrum vulgare
S.repen = Salix repens
Q.robur = Quercus robur
R.catha = Rhamnus cathartica
Cyno off = Cynoglossum officinale
Sen jac = Senecio jacobaea
G.cruci = Gentiana cruciata
H.pilos = Hieracium pilosella
G.moll = Geranium molle
L.catha = Linum catharticum
S.nutan = Silene nutans
A.hirsut = Arabis hirsuta
V.canina = Viola canina
V. Hirta = Viola hirta
V.rupest = Viola rupestris
O. repe = Ononis repens
F. adian = Fissidens adianthoides
V.curt = Viola curtisii.

**due to overhanging Populus tree branches from outside the reference plot 85, the average of the (high) tree layer in the reference plots is 4 meters which is relatively high; without the in hanging tree branch the height is 2 meters.*

	P.T.	
	EXCL.	**REF.**
Plot number	80 & 81	80 & 81
Number of sites	2	2
Species specific features		
MOSSES		
Species presence	Hypnum cup.	
LICHENS		
Number of species	6	2
Cover (%)	26.0	2.5
Species	Cladonia furcata C.fol C.rang C.cocc C.fimb C. grayi	Cladonia furcata C. fol
species		
Grass cover (%)		
Shrub cover excluding Hipp. rhamnoides (%)		
Ruderal indicator ^{a} Disturbance indicator ^{b}		
(High) tree layer (m)		
Anthyllido-Silenetum specific features		
# typical species		
Species presence (typical examples)		
# Viola species		
Species presence		

A.S.		H.L.		BC-C	
EXCL.	**REF.**	**EXCL.**	**REF.**	**EXCL.**	**REF.**
82	82	83	83	84, 85 & 86	84, 85 & 86
1	1	1	1	3	3
Cladonia furcata C.fol C.rang C.cocc C.fimb C. grayi					
C.mono L.vulga S.repen Q.robur R.catha	C.mono L.vulga				
		10	36		
		40	2		
Cirsium vulgare [a]	-	-	Cyno off[b] Sen jac[b]		
				8	2*
11	19				
G.cruci H.pilos G.moll L.catha S.nutan A.hirsut	G.cruci H.pilos G.moll L.catha S.nutan A.hirsut V.canina V.hirta V.rupest O.repe F.adian				
0	4				
0	V.canina V.hirta V.rupest V.curtisii				

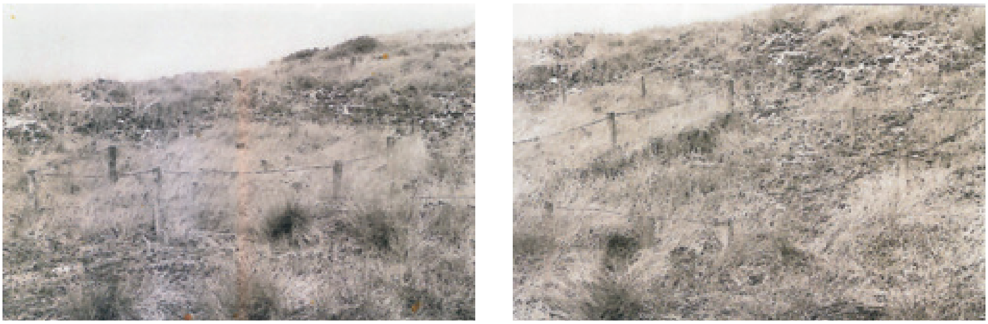
Fig. 2. Photographs of the 1990 and 2015 situation of the exclosure and reference plots.

Fig. 2a. Photographs of the exclosure and reference plots 80 and 81 with southern exposition with a Phleo-Tortuletum plant community.

Location 80 exclosure and reference in 1990:

Location 80 exclosure and reference in 2015:

Location 81 exclosure and reference in 1990:



Location 81 exclosure and reference in 2015:

Fig. 2b. Photographs of the exclosure and reference plots 82 on the northern slope with the Anthyllido-Silenetum.

Location 82 exclosure and reference in 1990:

Location 82 exclosure and reference in 2015:

Fig. 2c. Photographs of the exclosure and reference plots of 83 Hippophae rhamnoides shrubland (Hippophao-Ligustretum).

Location 83 exclosure and reference in 1990:

Location 83 exclosure and reference in 2015:

Fig. 2d. Photographs of the exclosure and reference plots of 84, 85 and 86 in the Bierlap dune valley with the Basal Community of Calamagrotis epigejos [Cladonio-Koelerietalia].

Location 84 exclosure and reference in 1990:

Location 84 exclosure and reference in 2015:

Location 85 exclosure and reference in 1990:

Location 85 exclosure and reference in 2015:

Location 86 exclosure and reference in 1990:

Location 86 exclosure and reference in 2015:

In five out of seven cases (82-86) the biodiversity (species number) dropped marginally to substantial due to excluding rabbits, answering the first research question. Southern exposed locations 80 and 81 form an exception, with a higher species number inside the exclosure mainly caused by the presence of lichen species.

As for the long-laiving shrub species, in most *Crataegus monogyna* was the shrub species present; in three of them *Crataegus* became more or less dominant. Also *Quercus robur* had a high presence in the exclosures and in some *Quercus* covered a substantial part or all of the exclosure. Both species even occurred in one of the southern exposed exclosures (plot 81) with a harsh climate. *Populus tremula* is the third species to dominate in one of the exclosures (plot 85) growing in from a *Populus tremula* forest edge. In the reference *Populus tremula* also occurs, but only as short root sprouts. In one case (location 83), both the exclosure and reference were invaded and dominated by the relatively short living shrub *Hippophae rhamnoides*, but the cover of other shrub species than *Hippophae* was higher inside the exclosure versus the reference (40% versus 4%); this difference of more cover by *Crataegus monogyna* (exclosure 38%; reference 2%) is very likely to the effect of rabbits. This answers the second and third research question. An outlier is the reference of plot 80; *Hippophae* invaded from one side the reference, which did not happen in the exclosure giving deviant results.

Our results indicate that apart from grazing on palatable grasses and herbs and digging, rabbits are keen on feeding on young seedlings with a high protein content and on young sprouts which are more palatable than other parts of trees and shrubs (e.g. Salman & Van der Meijden 1985). The role of the in 1990 introduced livestock is unclear and impossible to separate from the rabbit's impact, because no plots were installed to separate the impact of both. With the outbreak of RVHD in 1989 the rabbit numbers collapsed again. Livestock took over the grazing and might explain the enduring grassland aspect of the references; livestock strongly prefer graminoid species (Lamoot et al. 2005) which might have induced shrub and tree sprouts to also invade some of the references. Whether the 40 years of this research on exclosures and their references is long enough to determine the difference between short and long-living tree and shrub species remains to be answered. But, the physiological lifespan of shrub and tree species is known. *Hippophae rhamnoides* lasts for 25-40 years, and *Crataegus monogyna* and *Quercus robur* last more than 150 years. In most cases *Hippophae* shrubland falls back to grasslands (Van der Hagen et al. submitted), which is on the verge of happening in the reference plot of location 83, while long-living shrub species may well be a trigger for afforestation in the exclosure plot of location 83 (fourth research question).

The above mentioned observations are discussed per location.
Location 80 and 81: open dune grasslands – open dune grasslands with small shrubs
The speed of development on the southern exposed areas with a *Phleo-Tortuletum* with summer temperatures up to 60°C (Brandt 1974) is low. Especially lichens and specific mosses are able to cope with the climate extremes on these southern expositions. A lichen-dominated stage can last over several decades, which seems to be the case inside the exclosures.

The exclosure plots 80 and 81 developed in a comparable way. In both exclosure plots shrubs have developed and the cover of the herb layer (grasses) is much higher due to the exclusion of rabbits. Surprisingly, the exclosures have an average higher number of species, especially of lichens. This higher biodiversity inside the exclosure is in contradiction with other findings (e.g. Olofsson et al. 2008; Ranwell 1960; Gillham 1955; Watt 1957, 1961, 1962; Zeevalking & Fresco 1977). Because of the rabbit proof fence, small amounts of in-blowing sand was trapped inside the exclosure. Over decades, the average level of the soil became 5 cm higher inside the exclosure than in its surroundings. This may have affected nutrient and water availability (e.g. the high presence of *Hypnum cupressiforme*) inside the exclosure. There are some explanations possible. First, autonomous or livestock induced blowout development causing an open sandy situation in the proximity of location 80 and in the reference plot. This sandy situation is less species rich than the lichen rich vegetation inside the exclosure. Second, the 2015 situation of the reference plot of location 80 is dominated by side intruded *Hippophae* being a less species rich plant community. Third, the rabbit proof fence of the exclosure caught sand to settle inside the exclosure. This in-blowing sand may be just stressful enough to maintain a vegetation rich in species without grass encroachment; grass encroachment in the references is prevented by livestock and/or rabbit grazing.

The combined comparison between the reference plots of location 80 and 81 and its exclosures is difficult. The development of the reference plot of location 80 differs greatly from plot 81. This is due to the lateral ingrowth of *Hippophae* in the reference plot of location 80. In 1990 the reference plot of location 80 was almost only open sand due to the presence of a natural blowout (Fig. 2a: 1990). The 1990 bare sand situation of the reference plot of location 80 cannot have been induced by livestock, because livestock was introduced end 1990. In 2015 side ingrowth of the pioneer species of *Hippophae rhamnoides* (Zoon 1995) has manifested changing the development of the reference drastically and incomparable to the reference plot of location 81 with no shrub intrusion.

Location 82: Closed dune grassland – shrubland

Excluding rabbits had a great impact on the vegetation of this northern exposed slope. Within 40 years most of the exclosure has been taken over by shrubs. Van Groenendaal et al. (1982) and Salman & Van der Meijden (1985) already described the survival of the young sprouts of *Crataegus monogyna* following the outbreak of myxomatosis. This exclosure suggests that it is also the case for four other shrub species (Table 2; online appendix Table 1b). Van Tongeren (2006) also describes the settling of different shrub species in a rabbit exclosure experiment in every following year over seven years. Typical species of the grassland community like *Gentiana cruciata, Silene nutans* and *Galium mollugo* are still present in exclosure and reference; they are quite robust species with robust roots. Inside the exclosure though, most typical species of the *Anthyllido-Silenetum* are lost like *Picris hieracioides, Euphrasia stricta, Fissidens adiantoides, Viola rupestris, Viola hirta, Viola canina, Taraxacum section Erythrosperma, Prunella vulgaris, Veronica arvensis* and *Ononis* repens. The reference has an open character and is partly sand overblown as indicated by *Viola curtisii, Cerastium semidecandrum, Phleum arenarium, Syntrichia ruralis* and *Bromus hordeacaeus*. The sand originates from a natural blowout in the southern exposed slope on the other side of the hill. This in-blowing sand must have changed the species composition of the reference, keeping it in a more pioneer situation. The sand caught in the vegetation under the shrub inside the exclosure adds up to the existing soil profile without changing the situation into a pioneer situation. The higher species richness in the more sandy and rabbit grazed reference is consistent with other exclosure research (Assendorp 1990; Olofsson et al. 2008). The development of shrub started during the exclosure of rabbits, but whether the post 1990 livestock grazing is partly responsible for the very short herb layer in the reference is not separable from the fluctuating rabbit influence.

Location 83: Grassland – Hippophae shrubland

At the start of the exclosures in 1975, both the exclosure and reference plots and their surroundings consisted of dune grassland (Boerboom 1960). In location 83, the manifestation of *Hippophae rhamnoides* by seeds and/or root ingrowth started later than the 1954 outbreak of myxomatosis in other parts of Meijendel. In 1990, about 30-40% of the cover was *Hippophae* (Fig. 2c). In 2015 both the exclosure and the reference as well as their surroundings are dominated by *Hippophae rhamnoides*. Considering the lifespan of about 40 years, these *Hipphophae* shrubs will have their peak around 2015 and will start decaying soon. In the absence of rabbits, young sprouts from *Crataegus* seeds have established earlier in the exclosure than in the reference and taken over the dominant position of *Hippophae*. The low presence of *Crataegus* in the reference plot might indicate that in the near future this plot will fall back into a dune grassland, like most *Hippophae* dominated shrubland did in Meijendel (Van der Hagen et al. 2022a).

The disturbance impact of livestock and/or rabbits is illustrated by the presence of two herb species: *Cynoglossum officinale* and *Jacobaea vulgaris*. Seeds of both species germinate more easily in a more or less open soil when organic matter and lime rich sand are mixed. This mixing is likely to be caused by livestock trampling and/or rabbit scrapes (Assendorp 1990) preferably in combination with dung (Burggraaf-Van Nierop & Van der Meijden 1984). *Hippophae* shrubs in the regressive succession phase open up and livestock pushes it aside to get to the preferred graminoids (Lamoot et al. 2005). Especially seeds of both mentioned species can be transported though the fleece of the animals.

Locations 84, 85 and 86: decalcified dune grassland – forest

In the former arable land of the Bierlap valley, the dominance of three different shrub/tree species in the exclosures is imminent. In the exclosure plot of location 84, again *Crataegus* is dominating in the exclosure together with the climber *Humulus lupulus*. The dune grassland part consists of *Calamagrostis epigejos* and *Carex arenaria*, which are poorly palatable for rabbits (Fig. 2d). After the introduction of livestock in autumn 1990, the amount of (dead) biomass was reduced significantly resulting in the short grazed 2015 situation (Fig. 2d; Ten Harkel & Van der Meulen 1996). Grazing by rabbits seems essential to prevent graminoids to become dominant in the dry dunes. If graminoids are dominant, especially with a large amount of dry organic material, grazing by horses can initially be an appropriate method to restore the original grassland vegetation (Gordon 2003; Köhler et al. 2016), facilitating rabbits. In the reference plot of location 85, rabbits (and maybe later on also livestock) did prevent *Populus tremula* to dominate the plot by root sprouts, as is the case in the exclosure.

In the exclosure plot of location 86, the 2015 situation is dominated by *Quercus robur*; this tree must have originated from seeds and most likely shortly after 1990 (Fig. 2d).

In 2015, the exclosures still consist of species poor grassland and all in combination with a high cover of a tree species. This means that there is a large impact on shrub and tree cover and its consequences in species diversity (14.3 versus 20.7) due to excluding rabbits and later on livestock. The results are consistent with similar research in coastal dunes in Cumbria (McNab n.y.) and arid and semi-arid grasslands of western North America (Dobkin et al. 1998). This means that rabbits are important in preventing shrub and forest development both for species, which propagate with seeds (e.g. *Crataegus monogyna, Quercus robur*) as for species with root dispersal (e.g. *Hippophae rhamnoides, Populus tremula*). Livestock favors graminoids (Lamoot et al. 2005) and controls the dominance of the biomass of grasses, open up the vegetation and herewith increases species diversity in the reference (Ten Harkel & Van der Meulen 1996).

Representativeness of the exclosures

The number of experimental locations and plots is small and in some cases the number of plots per vegetation type is only one, hampering statistical analysis. Also the rabbit proof fence may have had additional effects, by sand entrapment; inside the exclosure of the southern exposed locations, the soil was on average a few centimeters higher than the direct surroundings. On the other hand, livestock might have had a large impact on damaging the vulnerable top layer of the vegetation in the references leading to a lower number of species. Nonetheless, the differences between the exclosures and its references over these four decades is immanent (see figures 2).

Fig. 3 shows the development of shrubs and trees (afforestation) in Meijendel (± 2.000 ha) over a period of 76 years. The viral diseases of myxomatosis (around 1954; Van Koersveld 1955), when more than 95% of the rabbits died, and RVHD (1989) speeded up the closing of the landscape. More than 85% of *Crataegus* in Meijendel originates from the first three years after the myxomatosis outbreak (Salman & Van der Meijden 1985).

Natura 2000 conservation consequences

The consequence of a temporary decimation of rabbits due to epidemic myxomatosis and RVHD and its changing virulence will remain visible in the near future. This means that due to undulating amounts of rabbits, waves of tree and shrub species get the opportunity to further close the dune landscape. The consequences of this phenomenon for nature conservation in a Natura 2000 area are great. Under European law, Grey dunes (H2130) are a priority habitat and they are critically endangered both in quantity and quality. Shrub and tree encroachment means the disappearance of the priority dune grasslands (Grey dunes H2130; Council of the European Communities 1992) and here-

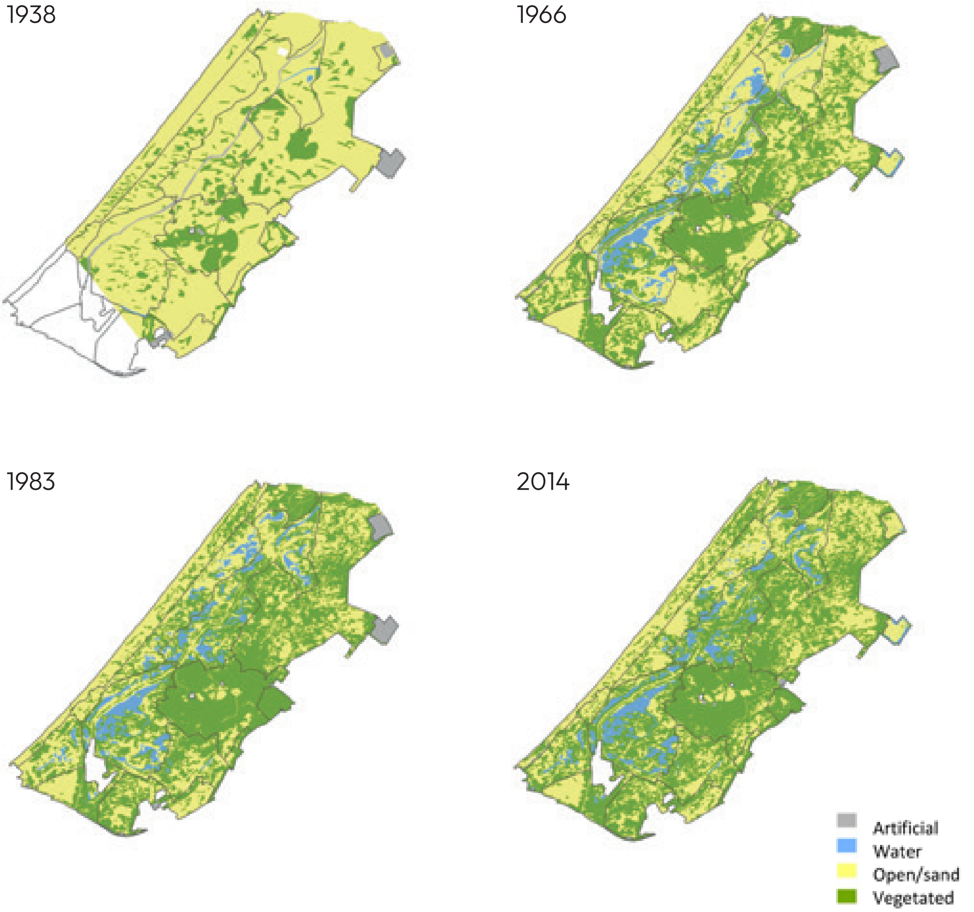


Fig. 3. Development of the open/sandy vegetation versus shrubland/forests in Meijendel (± 2.000 ha) in 1938, 1966, 1983 and 2014 based on aerial photographs. The myxomatosis outbreak was in 1954; the Rabbit Viral Hemorrhagic Disease outbreak was in 1989.

with a very important focal point of nature conservation. The rabbit proof fence had a great impact on the development of the vegetation, proving the hypothesis that rabbits have a crucial role in maintaining an open dune grassland landscape. The biodiversity within the exclosures has dropped, except for the southern exposed exclosures. The lack of rabbits may cause encroachment of dune grassland by long-living species, resulting in a loss of grassland habitat for a century or longer. This means that dune grasslands are overrun by long-living shrubs and trees, which may be considered a loss of dune grasslands for a century or more. These differences found between the exclosures and their references may have great implications concerning active nature management and achieving the Natura 2000 goals. As rabbit numbers strongly vary, it is necessary to actively control the indigenous tree and shrub growth in Meijendel to prevent long-term encroachment. In 2019 the associated costs are about 5 million euros (Van der Hagen 2019) for the Meijendel area alone. Other dune areas in north-western Europe will most probably face the same situation.

APPENDIX TABLES

Appendix table 1a. Changes in species composition of the exclosures and their reference relevés of the Phleo-Tortuletum; major differences are highlighted in bold.

PLOTCODE DUNEA	PQ 80A EXCL.	PQ 81A EXCL.	PQ 80B REF.	PQ 81B REF.
Datum (year/month/day)	20150706	20150701	20150706	20150706
Area (m^2)	25	25	25	25
Exposition (`NWZOVX')	Z	Z	Z	Z
Inclination (degrees)	5	20	7	7
Total cover (%)	**85**	**98**	**50**	**40**
Cover tree layer (%)	0	0	0	0
Cover shrub layer (%)	7	10	**45**	1
Cover herb layer (%)	**40**	**70**	**3**	**20**
Cover moss layer (%)	70	60	25	30
Cover humus layer (%)	10	0	10	0
Height (high) tree layer (m)	-	-	-	-
Height low tree layer (m)	-	-	-	-
Height (high) shrub layer (m)	0.6	1	1	0
Height low shrub layer (m)	0	0.4	0	0.2
Av. height (high) herb layer (cm)	15	25	15	15
Av. height low herb layer (cm)	5	10	5	10
Max. height herb layer (cm)	60	60	70	40
Number of species	21	33	22	19
Hippophae rhamnoides	**8**		**38**	
Crataegus monogyna		**8**		**1**
Quercus robur		**2**		
Phleum arenarium	4	2	2	2
Syntrichia ruralis	3	18	18	18
Hypnum cupressiforme v. lac.	8	**38**	2	8
Senecio jacobaea	3	2	2	2
Leontodon saxatilis	2	2	2	2
Ononis repens	2	2	3	8
Ceratodon purpureus	8	2	3	3
Carex arenaria	3	4		4
Cerastium semidecandrum	4	2	3	
Festuca rubra	2	**18**	2	

PLOTCODE DUNEA	PQ 80A EXCL.	PQ 81A EXCL.	PQ 80B REF.	PQ 81B REF.
Datum (year/month/day)	20150706	20150701	20150706	20150706
Senecio inaequidens	1	2	2	
Corynephorus canescens	8		2	
Cladonia furcata	**2**		**3**	
Cladonia foliacea	**38**			**2**
Elytrigia atherica	8	3		
Koeleria macrantha	2	**18**		
Myosotis ramosissima	2	2		
Saxifraga tridactylites	3	2		
Erophila verna	2	2		
Cladina rangiformis	**8**	**2**		
Cladonia coccifera		**2**		
Cladonia fimbriata		**2**		
Cladonia grayi		**2**		
Homalothecium lutescens		3		
Senecio sylvaticus		1		
Orobanche caryophyllacea		2		
Galium mollugo		18		2
Tortella flavovirens		2		18
Galium verum		3		3
Calamagrostis epigejos		3		4
Rubus caesius		**18**		8
Cynoglossum officinale		2	2	2
Erigeron canadensis		2	2	2
Erodium lebelii		2	2	2
Arabidopsis thaliana		2	2	
Polygonatum odoratum			2	
Eupatorium cannabinum			2	
Solanum dulcamara			2	
Viola curtisii			2	
Sonchus arvensis			1	
Festuca filiformis				2
Pseudoscleropodium purum				2
Number of Lichens	**6**		**2**	
Average cover lichens (%)	**26**		**2.5**	

Appendix table 1b. Changes in species composition of the exclosures and their reference relevés of the Anthyllido-Silenetum; major differences are highlighted in bold, the typical species of the syntaxon are highlighted in bold italics.

PLOTCODE DUNEA	PQ 82A EXCL.	PQ 82B REF.
Datum (year/month/day)	20150701	20150706
Area (m^2)	40	65
Exposition (`NWZOVX')	NO	NO
Inclination (degrees)	30	30
Total cover (%)	**90**	**50**
Cover tree layer (%)	-	-
Cover shrub layer (%)	**70**	**3**
Cover herb layer (%)	**30**	**45**
Cover moss layer (%)	0	30
Cover humus layer (%)	-	-
Height (high) tree layer (m)	-	-
Height low tree layer (m)	-	-
Height (high) shrub layer (m)	**1.5**	**0.8**
Height low shrub layer (m)	0.5	0
Av. height (high) herb layer (cm)	30	10
Av. height low herb layer (cm)	5	5
Max. height herb layer (cm)	80	60
Number of species	**37**	**49**

Crataegus monogyna	**68**	**2**
Ligustrum vulgare	**18**	**2**
Eupatorium cannabinum	8	
Salix repens	**8**	
Quercus robur	**2**	
Rhamnus cathartica	**2**	
Rumex acetosella	2	
Koeleria macrantha	2	
Asparagus officinalis s. officinalis	2	
Asparagus officinalis s. prostratus	2	
Bryonia dioica	**2**	
Solanum dulcamara	2	
Veronica chamaedrys	2	
Rosa canina	**2**	

PLOTCODE DUNEA	PQ 82A EXCL.	PQ 82B REF.
Datum (year/month/day)	20150701	20150706
Lonicera periclymenum	2	
Cirsium vulgare	**1**	
Rubus caesius	18	18
Calamagrostis epigejos	8	4
Galium mollugo	8	3
Carex arenaria	3	4
Aira praecox	3	2
Festuca rubra	3	2
Galium verum	3	4
Gentiana cruciata	2	4
Geum urbanum	2	2
Hieracium pilosella	2	4
Linum catharticum	2	4
Lotus corniculatus v. corniculatus	2	4
Luzula campestris	2	4
Polygonatum odoratum	3	3
Polypodium vulgare	3	2
Sedum acre	2	2
Silene nutans	3	4
Festuca filiformis	3	4
Senecio jacobaea	2	4
Cerastium fontanum	2	2
Arabis hirsuta	2	2
Pseudoscleropodium purum	2	3
Syntrichia ruralis		18
Cerastium semidecandrum		3
Leontodon saxatilis		2
Phleum arenarium		3
Ononis repens		8
Ceratodon purpureus		2
Hypnum cupressiforme v. lacunosum		4
Tortella flavovirens		2
Poa pratensis		3
Cladonia furcata		2
Viola curtisii		3

PLOTCODE DUNEA	PQ 82A EXCL.	PQ 82B REF.
Datum (year/month/day)	20150701	20150706
Sonchus arvensis		1
Picris hieracioides		2
Plantago lanceolata		3
Prunella vulgaris		2
Taraxacum sect. Erythrosperma		2
Veronica arvensis		3
Viola canina		2
Viola hirta		4
Viola rupestris		2
Rosa rubiginosa		1
Erodium cicutarium		2
Euphrasia stricta		3
Bromus hordeaceus		2
Fissidens adianthoides		2
Number of syntaxon species	**11**	**19**
Number of Viola species	**4**	**0**

Appendix table 1c. Changes in species composition of the exclosures and their reference relevés of the Hippophae rhamnoides shrubland (Hippophao-Ligustretum); major differences are highlighted in bold.

PLOTCODE DUNEA	PQ 83A EXCL.	PQ 83B REF.
Datum (year/month/day)	20150701	20150701
Area (m^2)	25	25
Exposition (`NWZOVX')	N	N
Inclination (degrees)	8	8
Total cover (%)	95	90
Cover tree layer (%)	-	-
Cover shrub layer (%)	70	70
Cover herb layer (%)	40	50
Cover moss layer (%)	40	20
Cover humus layer (%)	-	-
Height (high) tree layer (m)	-	-
Height low tree layer (m)	-	-
Height (high) shrub layer (m)	3	2
Height low shrub layer (m)	1.5	1.5
Av. height (high) herb layer (cm)	40	30
Av. height low herb layer (cm)	10	10
Max. height herb layer (cm)	90	70
Number of species	14	15
Hippophae rhamnoides	**18**	**68**
Crataegus monogyna	**38**	**2**
Solanum dulcamara	2	
Festuca filiformis	2	
Senecio inaequidens	2	
Pseudoscleropodium purum	**38**	18
Rubus caesius	18	3
Dryopteris dilatata	8	2
Teucrium scorodonia	8	3
Calamagrostis epigejos	8	18
Carex arenaria	**3**	18
Galium verum	2	2
Rosa canina	2	2
Urtica dioica	**3**	2

PLOTCODE DUNEA	PQ 83A EXCL.	PQ 83B REF.
Datum (year/month/day)	20150701	20150701
Senecio jacobaea		8
Cynoglossum officinale		2
Humulus lupulus		2
Poa pratensis		2
Number of shrub species	3	2
% cover excl. Hippophae	40	4

Appendix table 1d. Changes in species composition of the exclosures and their reference relevés of the BC Calamagrotis epigejos [Cladonio-Koelerietalia]; major differences are highlighted in bold. Species can be present in the different layers: t1=tree layer 1, s1= shrub layer 1; hl= herb layer; ml= moss layer.

PLOTCODE DUNEA	PQ 84A EXCL.	PQ 85A EXCL.	PQ 86A EXCL.	PQ 84B REF.	PQ 85B REF.	PQ 86B REF.
Datum (year/month/day)	20150701	20150701	20150701	20150706	20150706	20150706
Area (m^2)	25	25	25	25	25	25
Exposition (`NWZOVX')	-	-	-	-	-	-
Total cover (%)	95	100	90	80	95	80
Cover tree layer (%)	**30**	**80**	**40**	1	5	3
Cover shrub layer (%)	**20**	**30**	**20**	7	3	1
Cover herb layer (%)	**80**	40	20	30	10	50
Cover moss layer (%)	<1	<1	60	60	85	40
Cover humus layer (%)	**-**	**-**	**25**	**-**	**-**	**-**
Height (high) tree layer (m)	**6**	**10**	**8**	**3**	**(8)**	**1**
Height low tree layer (m)	-	-	-	-	-	-
Height (high) shrub layer (m)	3	3	3	3	0.5	0.4
Height low shrub layer (m)	0	0	1.5	0	0	0
Av. height (high) herb layer (cm)	**50**	**80**	**20**	**20**	**30**	**30**
Av. height low herb layer (cm)	**30**	**20**	**10**	**5**	**10**	**5**
Max. height herb layer (cm)	100	30	60	80	50	60
Number of species	12	19	12	23	23	16
Syntaxon	FG	FG/Pop	FG	FG	FG/Pop	FG

PLOTCODE DUNEA	PQ 84A EXCL.	PQ 85A EXCL.	PQ 86A EXCL.	PQ 84B REF.	PQ 85B REF.	PQ 86B REF.
Datum (year/month/day)	20150701	20150701	20150701	20150706	20150706	20150706
Calamagrostis epigejos	**8**	**8**	**18**	**3**	**2**	**8**
Carex arenaria	**3**	**3**	**3**	**4**	**4**	**18**
Holcus lanatus	**2**	**3**		**8**	**3**	**2**
Festuca filiformis		**3**	**3**	**8**	**2**	**38**
Rubus caesius	8					
Quercus robur	2		**38**			1
Quercus robur	2	8	18		2	
Crataegus monogyna	**38**			2		
Euonymus europaeus	**18**					
Humulus lupulus	3			2		
Humulus lupulus	**38**					
Urtica dioica	3					
Rubus sec. Rubus	**18**					
Brachythecium rutabulum	2					
Agrostis gigantea		18	2		3	2
Lonicera periclymenum		3	2			2
Prunus serotina		8	2			
Lonicera periclymenum		**8**	**18**			
Populus tremula		**82**			2	
Populus tremula		**18**			3	
Rhamnus frangula		2				
Prunus padus		2				
Populus tremula		3				
Prunus padus		2				
Rhamnus frangula		2				
Aulacomnium androgynum		2				
Kindbergia praelonga		2				
Dryopteris dilatata		2				
Acer pseudoplatanus		1				
Rosa canina			2	2		
Solanum dulcamara			2			
Dicranum scoparium			**38**	2	18	3

PLOTCODE DUNEA	PQ 84A EXCL.	PQ 85A EXCL.	PQ 86A EXCL.	PQ 84B REF.	PQ 85B REF.	PQ 86B REF.
Datum (year/month/day)	20150701	20150701	20150701	20150706	20150706	20150706
Hypnum cupressiforme v. lacunosum			**18**	**18**		**38**
Pseudoscleropodium purum	2	3		**38**	**68**	**18**
Crataegus monogyna				8	2	
Luzula campestris				**8**	**3**	**4**
Teucrium scorodonia		2		8	3	
Agrostis capillaris			2	3	3	
Poa pratensis				**2**	**2**	
Veronica officinalis				**2**	**2**	
Anthoxanthum odoratum		2		2	2	
Aira praecox				**2**		**3**
Senecio jacobaea				**3**		**8**
Crataegus monogyna		3		2		
Glechoma hederacea				2		
Rubus caesius				2		
Rubus sec. Rubus				2		
Rhytidiadelphus squarrosus				3		
Rosa canina				2		
Ceratodon purpureus					2	
Betula pendula					2	
Geum urbanum					1	
Viola riviniana					2	
Rosa rubiginosa					2	
Polytrichum piliferum					2	3
Cladina rangiferina						2
Galium verum						2
Rumex acetosella						2
Number of shrub species	4	7	3	3	5	1

Chapter 6

Dutch *Zeedorpenlandschap* dune grasslands and their value for international nature conservation

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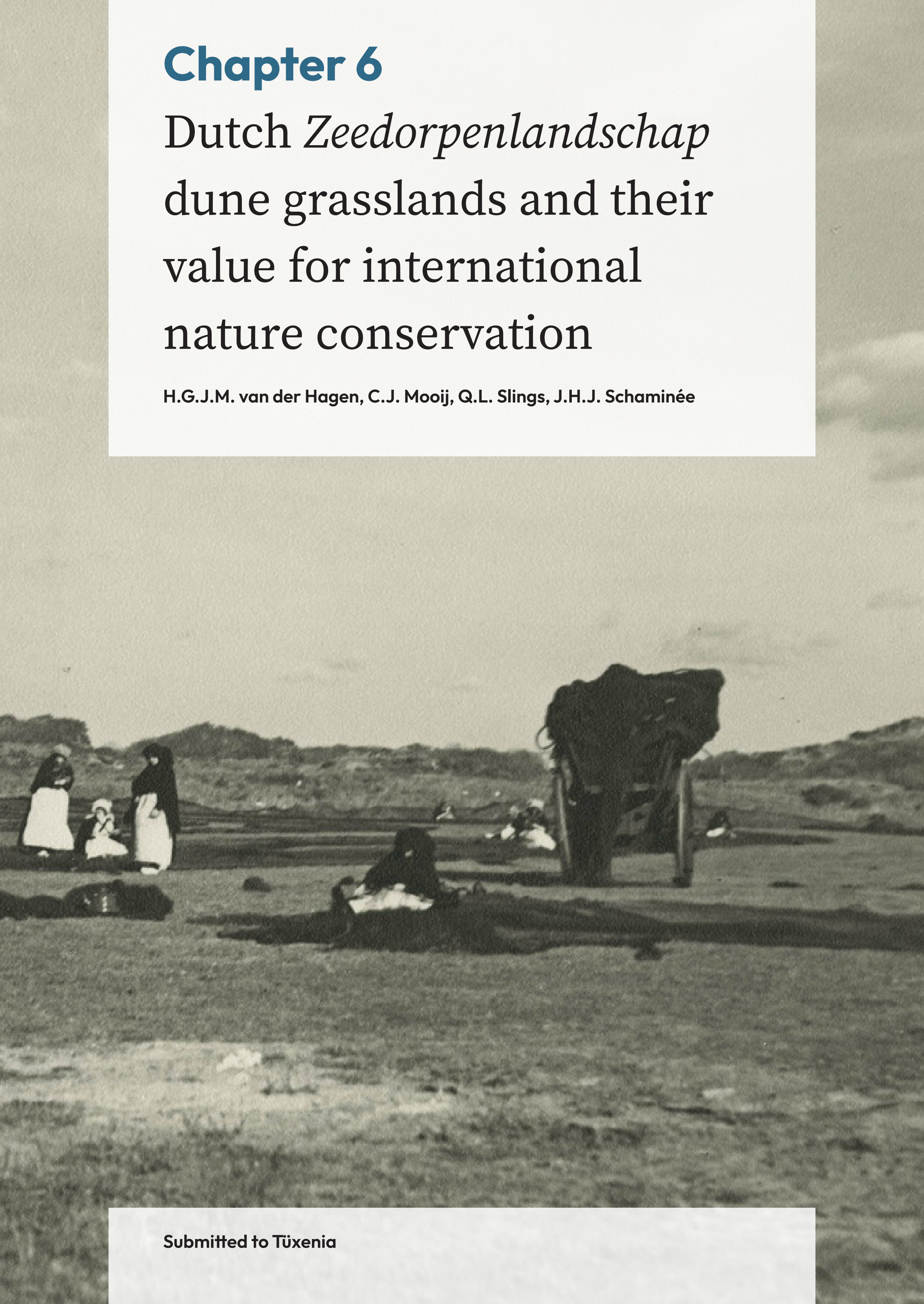

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ABSTRACT

The *Zeedorpenlandschap* is a part of the Natura 2000 habitat type Grey dunes (H2130), and is a landscape type with many rare plant species and various species-rich plant communities that are confined to calcareous dunes along the North Sea. The best examples are found along the Dutch coast, but they are also present on the Belgian and North-Western French coast. This landscape type is the result of traditional land use by inhabitants of coastal villages (in Dutch: *zeedorpen*) with different forms of small-scale disturbances alternating with periods of overexploitation. In this respect, there is striking resemblance with the machair (H21A0, another coastal Natura 2000 habitat type) from the Atlantic coasts of Scotland and Ireland, the Aizjomi landscape from the Baltic coast, and the Mielles from the North-Western French coasts.

Typical Dutch plant associations are the *Sileno-Tortuletum ruraliformis* and the *Anthyllido-Silenetum*. Our study focuses on the current botanical qualitative status of the plant communities of the Dutch *Zeedorpenlandschap*, by analysing spatial and temporal changes in plant species composition in the light of environmental variables. A large database was constructed containing recent and past vegetation relevés. The vegetation around six *zeedorpen* was studied in four different time periods. In 2016, soil samples were taken at all locations with *Anthyllido-Silenetum* community and compared with data collected in calcareous grasslands, characterized by the *Taraxaco-Galietum veri*, which occurs in dune areas away from the *Zeedorpenlandschap*.

The plant communities of the *Zeedorpenlandschap* prove to be rather stable over time, though obvious differences occur in space and time, showing a decline in characteristic species between the first (pre 1970) and second period (between 1970-1985), with a limited species recovery during the last period (post 2000). The observed changes are linked to changes in various environmental variables, in this case to pH, organic matter content, distance to villages (*zeedorpen*), and the occurrence of shell fragments in the organic topsoil. The last variable might relate to natural processes such as blow-outs as well as human-induced disturbance.

In the Natura 2000 network, the Atlantic machairs in Western Ireland and Scotland form a separate habitat type. Floristically however, they are strongly related to the plant communities of the *Zeedorpenlandschap*, specifically the *Anthyllido-Silenetum*, as well as showing similarities in environmental factors and historic land use. However, due to their restricted distribution, a significant number of the differentiating and characteristic plant species of the North Sea coast habitat are missing in the vegetation of the Atlantic machairs. Nevertheless, the floristic and environmental similarity indicates that the machair can be considered as a counterpart of the plant communities of the *Zeedorpenlandschap*, the “machairs of the North Sea coast”. For a better evaluation, more comparative phytosociological and synecological studies are needed.

KEYWORDS Sileno-Tortuletum ruraliformis, Anthyllido-Silenetum, Taraxaco-Galietum veri, grey dunes, Zeedorpenlandschap, Machairs, Aizjomi landscape, Mielles, nature management, disturbance.

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Erweiterte Deutsche Zusammenfassung am Ende des Artikels

1. INTRODUCTION

The coastal 'grey dunes' of the Netherlands are a priority habitat according to the Natura 2000 legislation (Habitat type H2130) (Council of the European Communities 1992; European Commission 2003). All short grasslands and bryophyte or lichen vegetation types along the Atlantic, Baltic and North Sea coast belong to this habitat type. They are especially abundant in the Netherlands, covering a large area and containing unique plant communities with high species diversity, including a number of rare species (Janssen & Schaminée 2003). Their quantity and quality, however, is under threat (Janssen & Schaminée 2003).

1.1 Zeedorpenlandschap

A specific landscape type within the grey dune habitat is found near historic villages (in Dutch *zeedorpen*) along the Dutch coast. They are surrounded by valuable plant communities with many rare species unique to this landscape type (Doing 1974, 1988, 1995; Janssen & Schaminée 2003). This *Zeedorpenlandschap* was first described by Doing (1974), who mapped the various landscape types of the dunes, using a combination of geomorphological, pedological, hydrological and topographical characteristics to describe the vegetation mosaics. Going from outer to inner dunes (west to east) Doing (1974; 1988) distinguished from the dry environments respectively, the A (Ammophila), R (*Rubus caesius*), H (Hippophae), K (Koeleria) and C (Corynephorus) landscapes. The *Zeedorpenlandschap*, type Ks (Koeleria – Silene) is located in the calcareous dunes in the provinces of Noord-Holland and Zuid-Holland, near the villages of Egmond aan Zee, Wijk aan Zee, Zandvoort, Noordwijk, Katwijk and Scheveningen (Slings 1994) (Fig. 1a). In the past, the villagers used their surrounding dunes for a variety of purposes. Examples are: livestock grazing, linen bleaching, repairing and drying fishing nets, manuring with the remains of fish and shrimps, collecting bird eggs and fruits (blackberry), poaching rabbits, collecting marram grass to weave baskets, cutting sods for roof cover, and cutting shrubs (specifically *Hippophae rhamnoides*, *Salix repens*) for heating and for fuelling baking ovens. Around 1850, extensive farming with small potato fields was introduced (Thurkow 1988). All these activities together influenced the dune ecosystem in a unique way (Janssen & Schaminée 2003; Slings 1994). Because of the variable amounts of fish catch, the exploitation of the dunes ranged from small-scale to a pronounced overexploitation.

In this paper, the *Zeedorpenlandschap* is defined as a part of the lime rich dune landscape in The Netherlands, located around these coastal villages and influenced by human activities. This has led to the development of the plant communities of *Sileno-Tortuletum* ruraliformis Doing 1993 and the *Anthyllido-Silenetum* De Leeuw in Braun-Blanquet et Moor 1938 (Schaminée et al. 1996; Weeda et al. 2002; Schaminée et al. 2010).

All these different human uses resulted in specific soil characteristics. The soil was enriched by cattle droppings or fish waste, by organic matter left over from cleaning fishing nets and by making small agricultural fields near the villages. Furthermore, as a result of small-scale sand drifts, created by e.g. rabbit burrowing, the decalcified topsoil was frequently overblown with fresh calcareous sand from deeper, more lime rich sands. Additionally, the topsoil contained more small shell fragments from land snails wintering in the topsoil layer (Fig. 2). The larger shell fragments and snail shells became fragmented by human and livestock trampling (Slings 1994).

1.2 Plant communities and species composition

The *Sileno-Tortuletum* ruraliformis and the *Anthyllido-Silenetum* are characteristic plant communities of the *Zeedorpenlandschap* (Doing 1993; Schaminée et al. 1996; Weeda et al. 2002; Schaminée et al. 2010). Of these two, the *Sileno-Tortuletum* is a pioneer community closely related to the *Phleo-Tortuletum ruraliformis*, but with a significantly higher species richness attributed to a slightly higher soil nutrient availability (Schaminée et al. 1996; Weeda et al. 2002; Schaminée et al. 2010). The *Anthyllido-Silenetum* is even more species-rich and generally occurs on north-facing slopes. In the northern region of the

Fig. 1. Study area with zeedorpen and names of the nature conservation areas (italics) (a). Map of the relevés selected in an area within a 1 kilometre radius from the zeedorpen (b).

Abb. 1. (a) Forschungsgebiet mit Namen der Küstendörfer und Namen der Naturschutzgebieten (kursiv). (b) Karte der Küstendörfer mit den Vegetationsaufnahmen innerhalb eines Distanzradius von einem Kilometer ausgehend vom Zentrum der Küstendörfer.

Dutch lime rich dunes, this plant community also occurs on relative flat areas but only on the higher parts and at the higher edges of dune slacks. The *Anthyllido-Silenetum* is more closed, with hemicryptophytes much more prominent than in the *Sileno-Tortuletum*. The *Anthyllido-Silenetum* is one of the rarest and most threatened plant communities in the Netherlands (Schaminée et al. 1996; Weeda et al. 2002; Schaminée et al. 2010). Its counterpart association in coastal sand dunes away from the *Zeedorpenlandschap*, is the *Taraxaco-Galietum veri* (Boerboom 1957 em. Weeda, Doing et Schaminée), which is most common on relatively flat to undulating parts of the dune landscape (Boerboom 1958) or Doing's R (*Rubus caesius*)-landscape (Doing 1988).

Characteristic plant species of the *Zeedorpenlandschap* are: *Silene conica, Anisantha tectorum, Artemisia campestris subsp. maritima, Poa bulbosa, Milium vernale, Alyssum alyssoides, Asparagus officinalis subsp. prostratus, Silene otites, Silene nutans, Picris hieracioides,*

Fig. 2. Shells and shell fragments of snails in the organic top soil layer. © Q.L. Slings.

Abb. 2. Schneckenhäuser und -fragmente in der oberen organischen Bodenschicht.

Eryngium maritimum, Calystegia soldanella, Bunium bulbocastanum, Anthyllis vulneraria, Orobanche caryophyllacea, Orobanche picridis, Orobanche purpurea, and *Anacamptis pyramidalis var. dunensis* (Slings 1994; Doing unpublished manuscript, Schaminée et al. 1996; Weeda et al. 2002; Janssen & Schaminée 2003; Schaminée et al. 2010; Londo et al. 2016).

1.3 International context

The *Zeedorpenlandschap*, as defined in this paper, appears to be confined to the Dutch coastal sand dunes, but is also present along the Belgian coast by the closely related association *Anthyllido-Thesietum* (Zwaenepoel 2014), but is not described as part of the *Zeedorpenlandschap* like Doing (1988; 1995) has in The Netherlands. Similar, a plant community depending on human activity might also be present along the North-Western coast of France called "Mielles" with the Hornungio-Tortulem ruraliformis (Gehu 1997; Duhamel et al. 2017), but the relevance is unclear yet. Sture (2012) describes the "Aizjomi" landscapes in Latvia. This has a resemblance in the human activities to the Dutch *Zeedorpenlandschap*. The dunes surrounding small sea side villages are under small scale agricultural use with a seemingly comparable dynamic utilization, depending on rhythms of nature and historical events. The great difference is that these dunes are poor in lime or lime is absent. This means that the characteristic *Zeedorpenlandschap* species are absent and so the Aizjomi landscape will not be further discussed in this paper.

Another related coastal landscape type is the “Machair”, on the Atlantic west coasts of Ireland and Scotland. Machairs are also determined by historic land-use as grazing, small agricultural use affected by organic waste (by humans or natural causes). The difference with the *Zeedorpenlandschap* is, that Machairs are more exposed to wind, waves and salt, and frequently endure severe storms in autumn and winter. Also the amount of precipitation is considerably higher. Both systems have quite a few species in common like *Asperula cynanchica*, but their different geographic position results in quite large floristic differences. For example, *Orobanche* and *Silene* species do not occur in the machair grasslands. At a European scale, Machairs are recognized as a valuable landscape type, protected under the Habitat directive as Special Areas of Conservation (H21A0) (European Commission 2003; Cooper et al. 2005; JNCC 2016). The *Zeedorpenlandschap* habitats are also protected under the Habitat directive, but only as a part of the grey dunes (H2130_A) and not as separate characteristic habitat type, let alone a landscape type. The similarities and differences are dealt with in the discussion chapter.

1.4 Decline and restoration

During the last century, the *Zeedorpenlandschap* declined because the land-use changed. From around 1885 onwards, the economic focus of several of the *zeedorpen* shifted from agricultural use in the surrounding dunes to a luxurious spa-bathing culture in the neighbourhood of the beach, like in Scheveningen (Slings 1994; Ehrenburg et al. 1995; Slings et al. 2007; Mooij 2018). At the same time, village expansion led to dune habitat loss (Slings 1994; Ehrenburg et al. 1995), which, through a decline of plant population size, can decrease genetic vitality of populations of the endangered species (Oostermeijer et al. 1994). Around some of the villages mass tourism developed, which led to a higher rate of loss of species, maybe due to a higher rate of disturbance (e.g. by bathers getting to the beach).

In the mid 1950’s, the rabbit population virtually collapsed (Van Koersveld 1955) due to myxomatosis. Starting in the mid-fifties, an increased nitrogen deposition led to grass encroachment and loss of plant biodiversity (Van Dijk 1992; Ehrenburg et al. 1995; De Bonte et al. 1999; Mourik 2004, Van den Bos 2007). In the 1990’s, in many areas, livestock grazing was introduced to preserve the valuable coastal vegetation types. Grazing was expected to affect the vegetation structure, and decrease the cover of dominant graminoids (De Bonte et al. 1999; Lamoot et al. 2005). It was also proposed to re-introduce or simulate the historic land uses required for the long-term survival of these habitats (Slings 1994; Freund et al. 2015). The effects of the vegetation of the *Zeedorpenlandschap* differ per area. In most cases, the introduction of livestock grazing could not stop the decline of the characteristic plant communities. Only near Wijk aan Zee, a positive effect of grazing on the quality and distribution of the plant communities was observed (Van den Bos 2007; Slings unpublished). South of Zandvoort, livestock did affect the vegetation structure, but only a minor recovery of the characteristic species was found after ten years of grazing (Ehrenburg et al. 1995; Mourik 2004). In Meijendel, *zeedorpen* species declined even further after the introduction of livestock (Van der Hagen et al. 2015; Van der Hagen et al. 2020b). On the other hand, in the 75 ha of the Noordwijkse Golfclub north of Noordwijk (operational at this site since 1974) most characteristic *zeedorpen* species are present (Inberg et al. 2007); in the surrounding dunes these species are missing and only the *Taraxaco-Galietum* verum exists there. Golf courses appear to mimic the minor disturbances needed, resulting in the establishment of species of the *Anthyllido-Silenetum*. This research is intended to give an overall review on the possible restoration of species since 1990.

1.5 Research questions and hypothesis

In this study, we qualitatively analysed vegetation and soil characteristics in all Dutch dune areas with *Zeedorpenlandschap* elements. The following questions were addressed: (1) Is the present species composition of the characteristic plant communities still comparable to the former one? (2) How did the quality of all *Zeedorpenlandschap* plant communities change over time? (3) What is the difference in botanical quality of each *Zeedorpenlandschap*? (4) What are the differences in environmental parameters between the *Anthyllido-Silenetum* and the *Taraxaco-Galietum veri*? (5) What are the floristic and environmental similarities and dissimilarities between the plant communities of the *Zeedorpenlandschap* (part of H2130A) and the Machairs (H21A0)?

The hypothesis is that thanks to recent management activities, the typical plant communities of the *Zeedorpenlandschap* still survive despite the disappearance of historic small scale land use and periodic overexploitation.

2. MATERIAL AND METHODS

Vegetation and species changes were studied over time by comparing new relevés with historic ones from the Dutch National Vegetation Database (DNVD) (Schaminée & Janssen 2006) as described in (Schaminée et al. 1996) and (Weeda et al. 2002). Spatial differences were studied by comparing the species composition of the relevés among different coastal villages along the Dutch coast. To test which environmental variables best explain these differences, we compared environmental variables between the plant communities of the *Zeedorpenlandschap* belonging to the association *Anthyllido-Silenetum* and dry calcareous grasslands of the association *Taraxaco-Galietum veri*. Nomenclature of the vascular plants follows Van der Meijden (2005), for bryophytes we followed Siebel and During (2006), and lichen names follow Van Herk & Aptroot (2004). Syntaxa names are according to Schaminée et al. (1996).

Table 1. Names of the study areas with size, owner and manager as given in figure 1a.

Tabelle 1. Namen der Forschungsgebiete mit Oberfläche, Eigentümer und der Manager wie gezeigt in Abbildung 1a.

AREA NAME/ GEBIEDSNAME	HA	OWNER/EIGENTÜMER	MANAGER
Noord-Hollands Duinreservaat	5,300	Provincie Noord-Holland	PWN
Nationaal Park Zuid-Kennemerland	2,500	Provincie Noord-Holland	PWN, Natuurmonumenten, Staatsbosbeheer, private owners
Zuidduinen	40	Zandvoort Municipality	Waternet
Amsterdamse Waterleidingduinen	3,400	Amsterdam Municipality	Waternet
Duinen van Noordwijk	640	Staatsbosbeheer	Staatsbosbeheer,
Coepelduinen	188	Staatsbosbeheer	Staatsbosbeheer
Berkheide	1,137	Staatsbosbeheer	Staatsbosbeheer, Dunea
Meijendel	1,875	Staatsbosbeheer, Den Haag Municipality	Dunea
Westduinpark	240	Den Haag Municipality	Municipality of Den Haag

2.1 Study area

The study area consists of dry grasslands in the calcareous part of the Dutch coastal dunes, between Egmond aan Zee in the province of Noord-Holland and Scheveningen in the province of Zuid-Holland (Fig. 1b) in nature reserves surrounding the following six *zeedorpen*: Egmond aan Zee, Wijk aan Zee, Zandvoort, Noordwijk, Katwijk, and Scheveningen. These nature reserves are also important for recreation, the production of drinking water, and as sea defence. Nearly all sites are protected under the EU Habitat Directive (Council of the European Communities 1992). From north to south, Table 1 gives the areas, the amount of hectares, the owner and manager(s). Most of the dune areas are accessible for visitors, although in most areas restricted to paths. Large parts of the area are grazed by various livestock, and locally – such as in the Amsterdamse Waterleidingduinen – also by large numbers of fallow deer, Dama dama (Van Til & Mourik 1999; Ehrenburg et al. 1995; Inberg et al. 2007, 2010).

2.2 Database

A database was created in Turboveg (Hennekens & Schaminée 2001) containing all historic relevés present in the DNVD (Schaminée & Janssen 2006) made in the area under investigation and classified as *Sileno-Tortuletum ruraliformis* or *Anthyllido-Silenetum*. The database was supplemented with relevés of the *Zeedorpenlandschap* not present in the DNVD and made available by the managers of the nature reserves in the study area.

2.3 Vegetation relevés

Between April 22 and July 8 in the year 2016, 96 new relevés were made in the *Sileno-Tortuletum* and the *Anthyllido-Silenetum* in the *Zeedorpenlandschap*, and the *Taraxaco-Galietum veri* as a reference community in the surrounding areas. The locations of the relevés were determined in the field on the basis of characteristic species of the abovementioned vegetation types. For the *Sileno-Tortuletum*, the selection was based on *Silene conica*, *S. otitis*, *Artemisia campestris subsp. maritima*, *Anisantha tectorum* and *Asparagus officinalis subsp. prostratus*, in combination with pioneer species like *Phleum arenarium* and *Syntrichia ruralis var. arenicola*. For the *Anthyllido-Silenetum*, keystone species were *Anthyllis vulneraria*, *Anacamptis pyramidalis*, *Orobanche purpurea*, *O. picridis*, *O. caryophyllacea*, *Asparagus officinalis subsp. prostratus*, *Silene nutans* and *Picris hieracioides*. Plots representing the *Taraxaco-Galietum veri* association were based on the occurrence of *Viola rupestris*, *Festuca filiformis*, *Gentiana cruciata*, micro-species of *Taraxacum section Erythrosperma* and other Viola species, like *V. canina* and *V. hirta* (Weeda et al. 2002). Relevés were made in 2x2 m plots; because of homogeneity reasons, occasionally a plot was reduced to 1x2 m. The presence and cover of species were recorded following the Braun-Blanquet scale as adapted by Barkman, Doing and Segal (Van der Maarel 1979).

2.4 Soil samples

Soil characteristics were studied in all vegetation relevés of the *Anthyllido-Silenetum* and the *Taraxaco-Galietum veri*. The *Sileno-Tortuletum* ruraliformis and *Phleo-Tortuletum ruraliformis* were not sampled, as there are no developed soil profiles to sample in these pioneer communities. The soil profile was sampled with a Wardenaar-type soil profiler (Fig. 3); www.Eijkelkamp.com, product nr. 05.08) in the centre of each plot. In the sample of this soil profiler, it is easy to distinguish the different layers based on differences in colour and easy to sample the soil for lab analysis. The thickness of the layers was measured in centimetres with a ruler. Subsequently, the profile was photographed, after which it was divided lengthwise. From one half, soil samples were taken from the centre of each layer for further analysis in the laboratory. On the other half, several characteristics were determined directly in the field, such as pH and the calcium carbonate reaction. For each soil layer, we determined the colour with the Munsell Color chart. To make sure that colours were identified in the same way, the samples were wetted with demineralized water before the colour was determined. Soil pH was determined with pH-indicator strips for two different ranges, from 4.0-7.0 and from 6.5-10.0. Soils were wetted with demineralized water before the pH strips were pressed into the soil to make a clear reaction of the strips possible. Content of calcium carbonate was quantitatively measured in the field with hydrochloric acid (10%) by assessing the effervescence (bub-

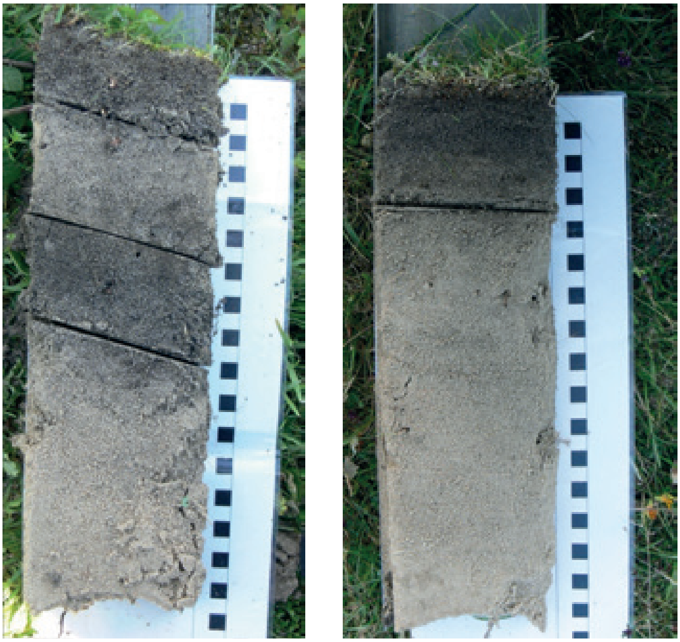


Fig. 3. Examples of two soil samples with four distinguishable soil layers from an overblown profile (left) and only two soil layers from a relatively stable area (right).

Abb. 3. Beispiele von zwei Bodenprofilen. Links ein Profil das mit mehreren Schichten von Sand überweht wurde. Rechts ein sehr stabiles, nicht von Sand überdecktes Profil.

ble) reaction (strong-weak-none). The reaction was classified in three classes, according to the field guide for humus forms (Van Delft 2006). The amount of four sizes of shell fragments and three sizes of root fragments were determined in every soil layer. Fig. 3 gives an example of a set of soil profiles sampled with a Wardenaar profiler.

For each soil layer, in the lab the pH-H2O, Organic Matter content (OM), P-Olsen, and Ca2+ were determined. The pH-H2O was measured in demineralised water according to Reeuwijk (2002). OM was measured in several steps according to Houba et al. (1997); after drying at 105 °C, the samples were weighed, subsequently heated to 550 °C and then reweighed to calculate the dry matter content, the moisture content and the organic matter content. Phosphorus was determined based on Olsen's method (Olsen et al. 1954) and measured according to Houba et al. (1997). The calcium content (Ca2+) was measured in demineralised water with an Atomic Absorption Spectrometer (Varian AA240FS fast sequential atomic absorption spectrometer).

2.5 Data analysis

The species composition of the historic data was compared with that of the newly collected relevés by means of the software package JUICE version 7.0 (Tichý 2002; Berg & Magnes 2019). A Detrended Correspondence Analysis (DCA) was carried out to relate species composition to gradients of theoretical variables (Hill & Gauch 1980; Jongman et al. 1995). For the DCA analysis, all vegetation layers were combined and the adapted Braun-Blanquet cover-abundance scale was converted to an ordinal scale (Van der Maarel 1979). A zero was entered for missing values. DCA analysis was performed using the vegan package in R (R core team 2013). Graphs of the site scores of the first two DCA axes were made in Excel.

For the temporal trend analysis, four time periods were distinguished: (1) <1970, (2) 1970-1985, (3) 1985-2000 and (4) >2000. The first period is over a longer period of time for a more equal distribution of the number of the relevés per period. The % presence and median cover abundance of characteristic species of the *Zeedorpenlandschap* were analysed for the study area as a whole and around each individual village.

For the spatial gradient analysis, we used all relevés within a zone of one kilometre around the six coastal villages (Fig.1b). Apart from multivariate analysis, differences in environmental variables between the plots assigned to the *Taraxaco-Galietum veri* and the *Anthyllido-Silenetum* were tested. For this test, we divided the relevés in two groups based on their vegetation type assigned by JUICE using Modified TWINSPAN Classification (Hill 1979; Roleček et al. 2009). The following environmental variables per layer were included: pH-H2O, OM, P-Olsen and Ca2+, shell material, root amount, number of soil layers and the distance to the nearest village. The latter was measured for each relevé in ArcMap 10.3.1. with a 'near' function from point (relevé) to polygon (nearest village). For the various soil characteristics, we tested whether or not the mean values of the groups significantly differed with T tests (in cases of normal distribution) or Mann-Whitney U tests (in cases of non-normal distributions that could not be normalized by data transformation).

3. RESULTS

3.1 Developments in time within plant associations

The two associations will be discussed separately. Within the DCA-diagram (axis 1-2) the relevés belonging to the *Sileno-Tortuletum* from the DNVD (pre 2016) and the new relevés of 2016 fully overlap, indicating the similarity in species composition (Fig. 4). Focusing on individual species, some small shifts occurred in their relative degree of presence (Table 2). From the group of characteristic *zeedorpen* species, in the fieldwork relevés some species were reduced compared to the data of the DNVD e.g. *Silene conica*. On the other hand, the presence of some species, e.g. *Milium vernale* and *Silene otites*, seems to have increased based on a comparison of relevés representing this association. In the group of accompanying species, shifts in species presence occurred. In most cases, only their relative % presence changed, e.g. *Daucus carota* and *Jacobaea vulgaris*. Some species, e.g. *Senecio inaequidens* (a relatively new exotic species from Southern Africa) and *Valerianella*

Table 2. Synoptic table with presence degree (%) and median abundance cover of species of the DNVD relevés and the 2016 fieldwork relevés of the Sileno-Tortuletum; zeedorpen species in blue, species that increased in the fieldwork relevés compared to the DNVD relevés in green and species that decreased in red.

Tabelle 2. Synoptische Tabelle mit Präsenz (%) und medianer Bedeckung der Pflanzenarten aus den Aufnahmen der DNVD und denen der Feldarbeit 2016vom Sileno-Tortuletum; Pflanzenarten der Küstendörfer werden in Blau, Pflanzenarten, die zwischen den Feldaufnahmen 2016 und denen aus der DNVD zugenommen haben, werden in Grün und Pflanzenarten, die abgenommen haben, in Rot wiedergegeben.

GROUP NO.	1		2	
NO. OF RELEVÉS	DNVD DATABASE: 215		FIELDWORK OF 2016: 33	
Alyssum alyssoides	6	1	6	+
Anisantha tectorum	42	1	48	+
Artemisia campestris subsp. maritima	26	2	30	2
Asparagus officinalis subsp. prostratus	24	+	24	+
Milium vernale	8	+	18	1
Orobanche caryophyllacea	3	+	6	+
Poa bulbosa	14	2	.	
Silene conica	59	+	45	1
Silene otites	24	+	33	1
Hypochaeris radicata	32	+	64	+
Daucus carota	34	+	61	+
Jacobaea vulgaris	22	+	61	+
Helictotrichon pubescens	22	+	58	+
Plantago lanceolata	34	+	58	2
Veronica arvensis	35	+	55	+
Ammophila arenaria	30	+	55	+
Vicia lathyroides	23	+	48	+
Senecio inaequidens	.		30	+
Valerianella locusta	.		12	+
Hieracium umbellatum	36	+	12	+
Ceratodon purpureus	22	1	3	+
Rhinanthus minor	14	+	.	
Crepis capillaris	12	+	.	

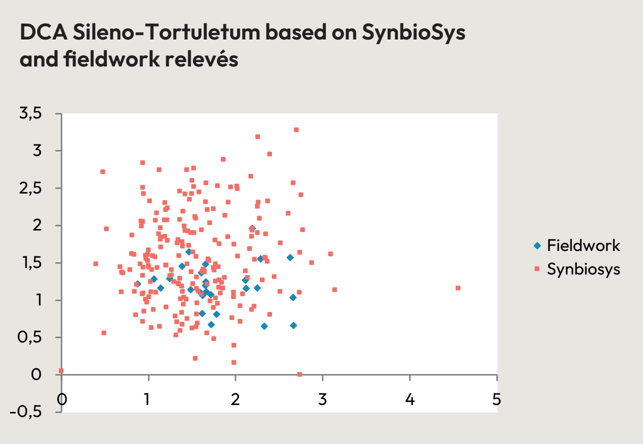


Fig. 4. Results of sites composition in the DCA analysis of the Sileno-Tortuletum based on the relevés of DNVD-Synbiosys and the 2016 fieldwork relevés. Eigenvalues of the DNVD species composition: 0.28 and 0.27 and for the fieldwork relevés: 0.27 and 0.25 for the first two axes.

Abb. 4. Anordnung der Vegetationsaufnahmen basierend auf Daten aus der DNVD sowie aus Feldbesuchen in 2016 mithilfe einer DCA Analyse der Sileno-Tortuletum. Eigenwerte der DNVD-Synbiosys Sortenkomposition sind 0.28 und 0.27 und für die Aufnahmen aus 2016 0.27 und 0.25.

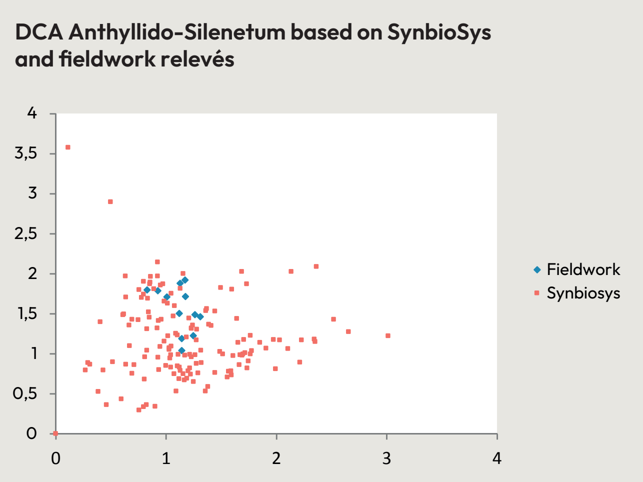


Fig. 5. Results of sites composition in the DCA analysis of the Anthyllido-Silenetum based on the relevés of DNVD-Synbiosys and the 2016 fieldwork relevés. Eigenvalues of the DNVD species composition of 0.23 and 0.19 and for the fieldwork relevés: 0.27 and 0.17 for the first two axes.

Abb. 5. Anordnung der Vegetationsaufnahmen in der Nähe der Küstendörfer in einer DCA Analyse mit Eigenwerten der DNVD-Synbiosys Artenkomposition von 0.23 und 0.19 für die beiden Diagrammachsen. Gleiches für die neuen Aufnahmen von 0.27 und 0.17 für beide Diagrammachsen.

locusta, were not present in the older DNVD relevés. Some species, e.g. *Rhinanthus minor* and *Crepis capillaris*, did not appear anymore in our field data (Table 2).

Also in case of the *Anthyllido-Silenetum* the DNVD relevés and the new relevés fully overlap (Fig. 5). Looking at the individual species, a number of species of the *Zeedorpenlandschap* had higher presence in the new fieldwork relevés e.g. *Anacamptis pyramidalis* and *Orobanche picridis* and to a lesser extent *Picris hieraciodes* and *Silene nutans*. Other species e.g. *Anthyllis vulneraria* and *Silene otites*, were less evident in the new data. Most accompanying species, e.g. *Jacobaea vulgaris* and *Ammophila arenaria* were present at a higher level. A few new species, e.g. *Senecio inaequidens* and *Claytonia perfoliata* (both exotic species) were observed in the *Anthyllido-Silenetum*. *Eryngium maritimum* was new in our data, although Doing (letter to Q.L. Slings) considers this species loyal to the *zeedorpen* species assembly. Many species, e.g. *Hieracium pilosella* and *Pimpinella saxifraga*, were recorded at a lower level or disappeared altogether, like *Erigeron acris* (Table 3).

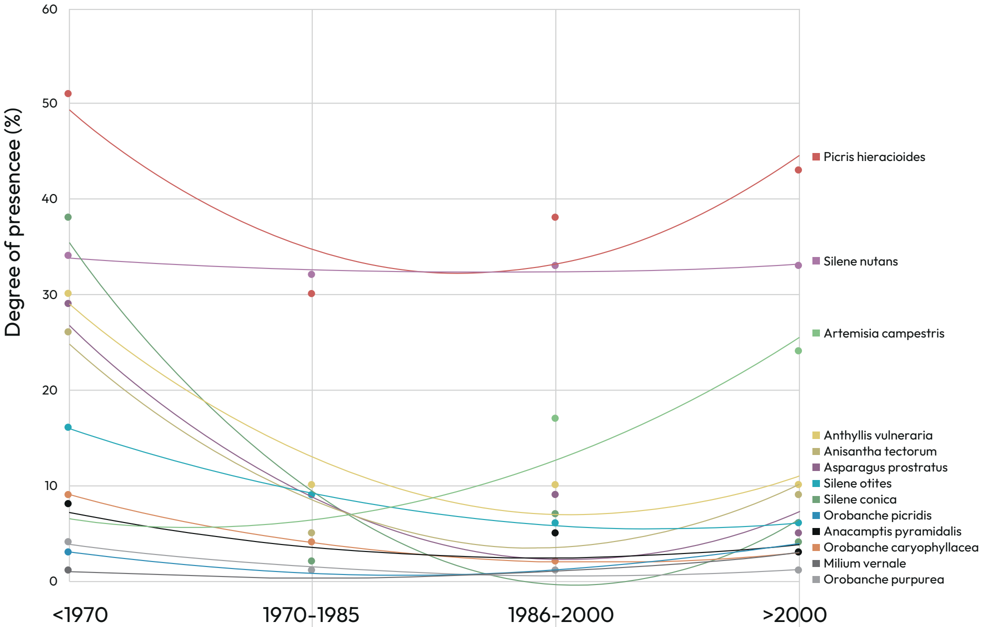


Fig. 6. Changes in presence of the typical species of the Zeedorpenlandschap in four time periods. Supplement 1 gives the degree of presence and median cover abundance.

Abb. 6. Veränderungen in der Präsenz von typischen Pflanzenarten von Küstendörfer in vier Perioden. Beilage 1 zeigt der Präsenz und medianer Bedeckung.

Table 3. Synoptic table with presence degrees (%) and median abundance cover of species of the DNVD relevés and the 2016 fieldwork relevés of the Anthyllido-Silenetum plant association; characteristic species of the zeedorpen species in blue, species that increased in the fieldwork relevés compared to the DNVD relevés in green and species that decreased in red.

Tabelle 3. Synoptische Tabelle mit Präsenz (%) und medianer Bedeckung der Pflanzenarten aus den Aufnahmen der DNVD und denen der Feldarbeit 2016 vom Anthyllido-Silenetum; Pflanzenarten der Küstendörfer werden in Blau, Pflanzenarten, die zwischen den Feldaufnahmen 2016 und denen aus der DNVD zugenommen haben, werden in Grün und Pflanzenarten, die abgenommen haben, in Rot wiedergegeben.

GROUP NO.	1		2	
NO. OF RELEVÉS	DNVD DATABASE: 146		FIELDWORK OF 2016: 12	
Anacamptis pyramidalis	8	+	25	1
Anthyllis vulneraria	67	+	50	1
Orobanche caryophyllacea	16	+	25	+
Orobanche picridis	14	+	50	+
Orobanche purpurea	1	r	.	
Picris hieracioides	68	+	83	2
Silene nutans	84	1	92	1
Silene otites	21	+	8	+
Jacobaea vulgaris	51	+	83	+
Pseudoscleropodium purum	36	2	83	2
Homalothecium lutescens	20	1	75	2
Taraxacum sectie Erythrosperma	26	+	67	+
Ammophila arenaria	38	+	67	+
Bromus hordeaceus	43	+	67	+
Vicia lathyroides	36	+	67	+
Cerastium fontanum	20	+	50	+
Veronica arvensis	12	+	50	+
Myosotis ramosissima	15	+	42	+
Plagiomnium affine	14	1	33	1
Cardamine hirsuta	13	+	33	+
Ranunculus bulbosus	34	1	33	+
Oenothera species	1	r	17	+
Senecio inaequidens	.		8	1
Eryngium maritimum	.		8	+
Claytonia perfoliata	.		8	+

GROUP NO.	1		2	
NO. OF RELEVÉS	DNVD DATABASE: 146		FIELDWORK OF 2016: 12	
Verbascum species	.		8	+
Taraxacum sectie Hamata	.		8	+
Hieracium pilosella	53	1	17	+
Pimpinella saxifraga	43	+	8	+
Sedum acre	38	+	8	+
Rhinanthus minor*	28	+	.	
Salix repens	28	2	.	
Rhytidiadelphus triquetrus	27	2	.	
Erigeron acris	25	+	.	
Cladonia rangiformis	20	2	.	

* almost certainly Rhinanthus angustifolius

3.2 Differences in time over all villages

Within one kilometre of the coastal village of Egmond aan Zee, Wijk aan Zee, Zandvoort, Noordwijk, Katwijk and Scheveningen (Fig. 1b), the 3,074 relevés were selected from the DNVD including our data. Some temporal trends in the data are visible (Fig. 6). All but three species had the highest % presence in the relevés from the first period. Many species showed a lower % presence in the second and third periods, but remained stable afterwards and even recovered, e.g. *Picris hieracioides* and *Milium vernale*. The % presence of *Anacamptis pyramidalis* and *Artemisia campestris subsp. maritima* increased in time, except that *Anacamptis pyramidalis* did not occur in the data from the second period (1970-1985). Species showing the strongest decline in % presence were *Anthyllis vulneraria*, *Asparagus officinalis subsp. prostratus*, and *Silene conica* (see also Table 3). *Artemisia campestris subsp. maritima* showed the strongest increase. *Poa bulbosa* only emerged in the relevés from the second period onwards.

3.3 Differences in species composition of the villages separately

Most characteristic species of the *Zeedorpenlandschap* are present in all areas, but their relative presence differs within the area of distribution (Fig. 7). Most species had a high % presence in Egmond aan Zee, decreasing southwards, getting higher again in the middle area of Noordwijk and Katwijk. Further south, % presence of key species dropped again with relatively low numbers in Scheveningen and with a low number of species present. The most northerly (approaching the lime poor coastal dunes) and southerly areas (mostly lost to urbanisation) had the lowest number of species. Katwijk was the

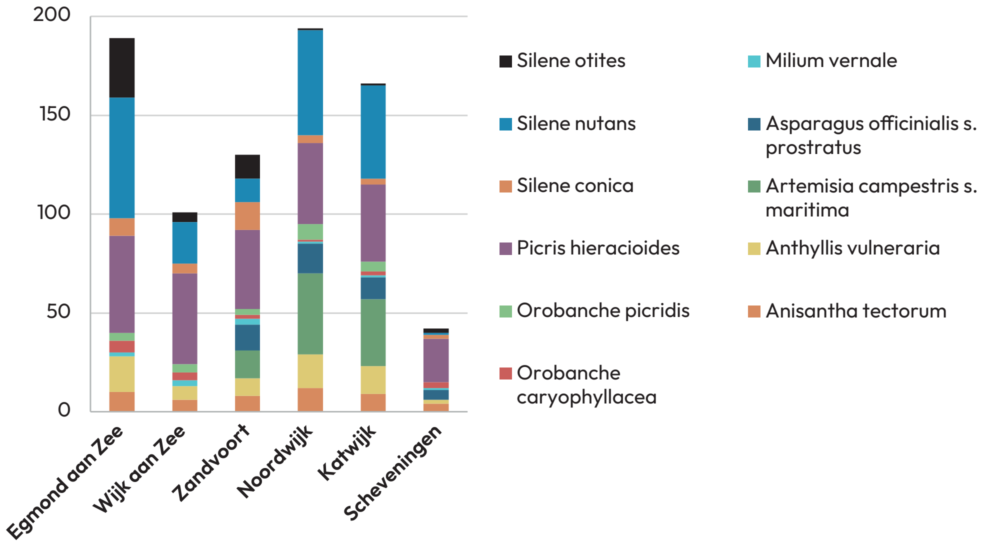


Fig. 7. Presence (%) in relevés focusing on the species of the Zeedorpenlandschap of all periods together around six different coastal villages; species are stacked. Supplement 2 gives the degree of presence and median cover abundance.

Abb. 7. Präsenz (%) in Vegetationsaufnahmen von typischen Pflanzenarten aus den sechs Küstendörfern aus allen Zeitperioden zusammen; Pflanzenarten sind gestapelt. Beilag 2 zeigt der Präsenz und medianer Bedeckung.

only village harbouring all characteristic species. Some species have a limited spatial distribution: *Alyssum alyssoides* only occurs near Katwijk, which has always been the case. In former days, *A. alyssoides* also occurred near Wijk aan Zee. *Artemisia campestris subsp. maritima* and *Asparagus officinalis subsp. prostratus* were long absent in the northerly part (Wijk aan Zee, Egmond aan Zee). Around 1909 *Artemisia campestris subsp. maritima* was planted for stabilisation purposes between Noordwijk and Katwijk and is now moving north and south; the plant originally had a SW-European distribution (Brummitt 2001; The Plant List 2013). The northern shift was also the case for *Asparagus officinalis subsp. prostratus*.

3.4 Environmental variables

Results of the T-tests and Mann-Whitney U tests showed that several variables were significantly different between the *Anthyllido-Silenetum* and the *Taraxaco-Galietum* (Table 4; see also Fig. 3). These variables were: pH of the first layer ($p = 0.037$), weighted average of pH ($p = 0.039$), OM-content of the second layer ($p = 0.007$), weighted average of OM-content ($p = 0.013$), distance to villages ($p = 0.005$), very small shells in the first layer ($p = 0.016$), small shells in the first and second layer ($p = 0.036$ and $p = 0.033$ respectively),

Table 4. Results of T-test and Mann-Whitney U tests to test differences in soil parameters between the Anthyllido-Silenetum and Taraxaco-Galietum. Significant results are bold and underlined. 1 refers to the first soil layer and 2 to the second. No number means the weighted average value of all layers.

Tabelle 4. Resultaten der T-Tests und Mann-Whitney U Tests, mit welchen die Differenz in Bodenparameters zwischen dem Anthyllido-Silenetum und Taraxaco-Galietum getestet wurde. Signifikante Resultate sind fettgedruckt und unterstrichen. Eine 1 hinter dem Umweltfaktor referiert an die erste Bodenschicht und eine 2 an die zweite. Wenn keine Nummer hinter dem Umweltfaktor steht, ist der gewogenes Durchschnittswert wiedergegeben.

ENVIRONMENTAL VARIABLE	MEAN/ MEAN RANK AS	STD. DEVIATION/ SUM OF RANKS AS	MEAN/ MEAN RANK TG	STD. DEVIATION/ SUM OF RANKS TG	T VALUE	Z VALUE	P-VALUE
pH1	7.58	0.75	6.97	0.75	2.21		0.04
pH2	16.63	199.50	10.82	151.50		-1.93	0.05
pH	8.04	0.34	7.73	0.37	2.19		0.04
Organic matter content 1	11.25	135.00	15.43	216.00		-1.39	0.17
Organic matter content 2	9.17	110.00	17.21	241.00		-2.68	0.01
Organic matter	1.64	0.70	2.21	0.36	-2.67		0.01
Phosphorus1	13.92	167.00	13.14	184.00		-0.26	0.80
Phosphorus2	15.67	188.00	11.64	163.00		-1.34	0.18
Phosphorus	15.58	187.00	11.71	164.00		-1.29	0.20
Calcium1	16.67	200.00	10.79	151.00		-1.96	0.05
Calcium2	15.25	183.00	12.00	12.00		-1.08	0.28
Calcium	14.92	179.00	12.29	172.00		-0.87	0.38
Distance to village	8.92	107.00	17.43	244.00		-2.83	0.01
Very small shell fragments1	17.29	207.50	10.25	143.50		-2.42	0.02
Very small shell fragments2	15.79	189.50	11.54	161.50		-1.45	0.15
Very small shell fragments	3.24	1.43	3.09	0.77	0.34		0.73
Small shell fragments1	16.71	200.50	10.75	150.50		-2.09	0.04
Small shell fragments 2	16.88	202.50	10.61	148.50		-2.13	0.03
Small shell fragments	16.58	199.00	10.86	152.00		-1.91	0.06
Large shell fragments1	14.08	169.00	13.00	182.00		-1.08	0.28
Large shell fragments2	14.38	172.50	12.75	178.50		-0.69	0.49
Large shell fragments	14.33	172.00	12.79	179.00		-0.61	0.55
Very large shell fragments1	13.50	162.00	13.50	189.00		0.00	1.00
Very large shell fragments 2	13.00	156.00	13.93	195.00		-0.93	0.36
Very large shell fragments	13.00	156.00	13.93	195.00		-0.93	0.36
Very small roots1	13.50	162.00	13.50	189.00		0.00	1.00
Very small roots2	11.46	137.50	15.25	213.50		-1.31	0.19
Very small roots	1.79	1.37	1.99	1.44	-0.37		0.72

ENVIRONMENTAL VARIABLE	MEAN/ MEAN RANK AS	STD. DEVIATION/ SUM OF RANKS AS	MEAN/ MEAN RANK TG	STD. DEVIATION/ SUM OF RANKS TG	T VALUE	Z VALUE	P-VALUE
Small roots1	17.79	213.50	9.82	137.50		-2.88	0.00
Small roots2	15.75	189.00	11.57	162.00		-1.43	0.15
Small roots	2.83	1.40	1.63	1.19	2.36		0.03
Large roots1	13.42	161.00	13.57	190.00		-0.05	0.96
Large roots2	11.58	139.00	15.14	212.00		-1.37	0.17
Large roots	14.58	175.00	12.57	176.00		-0.67	0.50
Very large roots	12.50	150.00	14.36	201.00		-1.34	0.18
Very large roots	12.00	144.00	14.79	207.00		-1.67	0.10
Very large roots	12.00	144.00	14.79	207.00		-1.35	0.18
Number of soil layers	12.92	155.00	14.00	196.00		-0.38	0.71

small roots in the first layer ($p = 0.004$) and the weighted average of the small roots ($p = 0.027$). All other tested variables did not show significant results.

The pH was significantly higher in the *Anthyllido-Silenetum* and the OM-content significantly lower. The distance to villages was significantly longer for the relevés of the *Taraxaco-Galietum*. The amount of very small and small shell fragments was significantly higher in the *Anthyllido-Silenetum* as well as the number of small root fragments.

3.5 Zeedorpenlandschap and Machairs: flora and soil

The machair (H21A0) and grey dunes (H2130_A) have many species in common like *Galium verum*, *Jacobaea vulgaris*, *Rubus caesius*, *Taraxacum section Erythrosperma*, *Carex flacca*, *Anacamptis pyramidalis*, *Anthyllis vulneraria* and *Carlina vulgaris*. On the other hand, a relatively extensive list of thirty *Anthyllido-Silenetum* species, that characterize and differentiate the Dutch *Zeedorpenlandschap*, are absent in the machairs of Ireland and Scotland, or even in Ireland and the UK as a whole (Table 5). Some of them are *Asparagus officinalis subsp. prostratus*, *Erodium lebelii*, all three *Orobanche* species, three *Silene* species, two *Viola* species, several *Trifolium* species, *Artemisia campestre subsp. maritima*, and *Gentiana cruciata* (Table 5). The machair missing species of the *Anthyllido-Silenetum* have a predominantly South-Western European or sub-Mediterranean distribution. The higher rates of precipitation in Western Ireland and Scotland and the lower average temperatures make the areas of the machairs less suitable for these species. But some species characteristic of the machairs are missing in the grasslands of the Dutch *zeedorpen* plant communities, e.g. *Agrostis stolonifera*, *Armeria maritima*, *Asperula cynanchica*, *Cynosurus cristatus*, *Glaux maritima*, *Plantago maritima*, *Potentilla anserina* and *Leucanthemum vulgare* (Table 5). Apart from *A. cynanchica*, which is also present in the Belgian dune grassland community, they indicate either soils rich in organic matter and nutrients or indicate salty soils due to salt spray.

Several soil characteristics of the machairs and *zeedorpen* plant communities are comparable. The lime content in both is high, in the machairs on average 23% up to 61% (Basset & Curtis 1985; Gaynor 2006). A typical feature for both is the presence of shell fragments in the organic top layer with a consequently higher pH in this layer (7-8.9) (Basset & Curtis 1985; Curtis 1991; this study). Also, the multi-layered soil profile points to periodic sand

Table 5. Differences in presence of species of the machair grasslands and the Anthyllido-Silenetum viewed from the Dutch Anthyllido-Silenetum perspective (excluding mosses and lichens). UK distribution is based https://www.brc.ac.uk/plantatlas/ (visited through September and October 2018).

Tabelle 5. Unterschied zwischen der Präsenz von Pflanzenarten des trockenen Teils der Machair und der Anthyllido-Silenetum aus der Perspektive der niederländischen Assoziation Anthyllido-Silenetum (ohne die Moos- und Flechtenarten). Die Verbreitung der Arten entstammt der Website https://www.brc.ac.uk/plantatlas/.

MACHAIRS	SPECIES TYPICAL OF MACHAIRS LACKING IN THE ANTHYLLIDO-SILENETUM	
	Agrostis stolonifera Armeria maritima Asperula cynanchica Carex pilulifera Cynosurus cristatus Cerastium fontanum Glaux maritima Leucanthemum vulgare Plantago maritima Potentilla anserina Succisa pratensis	

Dutch syntaxon	Species typical in the Anthyllido-Silenetum lacking in machairs	Number of missing characteristic species of each syntaxon level
Class Koelerio-Corynephoretea	Corynephorus canescens Erophila verna	2 of 15
Order Cladonio-Koelerietalia	Clinopodium acinos Vicia lathyroides	2 of 7
Alliance Polygalo-Koelerion	Erigeron acris	1 of 13

MACHAIRS	SPECIES TYPICAL OF MACHAIRS LACKING IN THE ANTHYLLIDO-SILENETUM	
Association Anthyllido-Silenetum	Asparagus officinalis prostratus Gentiana cruciata Hieracium umbellatum Orobanche caryophyllacea Orobanche picridis Rhinanthus angustifolius Rhinanthus angustifolius x minor Sanguisorba minor Silene nutans Silene otitis Viola hirta Viola rupestris	**12 of 28**
Sub-Association	Cerastium arvense Centaurea jacea Pyrola rotundifolia	3 of 14
Class: remaining species	Anisantha tectorum Artemisia campestre maritima Erodium lebelii Milium vernale Orobanche purpurea Silene conica Trifolium arvense Trifolium scabrum Tuberaria guttata Trifolium striatum	10 of 28
Class: species Molinio-Arrhenatheretea	Knautia arvensis Orchis morio	2 of 9
Class: species Nardetea	Euphorbia stricta Viola canina	2 of 7
Additional species	Diplotaxis tenuifolia Euonymus europaeus Festuca arenaria Genista tinctoria Linaria vulgaris Moehringia trinervia Polygonatum odoratum Stellaria pallida Thesium humifusum	9 of 40

accumulation with lime rich sand in the machair as well as in the plant communities of the *Zeedorpenlandschap*, with incoming shell fragments of different origin. In the *zeedorpen* plant communities of the mainland, they originate from human-deposited fishery remains as well as from the shell rich sands blown inland. In the machairs, the influx of lime can be attributed to a high erosion rate in combination with strong wind and wave action in the surf zone of rocky shores (Gaynor 2006). The influx of lime in the Dutch *Zeedorpenlandschap* is locally due to small-scale blowouts lifting sand up from deeper soil strata. Both processes apparently yield a similar soil profile and lime content.

4. DISCUSSION

Our hypothesis is that due to other human activities, the typical plant communities of the *Zeedorpenlandschap* still survive despite the disappearance of historic, small scale land use. The questions formulated are discussed and placed into an international context with the machairs.

On the changes in the flora and vegetation of the *Zeedorpenlandschap*, only relative qualitative statements can be given due to the dataset (such as difference in number of relevés, inconsistency in moss species, possible heterogeneity in larger relevés), but the data set has a great enough weight to show trends, and give some insights on the changes in time and place. A quantitative comparison is impossible, because over time and in areas along the coast, there are no consistent vegetation maps available.

4.1 Is the species composition of the characteristic plant communities still comparable to the former quality?

Results showed that the *Sileno-Tortuletum* and *Anthyllido-Silenetum* communities did change in quality, because of a dip in the 1970-2000 period, but regained the quality, because the typical species of these plant communities did not decline in % presence. Some characteristic species even increased in both plant communities (e.g. *Milium vernale*, *Picris hieracioides*). About 20-30 years ago, *Milium vernale* was a special botanical excursion target (pers. comm. Q.L. Slings) and has in recent years become locally even quite abundant. Some species were only found in the 2016 fieldwork (e.g. *Valerianella locusta* and the relative recent alien *Senecio inaequidens*). Also some species did not occur in our 2016 relevés (e.g. *Rhinanthus minor*; maybe in former relevés, this was confused with R. angustifolius). In both associations, species with presence % increase were mostly those growing well in relatively nutrient-rich circumstances like *Picris hieracioides*, *Veronica arvensis* and *Valerianella locusta* (Van der Meijden 2005) (SynBioSys 2.6.6). A trend towards species nutrient-rich conditions is visible, which might result in dominance of a few species and a decrease in species richness (Kooijman et al. 1998; De Bonte et al. 1999; Field et al. 2014). Based on our results though, the plant communities seem quite stable after the 1970-2000 recovery.

4.2 How did the quality of the Zeedorpenlandschap plant communities change in time?

The relative results of temporal patterns show that all the species of the *Zeedorpenlandschap* were well developed in the first period and declined afterwards. It also showed that most species were less frequent in relevés made in the second time period (1970-1985). In the last period after 2000, some species recovered to some extent and some other species totally recovered. These results are not in line with earlier studies in the northern part of the research area (Fig. 1). They found a constant decline in species (Bij 't Vuur 1993; Slings 1994; Van den Bos 2007), but most of these studies describe the *Zeedorpenlandschap* during the 1980s and early 1990s when – as our analysis shows – the species richness was at its lowest point.

4.3 What is the difference in botanical quality of each Zeedorpenlandschap?

The results of our spatial analyses showed that the relative presence of characteristic species was positive, but varied between the *zeedorpen*. In a few cases the typical species did not show this trend, especially at Scheveningen and to a lesser degree in Egmond aan Zee and Zandvoort. In Scheveningen, especially in the north on the edge of Meijendel, a considerable area was lost to urbanisation and an earlier change from an economic activity to a luxury beach resort (Mooij 2018).

The qualitative decline in plant communities of the *Zeedorpenlandschap* during the 1980s and 1990s might be explained by increasing soil enrichment by atmospheric nitrogen deposition as a result of human activity since the 1940s (Galloway et al. 2008; Noordijk 2007) preceded by an acidification by sulphur dioxide, as well as the collapse of the rabbit population due to viral diseases, and the planting of Marram grass to stabilize the dunes (e.g. Salman and Van der Meijden 1985; Van der Meulen et al. 1996; Van Turnhout et al. 2003).

Enriched soils result in the dominance of a few species and lead to a decline in species richness (Kooijman et al. 1998; Ford et al. 2016). Furthermore, high external nitrogen input makes biological nitrogen-fixation as a nitrogen source redundant, leading to topsoil acidification, and this further decreases plant diversity (Aggenbach et al. 2017). The observed recovery since 2000 might be related to reductions in N-deposition (Noordijk 2007) due to policy measures (Jones et al. 2014), although the levels of nitrogen deposition are still too high for biodiversity. At high pH levels, lime rich dune grasslands are often P-limited because it forms complexes with calcium and therefore phosphorus is less available for plants (Kooijman et al 1998; Kooijman & Besse 2002; Vitousek et al. 2010). Due to disturbance connected with human activities, lime fragments are mixed with organic material (OM); in such a case lime is a catalytic converter for OM, setting free large amounts of nutrients, including phosphates, from which Leguminosae profit; Leguminosae being more frequent and abundant in the *Anthyllido-Silenetum*. The OM content of the soil in the *Anthyllido-Silenetum* is lower than in the *Taraxaco-Galietum*, suggesting a higher breakdown of OM in the *Anthyllido-Silenetum*. Consequently, the P-availability must be higher for the Leguminosae; the N-synthesis needs a lot of energy, which in its turn needs a lot of phosphates. Apart from losses by urbanization (e.g. Scheveningen-north), this would suggest that other factors positively affected the plant communities of the *Zeedorpenlandschap* over the last two time periods, such as human actions (Slings 1994). Changes in disturbance (Roxburgh et al. 2004) may help in management if there is a subtle balance between not too little and not too much disturbance, such as recreational use (including walking the dog), side effects of golfing(searching for golf balls in the so-called rough) (Inberg et al. 2007), illegal football match viewing on a dune slope and/or a warming climate (Jongmans et al. 2013; Van der Hagen et al. 2020b). Installing grazing by livestock has contrasting results (Van den Bos 2007; Mourik 2004; Slings unpublished) and overgrazing might lead to lack of seed setting and to a loss of abundance of characteristic species. Also rabbit recovery from viral diseases is likely to affect more of the representative *Zeedorp* species of the *Anthyllido-Silenetum*, by warren excavation bringing more lime into the topsoil. If (hibernating) snails are still an important factor in the top layer of the OM (like in Fig. 2), this is unclear due to lack of data.

4.4 What are the difference in environmental variables between the Anthyllido-Silenetum and Taraxaco-Galietum veri associations?

The results of the statistical analysis showed that species composition was explained by several environmental variables. Overall, the comparison of the means tests showed several significantly different environmental variables between the *Anthyllido-Silenetum* and *Taraxaco-Galietum*, indicating that plant communities of the *Zeedorpenlandschap* differ from the other lime holding dune grasslands, specifically the *Taraxaco-Galietum* in the other parts of the dunes. A crucial factor seems the (snail) shell fragments in the top organic layer, in former days probably present due to the crushing of hibernating snails during livestock grazing.

4.5 International context: the Machair grasslands

Machairs (Gaelic for flat land) are confined to the coasts of North-Western Ireland (from Galway Bay to Malin Head) and Western Scotland (Bassett & Curtis 1985). By EU Habitat directive definition H21A0 only exists in these regions. They show a high degree of mutual similarity (Gaynor 2006). Some variation is caused by different land-use and/or management (Gaynor 2006). Like the Dutch *Zeedorpenlandschap*, machairs are a landscape type strongly influenced by traditional land use over long periods of time. According to Richie (1971), the machair landscape is at least 6000 years old. Crawford (1981) postulates an age of the Scottish machairs of at least 5000 years. Bassett & Curtis (1985) estimate that humans influenced the Irish machairs for at least 8000 years. Ryle et al. (2009) suggest that there are minor differences between the machairs and regular lime rich dune grasslands in their vicinity, and find the differences often subjective. Many of the typical species from the *Anthyllido-Silenetum* are missing in the machair (e.g. several *Silene* and *Orobanche* species on the Association level). It is impossible to separate the parts of the machairs influenced by humans from regular dune grassland communities, based on species composition (Table 5). On the other hand, *Asperula cynanchica*, a typical species of the machair, was present in the Netherlands and is still to be found sparsely along the Belgian coast.

Machairs only exist in areas with an average wind speed of 7 m/sec and a maximum of 50 m/sec (Ireland and Scotland) (Gaynor 2006) also leading to a higher impact of salt spray. This fierce Atlantic Ocean dynamic is lacking on the Dutch (mainland) coast because of the sheltered North Sea. This also explains the absence of machairs on the sheltered coasts of England, Wales and the south part of Scotland. Sand transport (including shells!) due to high wind speeds has filled in the undulations in the machair, explaining the word machair (flat land). In contrast, blow-out dynamics in the more pronounced undulating Dutch *Zeedorpenlandschap* was probably connected to local livestock grazing, even overgrazing, and human trampling; since the 1960's livestock grazing disappeared. In the last decades human trampling, in combination with dogs, became more important, but in parts a bit away of the village without serious damage to the vegetation. There is also a difference in the type of shells. In Ireland and the UK, these shells are rougher and harder; on the (Dutch) mainland coast they are finer and softer and break down more easily, especially when of snails.

The Dutch *Zeedorpenlandschap* is part of the calcareous Younger Dunes dating from 800-900 AD onwards. The human influence in the *Zeedorpenlandschap* of the dunes dates back to the Middle Ages (12th century) and the human use changed periodically from minimal levels up to overexploitation. The use was partly depending on the fluctuating amount of fish brought ashore from the North Sea (Mooij 2018). This influence significantly declined in most places from 1900 onwards. For instance, grazing stopped almost everywhere around 1900; near Katwijk, it continued into the early 1960's (Mooij 2018). Livestock grazing has gradually been reintroduced in several areas, with variable success (e.g. Ehrenburg et al. 1995).

Doing (1974; 1988) described the *Zeedorpenlandschap* as a limited zone of about one kilometre around the *zeedorpen*, separating it from the rest of the dune landscape further away; in Doing's terms: mainly in the Ks-, but also in the A- and R-landscape zone. There were as far as we know two exceptions. In Meijendel, the Anthyllido-Silentum even occurred up to five kilometres away from Scheveningen (Boerboom 1958; Van der Hagen et al. 2022b), and Egmond aan Zee (pers. comm. Q.L. Slings). Apart from its deliberate planting, the current presence of Rosa spinosissima might be an indication of the former presence of the *Zeedorpenlandschap*.

In the EU Habitats Directive, the machairs are distinguished as a specific habitat type at the landscape level (H21A0). Although the *zeedorpen* plant communities are a very specific set of plant communities, they are still just listed under the lime rich grey dunes (H2130_A). Why is there such a difference in approach when both are strongly influenced by human interference, apart from Atlantic Ocean influence on the machair? Should the zone of the *Zeedorpenlandschap* be separated from the grey dune complex and be considered as 'Machairs' of the European mainland? This preliminary floristic and abiotic review and field study forms a basis for further discussion to determine whether the *zeedorpen* plant communities are merely part of the grey dune habitat H2130_A or could form a separate habitat type H2130_D (see also Ryle et al. 2009). All in all, there are good reasons to give them fuller credit.

5. CONCLUSIONS

Based on our qualitative study we can conclude that species composition of the plant communities of the *Zeedorpenlandschap* did not change significantly. The species number and the abundance of the species of the vegetation surrounding the *zeedorpen* declined during the period 1980-2000 but recovered at the turn of the millennium, although the frequencies and abundances of the characteristic species vary among *zeedorpen*. The observed changes in species composition are mainly due to new species and invasion by the non-native species Senecio inaequidens.

Species and consequently plant communities of the *Zeedorpenlandschap* are associated with several soil characteristics (pH and small shell fragments). A better insight into the relationships between vegetation, environmental and soil conditions and management is necessary and requires an extended in-depth study, with far more relevés and soil samples, including vegetation mapping and a comparison with older maps to have a quantitative result. Furthermore, a better understanding of the local and detailed activities over decennia to reconstruct the landscape history of the *Zeedorpenlandschap* is needed to link processes with the observed changes in frequency and abundance of the characteristic species. A first report was made by Mooij (2018) to relate traditional land use to the present vegetation.

The windswept and extremely wet Atlantic environment of machairs undoubtedly forms a major difference with the Dutch *Zeedorpenlandschap*. In the Netherlands, the area of the plant communities of the *Zeedorpenlandschap* should be separated from the regular dune grassland communities of the grey dunes (H2130_A): H2130_D, the 'machairs of the European mainland'.

ERWEITERTE DEUTSCHE ZUSAMMENFASSUNG

Einführung

Die Küstengraudünen der Niederlande sind ein priorisierter Lebensraum der Natura 2000 Gesetzgebung (H2130; Council of the European Communities 1992; European Commission 2003). Die Pflanzengesellschaften dieser Graudünen sind in großer Vielfalt in den kalkhaltigen Küstendünen der Niederlande anwesend (Janssen & Schaminée 2003). Eine spezielle Pflanzengesellschaft und besonderer Landschaftstypus befindet sich in der Nähe der alten Küstendörfer. Die dortige Pflanzengesellschaft unterscheidet sich von den regulären durch spezifische Pflanzenarten (Schaminée et al. 1996). Dieser Landschaftstypus ist von Doing (1974; 1988) auf Niederländisch als *Zeedorpenlandschap* beschrieben worden und kommt rund um die Küstendörfer Egmond aan Zee, Wijk aan Zee, Zandvoort, Noordwijk, Katwijk und Scheveningen vor (Abb. 1). Früher wurden Fischernetze in den Dünen repariert, wobei organisches Material in den Dünen liegenblieb. Weiterhin wurden dort Leinenstoffe gebleicht, Brennmaterial und Heu gesammelt, Weidevieh gehalten und in kleinem Umfang Felder bestellt, wobei man vom nahen Grundwasser profitierte. Diese Einflüsse hatten einen Effekt auf den Boden und dessen Aufbau und damit auf das Vorkommen spezieller Pflanzenarten sowie die Zusammensetzung der Pflanzengesellschaften. Es betrifft das *Sileno-Tortuletum* und das *Anthyllido-Silenetum*. Die herkömmlichen Pflanzengesellschaften der Graudünen sind das *Phleo-Tortuletum* und *Taraxacum-Galietum* (Schaminée et al. 1996).

Die Pflanzengesellschaften der *Zeedorpenlandschap* sind überwiegend in den Niederlanden anwesend. Aus internationaler Perspektive ist das *Anthyllido-Thesietum* mit Pflanzengesellschaften der belgischen Küste verwandt. Möglicherweise ist das Hornungio-Thesietum in Nord-Frankreich verwandt. Aufgrund von Folgen menschlicher Einflüsse gleichen die Aizjoms in Lettland sich mit der *Zeedorpenlandschap*, mit dem Unterschied dass der Boden der Aizjoms keine Kreide befasst. Die Machairs an der Westküste Irlands und Schottlands ähneln den Pflanzengesellschaften der *Zeedorpenlandschap* am meisten.

Die Qualität und Quantität der Pflanzengesellschaften hat sich in den letzten hundert Jahren im negativen Sinne verändert, überwiegend durch reduzierte und/oder modifizierte Bodennutzung (Slings 1994; 2007). Auch der Einfluss exzessiver Stickstoffdeposition hatte große Folgen für die Qualität der Pflanzengesellschaften, was sich vor allem in der Dominanz von Gräsern beobachten lässt. Die Hypothese dieser Studie ist, dass diese Pflanzengesellschaften durch oben genannte Faktoren weiterhin in Qualität abnehmen. Um diese Hypothese zu testen werden fünf Fragen beantwortet: (1) Sind heutige (charakteristische) Pflanzenarten vergleichbar mit historischen? (2) Welche quantitativen Änderungen sind im Laufe der Zeit aufgetreten? (3) Welche qualitativen Änderungen bestehen zwischen den einzelnen Küstendörfer? (4) Welche Bodeneigenschaften und andere Faktoren sind für diese Änderungen verantwortlich? (5) Welche Position beziehen die Pflanzengesellschaften der niederländischen *Zeedorpenlandschap* als Unterteil der Graudünen (H2130A) im Vergleich zu den irländischen und schottischen Machairs (H21A0)?

Material und Methoden

Um die Forschungsfragen zu beantworten, wurden alle Vegetationsaufnahmen mit Koordinaten aus der Nationalen Datenbank DNVD selektiert (Schaminée et al. 1996; Weeda et al. 2002) sowie zusätzliche Aufnahmen von Naturparkwächtern entlang der Küste gesammelt und in einer separaten Datenbank gesammelt. Zwischen dem 22. April und 8. Juli 2016 wurden 96 neue Aufnahmen in beiden Pflanzengesellschaften der Küstendörfer und des *Taraxaco-Galietum* gemacht. Diese Aufnahmen hatten meist eine Maße von 2x2 Meter, manchmal jedoch 2x1 Meter zwecks Homogenität der Aufnahme.

Um zu testen welche abiotische Faktoren das Bestehen des *Anthyllido-Silenetum* versus des *Taraxaco-Galietum* bestimmen, wurden anschließend Bodenprofile aus 30-35 cm Tiefe in der Fläche der Vegetationsaufnahmen mit einem Wardenaar Profilstecker gestochen. Im Feld wurden die Farben der verschieden Bodenschichten (Abb.2) mit einem Munsell Color Chart (Munsell Color Company 1954) bestimmt der pH mit ColorpHast™ gemessen und der Kalkzustand des Bodens mit 10% HCl einer von drei Kategorien zugewiesen. Im Labor wurden pH-H_2O, der Anteil organischen Stoffs (OM), Phosphat-Olsen und Ca^{2+} bestimmt.

Die Daten wurden in TURBOVEG, JUICE und DCA (in R) analysiert. Für die Zeitanalyse wurden vier Zeiträume festgelegt: vor 1970, 1970-1985, 1985-2000 und nach 2000. Für die Raumanalyse wurden die Aufnahmen in einem Kreis von einem Kilometer Radius rundum die Küstendörfer mit ArcMap 10.3.1 selektiert. Die Signifikanz der zwei Gruppen bestehend aus Aufnahmen der Küstendörfer versus Aufnahmen der Nicht-Küstendörfer wurde mit den T-test und Mann-Whitney U-test geprüft.

Ergebnisse

Nur kleine Unterschieden ergaben sich zwischen den Aufnahmen aus der Nationalen Datenbank und den 96 neue Aufnahmen (Abb. 3, 4). Die DCA Analyse ergab keinen Unterschied zwischen beiden Gruppen. Einige Unterschieden sind, dass die Präsenz von *Silene conica* abnahm, während sich die von z.B. von *Milium vernale* und *Silene otites* erhöhte. Zudem erschienen auch neue Pflanzenarten, wie Senecio inaequidens (eine neuerliche exotischer Art) und *Valerianella locusta*. Einige Arten, wie *Rhinanthus minor* und *Crepis capillaris*, verschwanden.

In Zeit und Raum gab es verschiedene Änderungen. Im Laufe der Zeit nahm die Qualität der Wiesen ab, verbesserte sich jedoch in der letzten Periode (Abb. 5). Im Räumlichen ist der gleichen Trend bemerkbar (Abb. 6), allerdings je nach Küstendorf verschieden. Auch neue Arten, von denen eine exotische, sind Teil der Veränderung.

Die Bodenfaktoren erwiesen, dass der Unterschied zwischen dem *Anthyllido-Silenetum* und dem *Taraxaco-Galietum* entlang der Küste mit lokalen Untersuchungen von Slings (1994) übereinstimmte. In der Küstendorf-Assoziation des *Anthyllido-Silenetum* waren pH1 (pH der ersten Bodenschicht) und pH (Gewogener Mittelwert des pH) signifikant höher und der Anteil organischen Stoffs niedriger. Auch waren sehr kleine und kleine Muschelfragmente und kleine Wurzeln in der Fischerdorf-Assoziation des *Anthyllido-Silenetum* signifikant häufiger anwesend (Tabelle 4).

Diskussion

Die Qualität des *Anthyllido-Silenetum* hat sich im Laufe der Zeit und im Raum negativ entwickelt, jüngst jedoch auch wieder verbessert. In dieser Studie waren die beiden Gruppen von Aufnahmen nicht gleich groß: 461 versus 45 Aufnahmen. Die konstatierte Variation ist möglicherweise auf diese Differenz zuzuschreiben. Die verbesserte Qualität der Assoziation, spezifisch im die jüngsten Zeitraum, wird wahrscheinlich durch eine verbesserte Luftqualität (NOx) bedingt. Auch hier kann die Anzahl der Aufnahmen einen Einfluss auf das Ergebnis haben. Verschiedene Bodenfaktoren standen statistisch zuverlässig mit den Unterschieden zwischen dem *Anthyllido-Silenetum* und dem *Taraxaco-Galietum* im Zusammenhang. Trotz vieler Informationen über das Management der Dünen entlang der Küste war es nicht möglich einen fundierten Zusammenhang zwischen der Verbesserung der Qualität des *Anthyllido-Silenetum* und den zahlreichen Managementmaßnahmen zu finden. Ein solides Resultat benötigt Daten in kleinerem Maßstab. Die Frage, ob das *Anthyllido-Silenetum* enger mit dem irländischen und schottischen Machair verwandt ist, als mit der ‚herkömmlichen' Dünenwiese (*Taraxaco-Galietum*), benötigt weitere Untersuchungen mit detaillierteren Daten zur Pflanzenzusammensetzung in Kombination mit dem Boden, sowie Daten von der ganze Küste Nordwesteuropas.

In der Europäischen Gesetzgebung von Natura 2000 ist *Anthyllido-Silenetum* und Phleo-Tortuletum ein Teil der kalkreichen Dünenwiesen (H2130_A, ein priorisiertes Habitat); das Machair ist ein separates Habitat (H21A0). Durch die limitierte Verbreitung van Pflanzenarten (Tabelle 5), die das *Anthyllido-Silenetum* in den Niederlanden charakterisieren, ist es möglich besser, das *Anthyllido-Silenetum* und Phleo-Tortuletum separat von den Graudünen zu platzieren (H2130_D) und nicht unter die kalkreiche Dünenwiesen (H2130_A) zu ordnen.

AUTHOR CONTRIBUTION STATEMENT

Harrie van der Hagen, Rienk Slings, Gerard Oostermeijer, Joop Schaminée co-supervised the MS thesis of Charlotte Mooij. Harrie van der Hagen used the basis of this thesis for this article, and structurally extended it with research on the Machair, Aizjoms and Mielles for the international context of the *Zeedorpenlandschap*. Text and figure suggestions were made by the co-authors as well as Gerard Oostermeijer, Karlè Sýkora and Frank van der Meulen.

Supplement 1. Synoptic table with degree of presence (%) and median abundance cover focusing on the species of the Zeedorpenlandschap of all zeedorpen together in four different time periods with number of relevés involved.

Beilage 1. Synoptische Tabelle mit Präsenz (%) und medianer Bedeckung mit Fokus auf alle Küstendorf-Pflanzenarten aller Küstendörfer zusammen, gelistet in vier Zeitperioden inklusive Anzahl der Aufnahmen.

TIME PERIOD	< 1970		1970-1985		1985 - 2000		> 2000	
NUMBER OF RELEVÉS	76		678		1314		990	
Alyssum alyssoides	3	+			1	1	1	1
Anacamptis pyramidalis	1	+			1	+	3	+
Anisantha tectorum	26	+	5	1	7	+	9	+
Anthyllis vulneraria	30	1	10	+	10	+	10	+
Artemisia campestris subsp. maritima	8	2	2	2	17	1	24	2
Asparagus officinalis subsp. prostratus	29	+	2	+	9	r	5	r
Milium vernale	3	r	1	2	1	1	4	1
Orobanche caryophyllacea	9	+	4	r	2	r	3	r
Orobanche picridis	8	r	1	+	5	r	3	r
Orobanche purpurea	4	1	1	+	1	+	1	+
Picris hieracioides	51	+	30	+	38	+	43	+
Poa bulbosa			1	2	1	1	1	+
Silene conica	38	1	2	r	7	r	4	+
Silene nutans	34	+	32	+	33	+	33	+
Silene otites	16	+	9	1	6	1	6	+

Supplement 2. Synoptic table with degree of presence (%) and median abundance cover focusing on the species of the Zeedorpenlandschap of all periods together around the six different zeedorpen with number of relevés involved.

Beilage 2. Synoptische Tabelle mit Präsenz (%) und medianer Bedeckung mit Fokus auf alle Fischerdorf-Pflanzenarten von allen Zeitperioden zusammen, gelistet per Fischerdorf inklusive Anzahl der Aufnahmen.

VILLAGE	EGMOND AAN ZEE		WIJK AAN ZEE		ZANDVOORT		NOORDWIJK		KATWIJK		SCHEVENINGEN	
Number of relevés	452		355		487		473		1236		433	
Alyssum alyssoides	.		.		.		.		1	1	.	
Anacamptis pyramidalis	.		7	+	.		2	+	1	+	.	
Anisantha tectorum	10	+	6	1	8	+	12	+	9	+	4	+
Anthyllis vulneraria	18	+	7	1	9	+	17	+	14	+	2	1
Artemisia campestris s. mar.	.		.		14	2	41	1	34	2	.	
Asparagus officinalis s. pros.	.		.		13	r	15	r	11	r	5	+
Milium vernale	2	1	3	1	3	1	1	+	1	+	1	1
Orobanche caryophyllacea	6	r	4	r	2	r	1	r	2	r	3	r
Orobanche picridis	4	r	4	r	3	r	8	r	5	r	.	
Orobanche purpurea	.		1	1	.		.		1	+	1	+
Picris hieracioides	49	+	46	+	40	r	41	+	39	+	22	+
Poa bulbosa	.		1	1	1	r	.		1	1	1	+
Silene conica	9	r	5	r	14	r	4	r	3	+	2	+
Silene nutans	61	1	21	1	12	r	53	1	47	+	1	r
Silene otites	30	1	5	+	12	r	1	1	1	+	2	1

Chapter 7

Synthesis

Harrie G.J.M. van der Hagen

SYNTHESIS

In 1989, I attended, together with five colleagues from the *Duinwaterleiding van 's-Gravenhage* (now called *Dunea*), an excursion to several coastal sand dune areas in England and Wales (Bakker et al. 1989). During this fieldtrip, we discussed the effects of livestock grazing with local dune managers. In some of the areas, livestock grazing has been applied continuously over a long period, sometimes for hundreds of years, as in Sandscale Haws and Tywyn Aberffraw. Returning to the Netherlands, we discussed the matter with our external advisory board of the *Duinwaterleiding*. It was decided to start an experiment with year-round livestock grazing in parts of Meijendel (Ten Haaf 1990) and to monitor the results.

MAIN QUESTIONS AND HYPOTHESIS

The main question was whether the 1990 introduction of livestock (Galloway cattle and Nordic fjord horses, later substituted with Konik horses) was capable to counteract the tall grasses and shrub encroachment, and rejuvenate the ecosystem with bare sand in the drier parts of the Meijendel coastal sand dunes. The main hypothesis of this PhD thesis is that the introduction of livestock in Meijendel coastal dunes at a density of 0.06-0.07 Large Livestock Units.ha-1.year-1 (1:12-18 ha) will lead to regressive succession by their grazing and trampling, as expressed by an increase of bare sand, a decrease in the area of shrubland and forest, and a subsequent increase of the area of dune grassland, as well as an improvement of the quality of the dune grasslands. The species poor, grass-encroached tall grasslands were expected to change into species-rich short dune grasslands with patches of bare sand.

A large amount of data was available, over a long time (up to 60 years) ranging from detailed false-colour photographs (scale 1:2,500), series of permanent plots, several exclosures, and the national database on vegetation plots. Every chapter of this thesis deals with a part of the main question and hypothesis, as explained in the General introduction (Chapter 1). Chapter 2 deals with the overall development of the three main classes of vegetation structure: bare sand, grasslands, and scrub and forest. In Chapter 3, the grassland class is divided into four subtypes, reflecting the processes in the dune landscape, such as: with blond sand slightly overblown vegetation, more or less closed species-rich grasslands, encroachments by tall grasses, and the combination of areas with dominant mosses and sparsely vegetated stands with grey sand. Chapter 4 evaluates 41 permanent plots, installed in 1953, to study the succession of the vegetation in Meijendel nature reserve. Chapter 5 focusses on seven exclosures, installed in 1975, to study the effect of rabbits on the expected progressive succession. Chapter 6 studies the vegetation of the so-called *Zeedorpenlandschap*, where livestock grazing was a traditional farming practice from neighbouring seaside villages; the analysis of the *Zeedorpenlandschap* is set in an European context.

In this synthesis, the developments observed in each chapter are placed in an ecological landscape context. For this purpose, we make use of two conceptual models that have been specifically designed for the coastal dune landscape. The Specific Hierarchic Model (SHM), developed by Bakker et al. (1979), forms the basis, putting the driving factors of the dune ecosystem in a hierarchical context, from climate down to fauna. This model was refined by Van Haperen (2009), who also linked the scheme of Bakker and co-workers to anthropogenic impacts at each level of the model (SHM: Box 1). Climate is considered to function at the top level of the system, whereas fauna and vegetation both act at the bottom level. This implicates that fauna and vegetation are subordinate, not only to climate but also to geology, relief, ground water, and soil. Livestock grazing is an additional faunal component, complementary to other grazers, like rabbits. Van Haperen (2009) also linked anthropogenic nitrogen deposition to the climate component in the model.

RESULTS

From the start of this PhD research, it was clear that the introduction of livestock grazing was not the only factor that could possibly explain the observed changes in Meijendel. Other factors had to be considered as well. Around 1990, several changes took place in this area and coincided. To be mentioned are: (i) an end to the planting of Marram grass (*Ammophila arenaria*) facilitating blow-outs, (ii) the reduction of nitrogen deposition, (iii) the average rise of temperature in the Netherlands (Fig. 1), speeding up around 1988, and (iv) – after the 1954 myxomatosis outbreak – the appearance of a second viral disease, the Rabbit Viral Haemorrhagic Disease (RVHD-1), that decimated the recovering rabbit population around 1989.

The first chapters are based on the analysis of four series of aerial photographs (1975, 1990, 2001, and 2009). The three grazed and three ungrazed areas, of about 50 ha each, are compared.

Chapter 2 concerns the analysis of the main types of vegetation structure in the area, the Crisp classes: bare sand (Cc1), grasslands (Cc2), and scrub and forest (Cc7). Contrary to the hypothesis, livestock grazing was not responsible for the changes observed, as tested in the Generalized Estimating Equations (GEE) model. Other factors than livestock are considered having a greater impact.

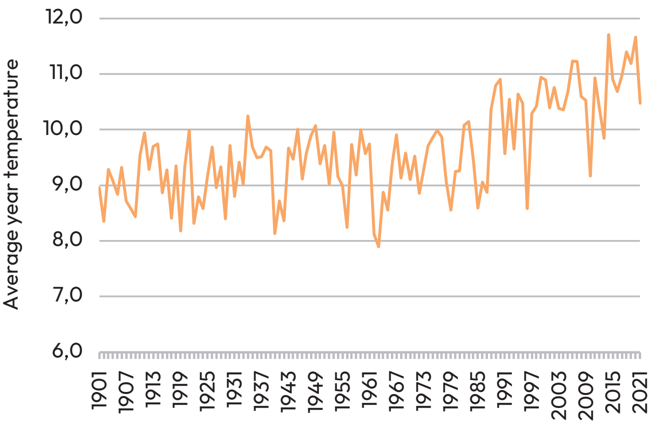


Figure 1. The average year temperature in The Netherlands. Note the relative sudden increase around 1988 (© KNMI data).

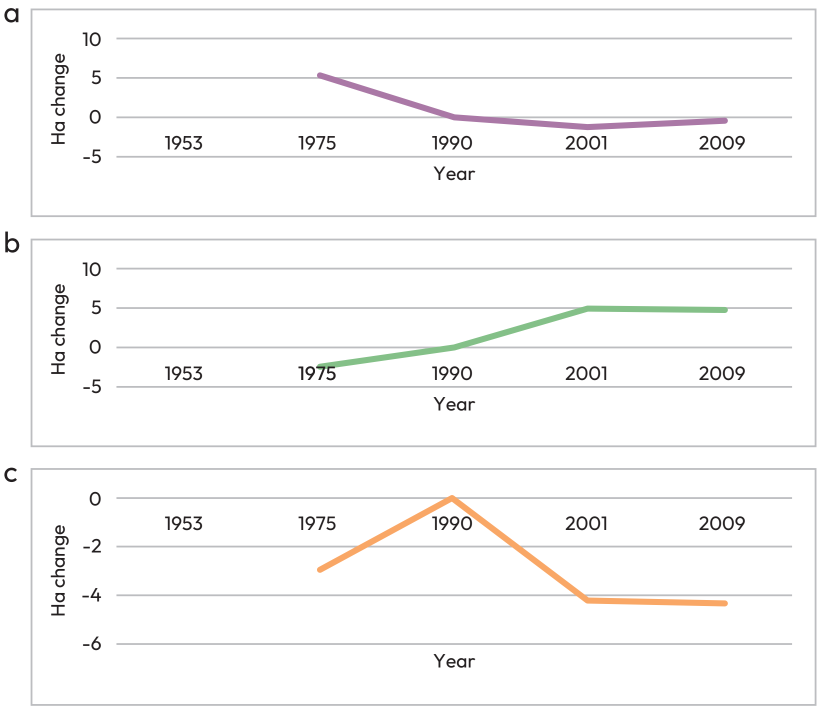


Figure 2. Average changes in the Crisp classes of (a) bare sand, (b) grasslands, and (c) shrubland, mainly Hippophae rhamnoides; high scrubs and forest is not included in aerial photograph results (see Chapter 2).

(1) In 1990, Marram grass planting stopped in Meijendel. As a consequence, after five to ten years, blow-outs arose autonomously (Fig. 2a), independently from livestock grazing, and possibly in combination with changing climate parameters (Aggenbach et al. 2018). In the next 10 to 25 years, these blow-outs will be likely to lead to a closed, species-rich dune grassland (Mensing 2002; Aggenbach et al. 2018).

(2) The reduction of nitrogen deposition at the end of the last century might have led to weakening of the algal crust, which is the first succession stage on bare sand. The weakening of the algal crust could have facilitated blow-out development since 2001 (Fig. 2a) independently from livestock grazing. Heavy rain showers in the summer – in combination with the weakened algal crusts – make these sites more vulnerable to erosion by rainwater and consequently more vulnerable to erosion by wind, leading to blow-outs (Box 1: SHM climate; Jungerius and Van der Meulen 1988).

(3) Livestock was hypothesised to reduce the area of shrubland, but the changes observed are predominantly linked to the 1954 outbreak of myxomatosis. It is import-

ant to recognize that rabbits have a preference for seedlings of shrub and trees. On a large scale, by this grazing, the rabbits blocked the progressive succession into shrubland and forest. The consequence of the myxomatosis outbreak was a window of opportunity for shrub species like *Hippophae rhamnoides* and *Crataegus monogyna* to flourish. These two species have a different life span: 35-45 years and up to 200 years, respectively. In the case of *Hippophae,* 35-45 years after the massive expansion due to myxomatosis, this shrub collapses (Fig. 2c) and falls back to grasslands (Fig. 2b) and seldom changes into high shrubland. *Crataegus* though, is more steadfast and gradually begins to dominate the landscape. The area of the grasslands is restricted to the area left over, squeezed in between bare sand and shrubland and forest.

Chapter 3 gives the results of four Fuzzy grassland classes indicating various processes: with blond sand slightly overblown vegetation (Fc2), the combination of stands with dominating mosses and sparsely vegetated stands with grey sand (Fc3+5), encroachments by tall grasses (Fc4), and species-rich more or less closed grasslands (Fc6). The changes in the grassland classes were tested using GEE, including data on nitrogen deposition and standardized rabbit counts. Changes occurred, but in contradiction to our hypothesis, there was no significant impact by the livestock on all four grassland classes within 11 and 19 years after the livestock introduction.

(1) In all four grassland classes, rabbits explain the changes observed, sometimes in combination with the decreasing nitrogen deposition since around 1990 (Fig. 2). Even in areas encroached by tall grasses (Fc4), livestock grazing is not the driving factor, despite the decrease of this vegetation type in the grazed areas; the presence of rabbits and nitrogen deposition however do explain such changes. We have no explanation for this outcome.

(2) The influence of rabbits is positively related to the amount of the blond sand overblown vegetation (Fc2) based on blow-out development (Fig. 2a) and rabbit meadows (Fc6). Burrow digging and scratching to dig for plant roots (Burggraaf-Van Nierop and Van der Meijden 1984) result in small-scale bare sand and grassland mosaics. As such, the species-rich short grasslands are being managed by rabbits.

(3) There is a negative correlation between rabbits and grasslands where the top layer is acidified (Fc3+5). These grasslands are almost not grazed by rabbits due to a lack of its preferred plants. However, due to their scratching and digging, lime-rich sand comes to the surface. The vegetation changes, as a response to the lime-rich situation, with an increase of highly palatable herbs and grasses for rabbits.

(4) At low densities of rabbits, the encroached grasslands (Fc6) may expand (Kooijman et al. 2017), whereas high numbers of rabbits may turn the grasslands, encroached by tall grasses, into a more open vegetation. In other words, rabbits are capable to change the encroachment by tall grasses into short herb-rich grasslands (Van der Hagen et al. 2022a; Q.L. Slings - personal communication).

(5) The post-1990 decrease in nitrogen deposition down to a non-critical level helps to reduce the encroachment by tall grasses. Due to the development of autonomous blow-outs, the sand with overblown vegetation (Fc2) leaves also less room for encroachments by tall grasses. These processes are seen along the entire Dutch coast, especially in the lime-rich part (Aggenbach et al. 2018). It is good to note that addition of climate factors to the GEE might have given more insight in explaining the changes seen.

Chapter 4 evaluates 41 permanent plots installed by Jan Boerboom to study vegetation succession. In 1953, all vegetation types were present from the sandy *Phleo-Tortuletum* up to the dune oak forests. The hypothesis was that livestock would cause regressive succession or at least slow down progressive succession. However, the opposite happened contradicting the hypothesis (Fig. 3).

(1) Only the more sandy plant communities (e.g. *Phleo-Tortuletum*) returned after 2003, which coincides with the autonomous expansion of bare sand (Fig. 2a; Chapter 2; Aggenbach et al. 2018). No indication exists that the introduced livestock is responsible for the observed changes.

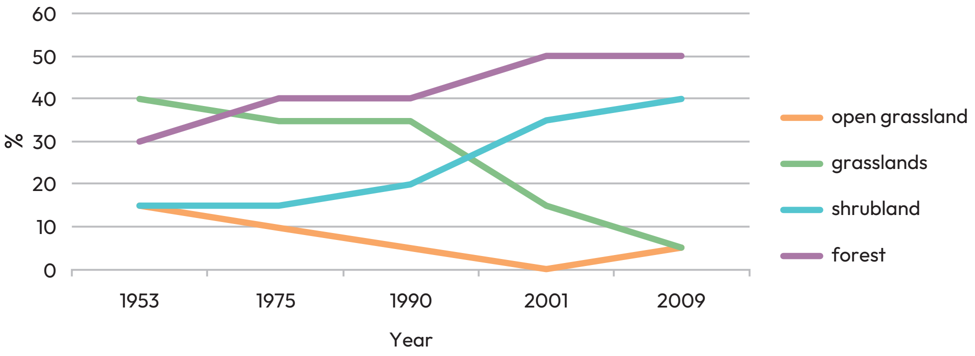


Figure 3. The vegetation changes in four clusters of succession across 41 permanent plots stages from 1953 to 2009 (based on Lammers 2015). 1954 is the outbreak of myxomatosis, 1989 is the outbreak of RVHD-1, and 1990 is the date of introduction of livestock. Note the difference in development between the permanent plots results and the aerial photograph results of figure 2, where high scrubs and forest are not included.

(2) In the pre-1990 period, before the introduction of livestock, progressive and regressive succession were in balance up to 1990 (51% versus 49%). After the 1954 myxomatosis outbreak, only a small shift was observed around 1970. Shrubs and small trees came up with a very modest increase in the vegetation relevés: a first indication of progressive succession.

(3) In the post-1990 period, a massive progressive succession occurred (10% versus 90%). Most of the species-rich grassland communities disappeared, including the *Anthyllido-Silenetum* of the *Zeedorpenlandschap*. Around 2004, again after 15 years, the progressive succession sped up (Fig. 6 in Chapter 5). The 1989 outbreak of RVHD is more likely to be responsible for this change than livestock grazing.

Chapter 5 evaluates seven exclosures with a rabbit proof fence and their reference sites. These exclosures were installed by Eric Wanders in 1975, to provide evidence on the impact of rabbits on succession. In all exclosures, shrub and forest species have established, even in the southern exposed ones, while this was not the case in most of the reference plots. The observed changes following the 1975 exclosure continue, whereas no differences are found in the references due to the introduction of livestock. There are two exceptions: (a) The two southern exposed exclosures bearing a closed moss and lichen dominated grassland; the reference plot is more open and less biodiverse due to the trampling of the heavy livestock, which is seen as a negative development. Notice that rabbits have a more subtle way of impact affecting the dune ecosystem (e.g. Wallage-Drees 1988; Bakker 2003). (b) In the middle dunes, both exclosure and reference plot developed into a *Hippophae* shrubland. *Crataegus monogyna* and *Rosa canina* are more dominant in the exclosure. *Cynoglossum officinale* and *Jacobaea vulgaris* only occur in the reference plot due to the disturbance from the livestock.

Chapter 6 evaluates the impact of the (former) agricultural activities, including livestock grazing, on the species composition of grassland communities of the *Zeedorpenlandschap* (Doing 1988; Slings 1994; Janssen and Schaminée 2003). We qualitatively compared them with grassland communities further away from the seaside villages. Changes over time (pre-1970, 1970-1985, 1985-2000, and post-2000) and space (six locations) are studied. Hypothesised was an overall loss in quality over time and at all locations. However, this was not the case in the post-2000 period, where even a small improvement was observed. Direct and indirect human disturbance, including recreation and golf, seem to mimic the former farming practices. Installing livestock grazing showed variable effects: sometimes positive, sometimes none (Ehrenburg et al. 1995; Mourik 2004; Van den Bos 2007; Van der Hagen et al. 2015). How to understand these differences? It is all about balance. Too much disturbance is destructive to the vegetation, while too little leads to progressive succession and conversion of the lime-rich coastal dunes of the Netherlands into less species-rich plant communities. Is the *Zeedorpenlandschap* a good example of the Intermediate Disturbance Hypothesis (Connell 1978; Collins et al. 1995; Roxburgh et al. 2004; Fox 2014; Brunbjerg et al. 2014)? Soil analysis showed that shell fragments in the organic top layer of the soil are a distinct characteristic of the *Anthyllido-Silenetum* compared to the *Taraxaco-Galietum*. The shell fragments originate from thin terrestrial snail shells. Snails hibernate in the organic top layer and can then be crushed by the livestock. In the post-2000 period, sand with small shell fragments from neighbouring blow-outs might serve as a lime supply, combined with effects of human trampling. From an European perspective, these human influenced dune landscapes of the *Zeedorpenlandschap* are not unique. The similarities and differences between Mielles in Northern France, Aizjoms in Latvia and Machairs in north-western Ireland and Scotland are discussed.

EVALUATION

According to the results of this PhD research (Chapter 2-6), the impact of the introduction of livestock grazing, at a density of 0.06-0.07 LLU.ha^{-1}.year^{-1} in Meijendel coastal dunes, is not the major factor explaining the observed changes in the vegetation over the last 50 years. Fluctuating numbers of rabbits, changing nitrogen deposition levels and climate change are likely to be more important and/or override the impact of livestock. The impact of these factors will be discussed further on, but not before some additional thoughts on livestock grazing are given. However, our findings do not imply that year-round livestock grazing at a density of 0.06-0.07 LLU.ha^{-1}.year^{-1} has no impact at all.

Livestock is considered to be a disturbance factor on a small scale (Assendorp 2010), which can be meaningful on its own, if properly applied (Nijssen et al. 2014). On the landscape scale, and given sufficient time, the effects of disturbance by livestock will disappear. Some examples are:

Due to livestock grazing, changes have been observed when *Hippophae* shrubland breaks up at the end of its lifespan. Livestock speeds up this break-down process, transforming scrubs into grasslands. And in the near-absence of rabbits, livestock is an alternative management tool, but it is key to realize that livestock does not replace the role of rabbits on burrowing, scratching and its key role in selective feeding on seedlings of shrubs and trees. In the near-absence of rabbits, livestock might have an impact, if applied in high density, and not necessarily year-round. This is observed in Solleveld (south of Meijendel), where a triple stocking rate of animals – under acidophilous circumstances – opened up a strongly degraded landscape that was almost totally encroached by tall grasses. These examples could be seen as a positive trend.

On the other hand, negative examples can be brought forward in relation to the weight of the animals. Unlike rabbits, livestock compact the soil, having a serious negative impact on the small fauna in dry dune grasslands, and consequently for the avifauna (De Bruyn 1997; Nijssen et al. 2014). Another negative effect can be observed in dune grasslands with an open vegetation structure. Repetitive grazing on grasses may lead to a horizontal growth of grasses smothering mosses and lichens (Van der Hagen 2011). Finally, the ecosystem has to adapt to the introduction of livestock, as it did centuries ago to rabbits (Van der Meijden 1992). It is certainly not advisable to stop the livestock grazing after the relatively short time since its introduction in 1990 (Assendorp 2010). This is in line with Victor Westhoff's guideline for nature conservation: stability in time, diversity in space (Westhoff 1983).

Herbivory

Putting livestock grazing in perspective, Van der Meijden (1992) made a rough estimate of the impact of herbivores in Meijendel. The largest impact of various herbivores turned out to be leaf and root lice with a consumption of 220,000 kg per annum. Livestock was second with 176,000 kg. Snails consumed an estimated 150,000 kg, followed by rabbits and the larvae of beetles each with 100,000 kg, and larvae of butterflies with an estimated 50,000 kg. Grasshoppers had the lowest impact with 1,000 kg. This overview implies that the impact of livestock grazing is larger than the impact of rabbits. However, these figures have to be put in a time perspective. After the introduction of the livestock grazing, the effects in parts of the area were clear and best visible along the fence lines. Over the last decade, however, the effects stood out less and the differences in the vegetation disappeared largely.

Apart from these estimated values for consumption, it is clear that some herbivore groups have a more specific impact. According to Van der Meijden (1992), rabbits consume in more or less comparable proportions to livestock, but the grazing is of a different character. Rabbits block progressive succession not only by grazing, but mainly by consuming a large share of the seedlings of shrub and tree species (Salman & Van der Meijden 1985). The two rabbit viral diseases, myxomatosis and RVHD-1, killed the vast majority of rabbits and so caused an explosion of opportunities for shrub and tree species, with all the consequences for progressive succession as described in chapters 2, 4 and 5.

On the other hand, when rabbits are present in numbers, their digging of warrens and making scratches (Burggraaf-Van Nierop and Van der Meijden 1984) leads to small scale sand deposits, and naturally collapsing warrens may lead to an initiation of blow-outs, especially under lime-rich conditions. On the other hand, tall grasses are tolerant to grazing by livestock, that therefore profit the most from their presence (Lamoot et al.

2005). According to Assendorp (2010), the impact gradually disappears after 5-10 years. The impact of other macro- and microfauna – as calculated by Van der Meijden (1992) – is even more complex than of livestock and rabbits. They are often bound to specific plant species and sometimes even limited to seeds, flowers, leaves or roots.

Though fauna is positioned at the lowest level in the SHM (Box 1), the impact of rabbits especially is clear and of higher significance than the impact of livestock. Therefore, the faunal component should be differentiated. A similar nuance could be given with regard to the position of vegetation and fauna in the model. According to Bakker et al (1981), vegetation and fauna are subordinate; according to Van Haperen (2009), vegetation and fauna function at the same level. Regarding to our findings, however, rabbits should be placed at a higher level than vegetation. And besides, rabbits are likely to have a great impact on relief (at a high position in the SHM), because burrowing may lead to blow-outs, whereas livestock do not do so or even block such developments due to trampling and subsequent soil compaction.

Climate and nitrogen deposition

The main reason for the introduction of livestock grazing in Meijendel was to counteract the strong encroachment on grassland by tall grasses and sedges (Kooijman et al. 1998). However, the start of this experiment coincided with a gradual decrease of the nitrogen deposition. Because nitrogen did not accumulate in the organic matter in the soil of lime-rich dunes (Aggenbach et al. 2017), it might be concluded that the impact of the nitrogen decrease since 1990 is larger than the effects of the grazing by livestock. So, we can assume that the decrease in nitrogen has led to the autonomous decrease of grass encroachment. Nowadays, the nitrogen load in the coastal region is nearing the pre-1920 situation, which in itself is a hopeful development for the re-establishment of species-rich dune grasslands.

Considering that blow-out development is not driven by livestock grazing, we have to look for other explanations. At least two possibilities can be brought forward. First, the interaction between nitrogen deposition and climate change. Changes in climate conditions, considered to be of importance for blow-out development by Aggenbach et al. (2018), might be linked to the changes in the conditions for algae to survive on bare sand. Cyanobacteria are the first life form on bare sand, followed by green algae, forming an algal crust (Van den Ancker et al. 1985; Pluis and De Winder 1989). The algae depend on nutrients from rainfall. The post-1990 decrease of nitrogen from a level of 30-35 kg.ha^{-1}.yr^{-1} to a level of 15 kg. ha^{-1}.yr^{-1} is near to a critical deposition, in respect of the most vulnerable dune grasslands. Bobbink (2021) and Kooijman et al. (2017) mentioned a critical low level of 10 kg.ha^{-1}.yr^{-1}. This low level might make these crusts more vulnerable for erosion by rainwater. The combination of heavy summer rains and hydrophobic sand is likely to promote this process. The lime-rich bare sand is thus exposed and becomes vulnerable for wind transport (Jungerius and Van der Meulen 1988), resulting in more blow-outs.

The second explanation is related to the idea that auto-cyclical patterns are of importance for large-scale changes in vegetation at the landscape level. In Box 2, several examples are given of auto-cyclical patterns, with different timespans, in different parts of the world, that could be linked to such large-scale changes. In the 1980's, blow-outs basically disappeared (Jungerius and Van der Meulen 1988; Mensing 2002) and only reappeared after 2001 (Aggenbach et al. 2018). Our suggestion is, that the observed blow-out developments along the Dutch coastal dunes could be likewise linked to such auto-cyclical patterns, possibly instigated by Atlantic Oscillations. Our suggestion is, that the observed blow-out developments along the Dutch coastal dunes are likewise linked to such auto-cyclical patterns, possibly instigated by Atlantic Oscillations.

Climate clearly is a dominant factor for the underlying components in the SHM (Box 1). According to Van Haperen (2009), the nitrogen deposition is part of the atmospheric deposition and, is linked to the climate component, together with carbon dioxide emissions. Despite nitrogen deposition is airborne, this high position in the model is disputable. The impact principally affects the soil, with clear differences between the lime-rich Rhenodunal and lime-poor Wadden district (Kooijman et al 2017).

RABBITS RULE

The importance of European rabbits as managers of vegetation development is documented extensively (e.g. Van Groenendael et al. 1982; Salman and Van der Meijden 1985; Van der Meijden 1992), and especially in southern European countries (e.g. Calvete et al. 1997).

On the other hand, in Junner Koeland, a floodplain grassland along the river Overijsselse Vecht near Ommen in the northeast of The Netherlands, Bakker (2003) documented all grazing by livestock, rabbits and common voles. The common vole had the highest impact, then the rabbits and then livestock in that landscape. It is not known if common voles play a comparable role in Meijendel.

The incentive of this thesis was evaluating livestock grazing in Meijendel, but in this PhD-thesis the crucial position of the rabbit – although on the lowest step in the SHM – has become clear, as the results of Chapters 2, 3, 4 and 5 reveal. Rabbits maintain the short grasslands consistently (Wallage-Drees 1988) and are perfectly able to counteract tall grass encroachments. If rabbits occur in sufficient numbers, the area of the short species-rich dune grasslands can be a very substantial part of the dune landscape. Due to the 1954 myxomatosis and the 1989 RVHD-1 outbreak, the consumption of the palatable seedlings of trees and shrubs almost stopped. This opened a window of opportunity for trees and shrubs to develop extensively (Fig. 4), with far reaching consequences for the openness of the dune landscape. Apart from the consumption of palatable seedlings, rabbits are also capable of holding back the expansion of shrubland (Smit and Ruifrok 2009). So - **Rabbits rule**.

HOW TO KEEP RABBITS RULING?

Viral diseases

The rabbit population in the Netherlands strongly fluctuates over the years, because of the impact of epidemic viral diseases: the 1954 myxomatosis outbreak and the two RVHD outbreaks, the RVHD-1 in 1989 and the RVHD-2 in 2014 (Van Koersveld 1955; Wallage-Drees 1988; Kerr 2012; Montizaan and IJzer 2016). When rabbits are exposed to the viruses for the first time, the diseases kill an estimated 90 to 95% of the infected animals (Wallage-Drees 1988; Drees and Van Maanen 2004). Myxomatosis is indigenous in the populations of the Brazilian rabbit (*Sylvilagus brasiliensis*) and the Californian rabbit (*Sylvilagus bachmani*); there it only causes mild symptoms of illness. RVHD-1 was first discovered in China in 1984. In 1986, 35 years after myxomatosis, RVHD-1 was detected for the first time in Europe, in Italy, possibly imported via the transport of dead or living rabbits from China. In 1991, RVHD-1 was introduced in Australia, and in 1997 in New-Zealand, to minimize environmental damage and food competition with sheep. The RVHD-1 virus killed again 90 to 95% of the wild rabbit population. The effect seemed even higher than that of myxomatosis (Drees and Van Maanen 2004). But through co-evolution of the animal and the virus, the virulence decreases and the resistance of the rabbit increases. In 2014, 25 years after RVHD-1, a new highly infectious mutant arrived in the Netherlands: RVHD-2 with again a high rate of rabbit losses. Again a slow recovery is seen up to the next iteration of the virus, whenever that may happen.

How to increase the number of rabbits?

Three alternatives must be considered to consistently increase the rabbit numbers: reduce the numbers of Red fox (*Vulpes vulpes*), restock the rabbit population or a combination of these two measurements. Reducing the Red fox helps, but is probably not a realistic option, because of social resistance. Local shooting in Australia led to a doubling of the rabbit population (Pech et al. 1991). Banks (2000) showed an increase by tenfold when killing all foxes.

The second alternative is repopulating an area with rabbits. This was a regular activity in Meijendel up to the 1980’s, as this area was an important hunting area of the Royal family. There was a preference to shoot fleshy rabbits instead of the meagre ones from the natural dune population. In Spain and France, it is customary to restock wild rabbit populations in natural areas (Van der Meijden 2018b; Calvete et al. 1997). The survival of the introduced rabbits proved to be a problem, with less than 3% survival in the first ten days. Guerrero-Casado et al. (2013) mention various options to achieve a more successful restocking. The physical condition of the animals should be good and shelter against predators should be optimized. To enhance the success, vaccination against RVHD must be carried out (like in domesticated rabbits). Young vaccinated rabbits had a 13,6 times higher chance of survival than non-vaccinated (Van der Meijden 2018b; Calvete et al. 2004). Recently, in addition, the vaccination has been shown to be effective for two years. If we want rabbits to rule again, large scale experiments in fox-excluded fenced-off areas should be considered (Dekker et al. 2022), executed with vaccinated, well-fed rabbits from nutrient-richer environments.

Despite including the rabbit in the Dutch Red List in 2021, shooting is still practiced at a large scale. For moving rabbits, the extensive and complex Natura 2000 procedures to bring rabbits from outside the dunes to repopulate Meijendel (and other dune areas) should be adapted into a far less complicated scheme. This set of procedures includes the methodology for rabbit catching by ferrets, the transport of the animals, and permits on vaccinating rabbits by veterinarians only. One could surmise that the paperwork disease is worse than the remedy getting rabbits.

FUTURE MANAGEMENT AND RESEARCH

Based on the results of this PhD thesis, a set of various management measures is advised, including the continuation of grazing by livestock for at least as long as the density of rabbits is (extremely) low. Note that grazing by livestock, however, is not more than a poor partial alternative. In 2015, we changed the grazing regime to an even lower density to enhance plants to flower more extensively. But also, apart from this, grazing by livestock should be continued, for reasons of ecosystem functioning, and as an expression of former activities. The aftermath of 1954 myxomatosis outbreak should be counteracted by cutting down trees and scrubs to safeguard the dunes as an open landscape. All management measures to safeguard a high biodiversity, especially the Natura 2000 priority habitat grasslands ('Grey dunes'), should be considered in the context of the Meijendel dune area being a semi-natural landscape (Westhoff 1949; Saris 2018) and not a natural or near-natural landscape. A better understanding of the impact of climate change, including auto-cyclical patterns (Box 2), is needed and should be studied to get insight if and when additional action, like initiating artificial blow-outs, is needed.

(1) Livestock grazing is most effective if applied in a flexible way (finger on the pulse management), linked to the needs and the conditions at a certain time and place (Nijssen et al. 2014), locally combined with mowing. Variables are the type and the size of animals, the number of livestock and the period of grazing. Such an ap-

proach mimics the former livestock farming in the *Zeedorpenlandschap* area around the seaside villages; in this landscape, mowing was a part of the historic practice. The remaining rabbit populations, indeed, perform the best at places with nutritious regrowth after mowing, as well as in the more nutrient-rich *Zeedorpenlandschap* (Brussel 2018).

(2) The rabbit viral diseases have resulted in an explosion of trees and shrubs in the grassland ecosystem of the Meijendel dunes (Fig. 3). Recently (2021), a 16-year program has been launched to cut down individual and groups of trees and shrubs to safeguard an open landscape in Meijendel (Van der Hagen et al. 2015). Long-lasting species like *Crataegus monogyna* and *Quercus robur*, together with introduced poplar species (especially *Populus canescens*), are the focus of this removal. Cutting is even more urgent, because the increase of bare sand (autonomously and artificially) also overblows into existing grasslands. The grasslands are increasingly squeezed in between bare sand and the advancing shrubland and forest. From the point of view of international nature conservation, it must be underlined that these grasslands are a priority Natura 2000 habitat (H2130 Grey dunes). As an additional management tool, burning could be proposed to be applied in coastal dunes. In Denmark burning has always been, and still is, a regular practice in managing heathland dunes, and research has been carried out on the vegetation and faunal aspects of this management measure (e.g. Vestegaard and Alstrup 1996; Brunbjerg et al. 2015). In the Netherlands, however, no systematically documented experiences exist with regard to this management tool.

(3) Assendorp (2010) states that the introduction of livestock is a disturbance factor, to which the Meijendel dune ecosystem has adapted since 1990, just like the ecosystem has adapted to the presence of the rabbit centuries ago. For the sake of continuity in ecosystem functioning, it seems not to be wise to end livestock grazing after such a short time.

(4) On-going climate change and cyclical patterns (Box 2) will affect the biotic (plant and animal shifts) and abiotic (with a focus on blow-outs) conditions in the Meijendel dunes, as well as along the entire Dutch coast. Aggenbach et al. (2018) found some correlations with climate parameters, but much is still not understood and needs further research. Apart from the effects mentioned before, climate change causes an increase of the soil temperature in the top 100 cm of 1.5°C over the last 40 years, resulting in accelerated soil processes (Bakema et al. 2022). In areas with a relative open vegetation, like coastal dunes, the increases in the soil temperature can even be more than average figures. This phenomenon has not been investigated in the coastal sand dunes yet, and should be considered in addition to impact of auto-cyclical patterns (Van der Hagen et al. 2022a).

(5) A further decrease of the nitrogen deposition is essential, probably down to the levels of a century ago (Noordijk 2007; Bobbink 2021). The question is whether the dune ecosystem now functions as well as in that former time frame. Experimental research is suggested on the typical dune cyanobacteria and green algae in the algal crusts, which likely flourished under a high level of nitrogen deposition. This research could investigate the increased vulnerability for algal crust erosion by rainwater due to a decreased input of nitrogen by atmospheric deposition.

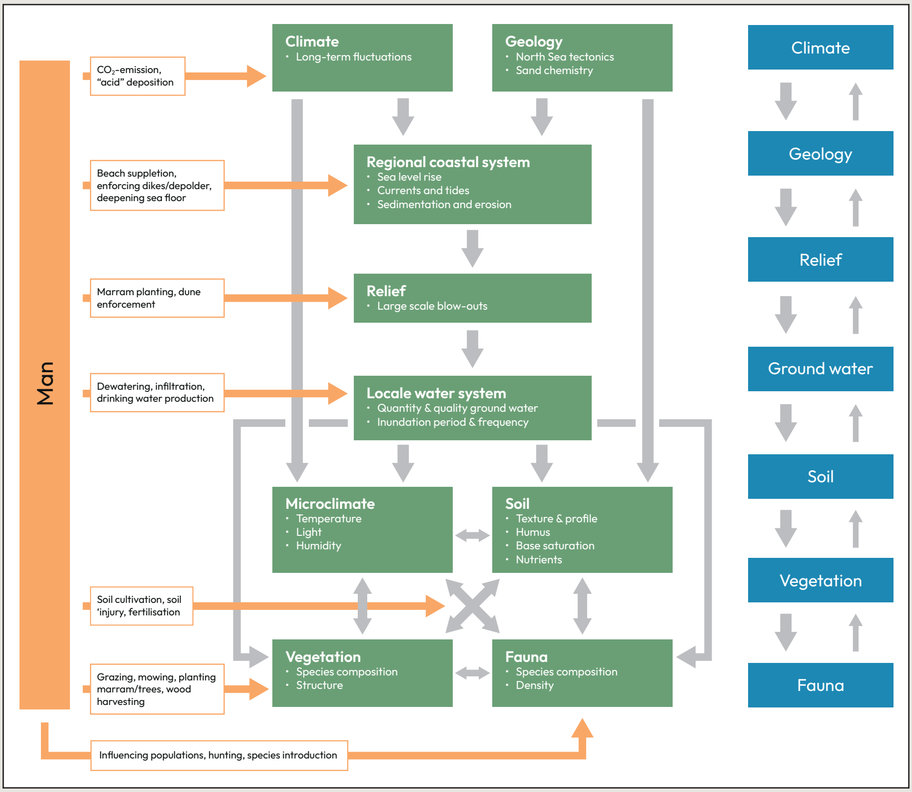
Outlook

The main challenge for the near future is to find an appropriate balance between the rabbit population and the number of introduced livestock. This in respect to an expected further decrease of the nitrogen deposition, anticipating known changes in climate conditions and awareness on auto-cyclical fluctuations. Only then, can the high biodiversity of the dune ecosystem be maintained. Given the current situation and the fairly fixed surrounding environment, coastal sand dunes must be regarded as a semi-natural landscape. This landscape is in demand of subtle, continuing and small-scale management activities, that are responding to yearly variations in the climate conditions. This outlook is not only valid for Meijendel; it has a general validity for the north-west European coastline and more specifically for the lime-rich coastal sand dune landscapes.

BOX 1. SPECIFIC HIERARCHIC MODEL: SIZING THE IMPACT OF INFLUENCES ON THE PHD THESIS RESULTS

The abiotic and biotic relationships in dune ecosystems of the Dutch coast are displayed in the Specific Hierarchic Model (SHM) developed by Bakker et al. (1979) (right section). From the top (climate), there is a dominant influence on the underlying component to the bottom (fauna). Changes taking place in the climate will affect all underlying components. The other way around, there is a subordinate influence. This means that, introducing livestock in Meijendel will have no influence on climate conditions, but is hypothesised to influence vegetation, possibly the soil component.

Van Haperen (2009) partly rearranged the top and bottom of the model (middle section), equalizing climate and geology, and vegetation and fauna. He also interrelated vegetation and fauna with microclimate and soil due to the fact that coastal sand dunes are a young ecosystem (see Assendorp 2010). Van Haperen introduced the regional coastal system, to be placed between climate/geology and relief. Bakker et al. (1979) and Van Haperen (2009) show that at all levels human activities interfere (left section). Nitrogen deposition (as part of “acid deposition”) is linked with the climate component. The components of geology, relief, hydrology and soil (Bakker et al. 1979) and regional coastal system (Van Haperen 2009) may be relevant for evaluating livestock grazing over areas of 50 ha not relevant in the context of this PhD thesis.



BOX 2. AUTO-CYCLICAL PATTERNS

The Littoral 2017 Liverpool symposium ‘Change, Naturalness and People’ brought the idea of the importance of auto-cyclical patterns for large scale changes in vegetation at the landscape level. DeVries-Zimmerman et al. (2020) discovered a fluctuating pattern in the ground water level in dune slacks in sand dunes along Lake Michigan. A rising water table from 1938, lowering in the years 1998 to 2014 and starting to rise in 2014 to 2017. The changes were linked with an auto-cyclical pattern in the water level of Lake Michigan of several meters with short term fluctuations of ~30 years and long term fluctuations of ~160 years already lasting for 4,700 years (Baedke and Thompson 2000). Van der Meijden (2018a) reviewed the vegetation development of Meijendel before the extraction of ground water for drinking water. Between 1750 and 1900, rainfall fluctuated with a substantial dip in between 1775 and 1825. The 30-year average annual rainfall decreased and rose again up to 200 mm (Van Straaten 1961). This temporary climate change must have an impact on the water level in dune slacks and also have an impact on the drier parts of the dune ecosystem. In 2003 and 2007, there were severe drought waves, which did not occur in the 1975-2001 timespan (except for 1976). The stormy winters of 2005 and 2007 might also have promoted sand movement in the post 2003 blow-outs (Aggenbach et al. 2018).

The question, that arises is: do these events fit into auto-cyclical patterns and do we have to adapt our management strategies to these possible patterns? González-Villanueva et al. (2013) mention a repetitive fixation and remobilization of the dunes of the Targa region in Spain. Gares and Nordstrom (1995) present data on the cyclic evolution of blow-outs along the New Jersey coasts with a four-stage pattern from formation to closure over 20 years. Sawakuchi et al. (2008) link the autonomous formation of blow-outs to wind extremes along the Brazilian coast. Jongmans et al. (2015) suggested a climate cycle of 50-60 years, which in figure 2 might explain the decrease of bare sand from 1975 onwards and the increase from 2001 to 2009 as an autonomous process. Although 40 years of data in this thesis is quite extensive, it is not enough to give sound conclusions. An explorative study by Van Rooijen et al. (2022) suggests, that the occurrence of open grassland vegetation in the dunes of Meijendel, based on NDVI (Normalized Difference Vegetation Index)-observations over 13 years, coincides with sea level fluctuations of the North sea. Seip & Grøn (2019) found an auto-cyclical pattern of ocean and sea oscillations of about 21 years. This is consistent with the sea level cycle (20-24 years) observed along the Dutch coast, which may be a factor of significance in promoting circumstances for increased aeolian activity.

If these auto-cyclical factors are key in promoting favourable conditions for open sand and open grassland vegetation as seen from 2003 onwards (Aggenbach et al. 2018), these factors will have an important interaction with the success (or lack of success) of measures taken to promote open vegetation, such as the idea introducing of livestock or artificially initiating artificial blow-outs. The success rates of these measures may be increased by incorporating these more-or-less predictable auto-cyclic factors in dune management schemes. At the least, we should consider these factors when planning to initiate a management measure unless great changes in climate conditions undermine these patterns.

Van Haperen (2009) partly rearranged the top and bottom of the model (middle section), equalizing climate and geology, and vegetation and fauna. He also interrelated vegetation and fauna with microclimate and soil due to the fact that coastal sand dunes are a young ecosystem (see Assendorp 2010). Van Haperen introduced the regional coastal system, to be placed between climate/geology and relief. Bakker et al. (1979) and Van Haperen (2009) show that at all levels human activities interfere (left section). Nitrogen deposition (as part of “acid deposition”) is linked with the climate component. The components of geology,

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Summary

During the last five decades, the vegetation in Dutch coastal dunes has changed considerably. The once open, sandy dunes dominated by species-rich grassland, has shifted into a more closed vegetation dominated by tall grasses, shrubland and forest. This rather monotonous vegetation is accompanied by a considerable loss of local biodiversity. These developments have been associated with several phenomena: (1) the sequential outbreaks of myxomatosis and Rabbit Viral Haemorrhagic Disease (RVHD) in rabbit populations (*Oryctolagus cuniculus*), (2) routine planting of Marram grass (*Ammophila arenaria*), shrubs and trees to stabilize and decorate the dunes, (3) high inputs of airborne nitrogen, (4) changes in land use, including abandonment of livestock grazing, notably in the *Zeedorpenlandschap*, and (5) the impact of changes in climate.

Livestock grazing was introduced in coastal sand dunes as a management tool, as elsewhere, because large grazers were thought to counteract the process of stabilisation, preventing encroachment by scrubs and forest, and to open up closed, monotonous grasslands. Due to the fact that the domestic livestock strongly prefer graminoid species, their extensive grazing seemed a logical choice to help restore the species-rich dry dune grasslands, and hopefully also to initiate blow-out formation, and to reduce the cover of shrubland and forest.

Late in 1990, year-round grazing by Galloway cows and Nordic Fjord ponies was introduced in the Meijendel dune area in the Netherlands. In 2005, the Fjord ponies were replaced by Konik horses. The livestock density was set and maintained at 0.06-0.07 LLU. ha^{-1}.year^{-1} (Large Livestock Units; 1:12-18 ha) as this level was seen as optimal for Meijendel. This PhD thesis evaluates the impact of the introduced livestock.

The main hypothesis tested whether the introduction of livestock will lead to regressive succession by grazing and trampling, as expressed by an increase of bare sand, a decrease in the area of shrubland and forest, and a subsequent increase of the area of dune grassland. It was also expected to lead to an improvement in the quality of the dune grasslands, with species-poor, grass-encroached stands changing into species-rich short dune grasslands with patches of bare sand.

The development of the vegetation is set in a landscape ecological context.

In **Chapter 2**, the main conclusion is that the changes observed are not linked to the introduced livestock. Principally, the lack of rabbits due to viral diseases, and the subsequent halt on their consumption of young palatable seedlings of tree and scrub species (e.g. *Hippophae rhamnoides* and *Crataegus monogyna*) by rabbits, led directly to progressive succession over large areas.

Notably, in the period 2001 to 2009, areas of bare sand have also developed autonomously, irrespective of livestock. Possible causal factors involved are the weakening of algal crusts on sand due to the decrease of nitrogen deposition, and changes in climate parameters. A decrease of shrubland also occurred, but not because of the livestock. Due to the limited 35 to 45 year lifespan of *Hippophae rhamnoides,* large scale and almost simultaneous collapse of this scrub led to natural regressive succession, resulting in a greatly increased area of grassland.

Chapter 3 shows that changes occurred in all four grassland classes. Contradicting our hypothesis, there was no significant impact within either 11 or 19 years after the livestock introduction. On the other hand, rabbits played a significant role in the changes in all four grassland classes in the 1975 to 2009 period. When at high density, the rabbits maintain the species-rich dune grasslands, and are capable of counteracting tall grasses encroached vegetation. The decrease of nitrogen deposition since1990 also explained part of the changes. Apart from rabbits and nitrogen deposition, changes in climate conditions, including auto-cyclic patterns, are likely to have had an impact on the observed results, but this needs more study.

Chapter 4 discusses the changes in the vegetation in 41 permanent plots. Up to 1990, progressive and regressive succession were in balance. After 1990, progressive succession was dominant, and livestock did not cause regressive succession. Above all, almost all grassland communities disappeared, including the rare plant community *Anthyllido-Silenetum*. Only the more sandy plant communities returned after 2003, which coincided with the autonomous increase in bare sand after 2001 (Chapter 2). The almost complete absence of rabbits due to viral diseases is likely to have played an important role in the progressive succession in the permanent plots.

The results of the 1975 rabbit exclosures in **Chapter 5**, when compared with its references, showed the pre-eminent role of rabbits. In the reference plots, the vegetation succession stopped or almost stopped. The livestock introduced in 1990 is not likely to have had such a strong effect on the developments. Only in the southern exposed exclosures, the lichen community was far less in quality in the reference plot than inside the exclosure, presumably due to livestock trampling.

In **Chapter 6**, the small-scaled impact of former human activities in the so-called *Zeedorpenlandschap* is discussed. Here, livestock grazing was a former practice of farmers who lived in the neighbouring coastal villages. A general decrease in grassland biodiversity of the *Anthyllido-Silenetum* from the pre-1970 period to 2000 occurred. In the post-2000 period, the situation improved, but not in Meijendel despite the introduced livestock grazing. This was the case in the majority of the six areas near these coastal villages. Human activities, such as recreation and golf sport, and in some cases livestock in low densities, seems to mimic the former farmers' activities. This is a delicate balance of disturbance: not too much and not too little. Soil research also revealed the fine-grained shell presence in the top-organic layer of the soil, and its necessity. In former days, this was linked to (hibernating) snails crushed by livestock. More recently, the small shell fragments possibly originate from blow-outs.

Based on the results of the data presented in this PhD thesis, other factors than livestock grazing explained the changes observed over the last 40 to 60 years. Fluctuating numbers of rabbits (more specifically the almost complete absence of the animal), the decrease of nitrogen deposition since 1990, and changes in climate parameters are likely to be more important and overrule the impact of livestock. This does not mean, that our findings implicate that year round livestock grazing at the Meijendel density of 0.06-0.07 LLU.ha^{-1}.year^{-1} (Large Livestock Units; 1:12-18 ha) has had no impact at all. In fact, it is not advisable to stop the livestock grazing in the relative short time since the introduction in 1990. This idea is in line with Victor Westhoff's guideline for nature conservation: stability in time, diversity in space.

Climate change, including auto-cyclical patterns, has an undisputed influence on the whole dune ecosystem, because climate is at the highest level in the Specific Hierarchy Model. If we place the results of this thesis in the perspective of the SHM, livestock is at the lowest fauna level and there is hardly any influence on the levels higher up in the hierarchy. However, in the case of the rabbit, it is absolutely clear that the impact of this animal within the dune ecosystem, and especially their absence, is immense: **Rabbits Rule**.

Based on these findings, a set of various management measures is advised. As a direct impact from the 1954 and 1989 rabbit viral diseases, the expansion of trees and scrubs should be reduced, especially in the still relatively open parts of the dune ecosystem. In this way, the potential area for the species-rich dune grasslands can increase. This increase is important because the dune grasslands are squeezed in between the autonomous or deliberate blow-out development and the shrubland and forest expansion. At least as long as the density of rabbits is so low, grazing by livestock should be continued. It is advisable to change stocking densities and test different types of livestock, including smaller livestock, conscious that larger livestock does not cause bare sand (blow-outs), and neither does it selectively consume seedlings of scrub and tree species. Suggestions are also given to improve the number of rabbits, to let **rabbits rule again** in the semi-natural landscape of the lime-rich coastal sand dunes of Meijendel, and similar lime-rich dune areas.

Samenvatting

In de afgelopen vijf decennia is de vegetatie in de Nederlandse kustduinen sterk veranderd. De ooit open, zandige duinen (de blanke top der duinen), gedomineerd door soortenrijk grasland, zijn veranderd in een meer gesloten vegetatie, gedomineerd door hoge grassen, struikgewas en bos. Deze vrij monotone vegetatie gaat gepaard met een aanzienlijk verlies aan plaatselijke biodiversiteit. Deze ontwikkelingen zijn in verband gebracht met verschillende verschijnselen: (1) de opeenvolgende uitbraken van myxomatose en Rabbit Viral Haemorrhagic Disease (RVHD) onder konijnenpopulaties (*Oryctolagus cuniculus*), (2) de routinematige aanplant van Helm (*Ammophila arenaria*) en struiken en bomen om de duinen te stabiliseren en te verfraaien, (3) de hoge toevoer van stikstof uit de lucht, (4) veranderingen in het landgebruik, waaronder het opgeven van veebegrazing, met name in het *Zeedorpenlandschap*, en (5) de invloed van klimaatverandering.

Begrazing door vee werd in de kustduinen ingevoerd als een beheersinstrument, net als elders, omdat men dacht dat grote grazers het stabilisatieproces zouden tegengaan, het oprukken van struikgewas en bos zouden voorkomen, en gesloten, monotone graslanden zouden veranderen in kruidenrijke graslanden. Aangezien de gedomesticeerde veestapel een sterke voorkeur heeft voor grassoorten, leek extensieve begrazing een logische keuze om bij te dragen tot het herstel van de soortenrijke droge duingraslanden, en hopelijk ook om zandverstuiving op gang te brengen, en de bedekking met struikgewas en bos te verminderen.

Eind 1990 werd in het duingebied van Meijendel, Nederland, jaarrond een begrazing door Galloway-koeien en Noordse Fjordpony's ingesteld. In 2005 werden de Fjordenpony's vervangen door Konikpaarden. De veedichtheid werd vastgesteld en gehandhaafd op 0,06-0,07 LLU.ha^{-1}.jaar^{-1} (Large Livestock Units; 1:12-18 ha). Dit niveau werd als optimaal beschouwd voor Meijendel. Dit proefschrift evalueert het effect van de geïntroduceerde veestapel.

De hoofdhypothese test of de introductie van vee zal leiden tot regressieve successie door begrazing en vertrapping, wat tot uitdrukking komt in een toename van kaal zand, een afname van het areaal struik- en bosland, en een daaropvolgende toename van het areaal duingrasland. Ook werd verwacht dat dit zou leiden tot een verbetering van de kwaliteit van de duingraslanden, waarbij soortenarme, met gras begroeide standplaatsen zouden overgaan in soortenrijke korte duingraslanden met plekken kaal zand.

De ontwikkeling van de vegetatie wordt in een landschapsecologische context geplaatst.

In **hoofdstuk 2** is de belangrijkste conclusie dat de waargenomen veranderingen geen verband houden met de geïntroduceerde veestapel.

In hoofdzaak heeft de afwezigheid van konijnen als gevolg van virusziekten, en de daaropvolgende stopzetting van hun consumptie van jonge, smakelijke zaailingen van boom- en struiksoorten (bijv. *Hippophae rhamnoides* en *Crataegus monogyna*) door konijnen, rechtstreeks geleid tot een progressieve successie over grote oppervlakten.

Opmerkelijk is dat in de periode 2001-2009 ook gebieden met kaal zand zich autonoom hebben ontwikkeld, onafhankelijk van de veestapel. Mogelijke oorzakelijke factoren zijn de verzwakking van algenkorsten op zand als gevolg van de afname van stikstofdepositie, en veranderingen in klimaatparameters. Een afname van het struikgewas deed zich ook voor, maar niet als gevolg van de veestapel. Door de beperkte levensduur van 35 tot 45 jaar van Duindoorn (*Hippophae rhamnoides*) leidde grootschalige en vrijwel gelijktijdige instorting van Duindoorn tot natuurlijke regressieve successie, met een sterk toegenomen areaal grasland als gevolg.

Hoofdstuk 3 laat zien dat er veranderingen optraden in alle vier de graslandklassen. In tegenstelling tot onze hypothese was er geen significant effect binnen 11 of 19 jaar na de introductie van de veestapel. Aan de andere kant speelden konijnen een belangrijke rol in de veranderingen in alle vier graslandklassen in de periode 1975 tot 2009. In hoge dichtheid houden de konijnen de soortenrijke duingraslanden in stand, en zijn ze in staat om de oprukkende vegetatie van hoge grassen tegen te gaan. De afname van stikstofdepositie sinds 1990 verklaart ook een deel van de veranderingen. Behalve konijnen en stikstofdepositie hebben waarschijnlijk ook veranderingen in klimaatomstandigheden, inclusief auto-cyclische patronen, invloed gehad op de waargenomen resultaten, maar dit moet nader onderzocht worden.

Hoofdstuk 4 bespreekt de veranderingen in de vegetatie op 41 permanente kwadraten. Tot 1990 was er een evenwicht tussen progressieve en regressieve successie. Na 1990 overheerste de progressieve successie en veroorzaakte het vee niet de verwachte regressieve successie. Bovenal verdwenen bijna alle graslandgemeenschappen, inclusief de zeldzame plantengemeenschap van het *Zeedorpenlandschap*: het *Anthyllido-Silenetum*. Alleen de meer zandige plantengemeenschappen keerden na 2003 terug, wat samenviel met de autonome toename van kaal zand na 2001 (hoofdstuk 2). De bijna volledige afwezigheid van konijnen als gevolg van virusziekten heeft waarschijnlijk een belangrijke rol gespeeld bij de geleidelijke successie in de permanente percelen.

De resultaten van de konijnen-exclosures van 1975 in **hoofdstuk 5**, als vergeleken met de referenties, toonden de overheersende rol van konijnen aan. In de referentiepercelen is de vegetatiesuccessie gestopt of bijna gestopt. Het ligt niet voor de hand dat het in 1990 geïntroduceerde vee nog een sterk effect op de ontwikkelingen heeft gehad. Alleen in de zuid geëxponeerde exclosures was de korstmossengemeenschap in het referentieperceel veel minder van kwaliteit dan binnen de exclosure, vermoedelijk als gevolg van vertrapping door het vee.

In **hoofdstuk 6** wordt ingegaan op de kleinschalige invloed van vroegere menselijke activiteiten in het zogenaamde *Zeedorpenlandschap*. Hier was het grazen van vee een vroegere praktijk van boeren die in de naburige kustdorpen woonden. Van de periode vóór 1970 tot 2000 deed zich een algemene afname voor van de biodiversiteit van het *Anthyllido-Silenetum*, een van de karakteristieke graslanden voor het *Zeedorpenlandschap*. In de periode na 2000 verbeterde de situatie, maar niet in Meijendel ondanks de geïntroduceerde begrazing door vee. Dit was dus wel het geval in het merendeel van de zes gebieden in de buurt van deze kustdorpen. Menselijke activiteiten, zoals recreatie en golfsport, en in sommige gevallen vee in lage dichtheden, lijken de activiteiten van de vroegere boeren na te bootsen. Het gaat hier om een delicaat evenwicht van verstoring: niet te veel en niet te weinig. Bodemonderzoek bracht ook het belang van de aanwezigheid van kleine schelpfragmenten in de top van de organische bodemlaag aan het licht. Vroeger werd dit fijn schelpenmateriaal in verband gebracht met (overwinterende) slakken die door vee werden vertrapt. Recent zijn de kleine schelpfragmenten mogelijk afkomstig van stuifkuilen in de directe omgeving.

Op basis van de resultaten van de in dit proefschrift gepresenteerde gegevens verklaren andere factoren dan begrazing door vee de veranderingen die in de afgelopen 40 tot 60 jaar zijn waargenomen. De fluctuerende aantallen konijnen (meer specifiek het bijna ontbreken van het dier), de daling van de stikstofdepositie sinds 1990 en de veranderingen in klimaatparameters zijn waarschijnlijk belangrijker; deze overrulen de invloed van het ingezette vee. Dit betekent niet, dat onze bevindingen impliceren dat het jaarrond begrazen door vee in de in Meijendel gebruikte dichtheid van 0,06-0,07 LLU.ha^{-1}.jaar^{-1} helemaal geen effect heeft gehad. In feite is het niet raadzaam de beweiding te stoppen in de betrekkelijk korte tijd die sinds de invoering in 1990 is verstreken. Dit idee is in overeenstemming met de richtlijn van Victor Westhoff voor natuurbehoud: stabiliteit in de tijd, diversiteit in de ruimte.

Klimaatverandering, inclusief auto-cyclische patronen, heeft een onbetwiste invloed op het hele duinecosysteem, omdat klimaat op het hoogste niveau in het Specifiek Hiërarchisch Model staat. Als we de resultaten van dit proefschrift in het perspectief van het SHM plaatsen, zit het vee op het laagste faunaniveau en is er nauwelijks invloed op de niveaus hoger in rangorde. Maar, in het geval van het konijn, is het absoluut duidelijk dat de impact van dit dier binnen het duinecosysteem, en dan vooral hun afwezigheid, immens is: **Rabbits Rule**.

Op basis van deze bevindingen wordt een pakket van verschillende beheersmaatregelen geadviseerd. Als direct gevolg van de konijnenvirusziekten van 1954 en 1989 dient de uitbreiding van bomen en struikgewas te worden teruggedrongen, vooral in de nog relatief open delen van het duinecosysteem. Op deze manier kan de potentiële oppervlakte voor de soortenrijke duingraslanden toenemen. Deze toename is belangrijk omdat de duingraslanden ingeklemd zitten tussen de autonome of bewuste ontwikkeling van kaal zand en de struik- en bosuitbreiding. Zolang de konijnendichtheid zo laag is, moet de begrazing door vee in ieder geval worden voortgezet. Het is raadzaam de bezettingsdichtheid te veranderen en verschillende soorten vee te testen, waaronder kleiner vee, in het besef dat groter vee geen kaal zand veroorzaakt en evenmin selectief zaailingen van struik- en boomsoorten verbruikt. Ook worden suggesties gedaan om het aantal konijnen te verbeteren, om konijnen weer te laten regeren in het half-natuurlijke landschap van de kalkrijke kustduinen van Meijendel, en vergelijkbare kalkrijke duingebieden.

Dankwoord

Werken aan een tienjarige PhD-studie aan het einde van een 35-jarige onderzoeksloopbaan bij Dunea heeft een voor- en een nadeel. Het voordeel is de ervaring die je hebt om op allerlei manieren onderzoeksresultaten te documenteren. Je weet dus hoe onderzoek uitvoeren werkt en je kent de klappen van de zweep over methoden, resultaten en discussies. Het nadeel is dat je al een werkgever bedient en waar je dus de dagelijkse werkzaamheden uitvoert. Het uitvoeren van beide taken betekende, dat het promotietraject tien jaar duurde in plaats van de geprognotiseerde vijf jaar. Na tien jaar zijn de 250 geclaimde dagen voor het promotietraject besteed zoals gepland. Deze ervaring was voor mij meer dan de moeite waard en een mooie afsluiting bij Dunea.

Allereerst dank ik mijn stilzwijgende, stimulerende vader Jan van der Hagen. Hij gaf mij de kans om te gaan studeren in plaats van de derde generatie te zijn op een in 1922 in Stevensbeek gesticht fruit- en akkerbouwboerderij; een kans die hij voor zover ik weet niet heeft gekregen. Mijn vader was misschien geïnspireerd door zijn jongste en liefste broer Jos, die van mijn grootvader de kans kreeg om natuurkunde te gaan studeren in Utrecht met een prachtige carrière. Bij vele gelegenheden gaf mijn vader ook graag zijn privéauto aan mij mee om met vrienden de sub-mediterrane flora te gaan bestuderen. Hiermee stimuleerde hij mijn gewenste richting in de ecologie. Gelukkig werd de boerderij voortgezet door mijn zus Karin en haar man Theo, en is de volgende generatie bezig om fruit om te zetten in alcohol. Ook mijn andere zus Gonny heeft de boerderij verlaten en is haar eigen hobbelige en vreugdevolle leven gegaan.

Ik ben mijn bijna levenslange vriend en promotor Joop Schaminée heel dankbaar. We hebben veel meegemaakt, professioneel en persoonlijk. We begonnen beiden onze studie in 1976, samen met Stephan Hennekens, Karel Giesen en Giel Bongers in een bij toeval samengestelde studentengroep voor de eerste kennismakingsweken met de universiteit en Nijmegen. We hadden beiden het voorrecht om onze vegetatiestudie te beginnen in een kalkrijk biotoop, met alle florabijzonderheden die daaraan verbonden zijn. Vooral de reis die Joop organiseerde naar de Zweedse eilanden Öland en Gotland is een van de dierbaarste waar ik deel van uit mocht maken. Vele, vele honderden excursies in verschillende samenstellingen volgden. Wat mijn promotie betreft: de altijd optimistische, stimulerende en hoopvolle Joop heeft me meerdere malen uit de modder van het promotietraject getrokken.

Victor Westhoff was de inspiratie om van cytogenetica, de expertise van mijn biologieleraar op de middelbare school, over te stappen op plantenecologie, een herbeleving van mijn jeugdherinnering aan de toen nog omringende fraaie natuur. Naar aanleiding van een verzoek om de effecten van recreatie op de vegetatie te bestuderen, koppelde Victor mij aan Frank van der Meulen. Terugkijkend had ik niet meer geluk kunnen hebben. En, Victor was altijd bereid om kritisch en stimulerend advies te geven over de Meijendel-ecologie. Meijendel, het gebied waar hij en Nettie Westhoff-de Joncheere rond 1940 onderzoek deden naar mieren en bossen. Tijdens bovengenoemde gedenkwaardige excursie naar Zweden leerde ik Nettie en Victor Westhoff op een meer persoonlijke manier kennen: verschillende karakters maar elkaar zeer aanvullend.

Frank van der Meulen, mijn copromotor, en zijn vrouw Ida hebben mij op een aantal beslissende momenten in werk en privé door het leven geloodst. In 1980, na zijn promotie in Zuid-Afrika, begon Frank zijn werk bij de Duinwaterleiding van ‘s-Gravenhage. Met Jean-Pierre Breuer deed ik een masterstudie over de vegetatie van Waalsdorp. Wij waren Franks eerste studenten en samen ontdekten we de rijkdom van Meijendel. Maar voor mij lonkte ook Afrika. Frank moedigde me aan om mee te doen aan een masterstudie op een koraalrif in Malindi, Kenia: zou het een opstapje kunnen zijn? Het liep anders, zonder enige spijt. In 1988 kon ik Frank’s baan invullen, en samen gingen we de onderzoeksweg op om een grondig inzicht te krijgen in de landschapsecologie van Meijendel. Het was altijd een genoegen om met Frank moeilijke zaken terug te brengen tot een plaatje of tabel, en het leven te bespreken onder het genot van een glas witte wijn, of twee.

Mijn copromotor Karlè Sýkora was lid van de Commissie Advies Duinbeheer van de Duinwaterleiding van ‘s-Gravenhage en haar opvolgers. De leden van de commissie gaven gevraagd en ongevraagde adviezen aan het bedrijf en natuurlijk ook aan mij, die ik graag in ontvangst nam. De meest gedenkwaardige gebeurtenissen waren de excursies, o.a. naar Ierland ter voorbereiding van mijn proefschrift, met levendige discussies (in een brede context) zowel in het veld als ‘s avonds onder het genot van een drankje. Karlè stimuleerde mijn nieuwsgierigheid en hij zorgde voor veel studenten die mij hielpen Meijendel te leren kennen. Bedankt Karlè voor al je stimulerende adviezen.

Het was geen verrassing dat ik aan de Wageningen Universiteit promoveer. Frank Berendse gaf direct zijn goedkeuring. Ook David Kleijn, de opvolger van Frank, gaf graag zijn steun, en gaf aan dat het best bijzonder is dat een particulier bedrijf een promotiestudie ondersteunt. Omdat ik ook nog een reguliere baan te vervullen had, kon ik slechts incidenteel deelnemen aan de activiteiten van de PEN-afdeling. Gelukkig gingen de door Karlè geïnitieerde Wageningse excursies ook onder David gewoon door, waardoor de band met de PEN-collega’s versterkt werd. Vooral met Jasper van Ruijven en Juul Limpens had ik inspirerende ontmoetingen, en zij waren altijd behulpzaam bij het regelen van onderzoeksbenodigdheden.

Mijn werkgever Dunea brengt met grote regelmaat de twee bestaansredenen naar voren: drinkwaterproductie en natuurbehoud. Vanaf mijn eerste kennismaking als student in 1980 met Meijendel heb ik met vier directeuren samengewerkt: de illustere en minzame Henk Bosch, de militair-achtige en constructieve Han Hieter, de economist Piet Jonker die natuur en water eindelijk statutair gelijk stelde, en de water- en natuurintegrator Wim Drossaert. Het is opmerkelijk en zeer prijzenswaardig dat zo'n relatief klein bedrijf in de natuurbescherming onderzoek initieert en ondersteunt om de kennis van het duinecosysteem te vergroten, zelfs zo ver dat het een proefschrift ondersteunt: alle lof! Een speciaal woord van dank gaat uit naar Jaap Mos, die mij op een zeer aimabele manier ertoe heeft kunnen bewegen dit proefschrift ook af te ronden, ondanks al het andere werk dat er lag.

Met Georgette Leltz, en vele anderen, ben ik in 1990 begonnen aan twee grote onderzoeken. Het herstel van duinvalleien en een milieueffectrapport over diepinfiltratie. Beide waren een fors karwei, maar enorm de moeite waard vanwege het succes van het herstel van tientallen hectaren duinvalleien. Na de fusie van de drinkwaterbedrijven van Leiden, Den Haag en Monster werd Georgette Leltz mijn super-leidinggevende en onderzoekscollega. Zij stimuleerde haar groep om grote dingen te doen in een positieve setting. Op haar instigatie vulde ik het nodige onderzoek in om de natuurkwaliteit, waar Dunea verantwoordelijk voor is, te verbeteren. Georgette's gedrevenheid dat de juiste beslissingen in het natuurbeheer ondersteund moeten worden door gedegen wetenschappelijk onderzoek was de basis van dit proefschrift. Voor mij was het eenvoudig om deze opdracht in te vullen, namelijk een bedrijfsrapport over 25 jaar over vee als beheermaatregel omzetten in dit proefschrift. Bedankt Georgette dat je mij in mijn kracht hebt gezet en deze kans hebt gecreëerd.

Dan Assendorp ontwikkelde samen met Wim Droesen de Dicranum software om false colour luchtfoto's te interpreteren. Maar ook eerder was hij betrokken bij het Meijendel onderzoek: planten- en bodemecologie van exclosures, die in 1975 door Erik Wanders werden geplaatst. Natuurlijk heeft Dan mij geholpen bij de enorme hoeveelheid berekeningen van de allereerste brede evaluatie van deze luchtfoto's, die decennia op gebruik hebben gewacht. De optimistische Dan stond altijd voor mij klaar met serieuze, zeer welkome en doordachte adviezen, en altijd met een knipoog. Veel dank Dan!

Als opgeleid veldecoloog had ik bijna geen opleiding in statistiek. Sinds mijn universitaire studie is statistiek een aparte en ingewikkelde discipline geworden. Georgette Leltz raadde me aan goede hulp te zoeken. Die heb ik gevonden: Wim Calame. Naast de berekeningen voor mijn doctoraalscriptie, passeerden tijdens de sessies ook tal van onderwerpen over duinecologie en het functioneren van Dunea de revue: altijd weer een inspiratiebron.

Mijn beste collega's en gepensioneerde collega's van Dunea, dichtbij het natuurbeheer en verder weg; het zijn er te veel om ze alle honderden te noemen. Van een ietwat verlegen, net afgestudeerde student in 1988, hebben jullie mij allemaal geholpen om de ecologie te begrijpen van het gebied dat ook jullie allemaal koesteren. Duinen lijken zo eenvoudig, gewoon een beetje zand en water, maar ze zijn oh zo ingewikkeld. Bedankt voor het delen van jullie kennis met mij! Van de helmplanter tot de fauna-ecoloog en de recreatiespecialist. Maar werken bij een drinkwaterbedrijf betekent ook levendige discussies over rivierwaterkwaliteit, leidingbeheer, elektrotechniek, IT-ondersteuning, geld voor onderzoek en stageplaatsen voor studenten (ook uit het buitenland waaronder La Reunion). En ik dank alle ecologen en hydrologen en andere specialisten van de collega drinkwaterbedrijven van PWN, Waternet en Evides, Kiwa Water Research, RIVM, Bureau Arens en Deltares voor de open discussies over onze gemeenschappelijke onderzoeksgronden, het vrijelijk delen van kennis en een luisterend oor voor mijn interesses.

Zo'n 50 studenten van de universiteiten van Wageningen, Nijmegen, Delft en Utrecht, als van hogescholen van Velp, Delft en Almere hebben mij bijgestaan in het opbouwen van mijn kennis van de kustduinen en de ontwikkelingen ervan. En ik kon mijn kennis delen met de studenten. Een speciaal woord van dank aan Erik Lammers en Charlotte Mooij om bij te dragen aan en coauteur te zijn van een hoofdstuk in mijn proefschrift. En, er zijn geen studenten zonder hun begeleiders, die mij weer de meest recente kennis gaven voor het beheer door Dunea. Via colleges deelde ik mijn kennis dan weer met studenten in hun leslokalen.

Geen natuurbescherming zonder gegevens. Tientallen vrijwilligers en specialisten hielpen mee met het verzamelen van gegevens over de meeste groepen planten en dieren. Elke discipline droeg bij aan mijn kennis van het gebied, informeerde mij over de speciale zorg voor specifieke soorten (bijvoorbeeld Rozenkransje en Sausijsbaardmos), gaf mij de mogelijkheid tot 'kruisbestuiving' van disciplines en tot publicatie van resultaten in het Dunea tijdschrift Holland's Duinen. Hans Toetenel noem ik hier in het bijzonder. Op zoek naar een werkwoord dat allitereert op 'rabbit', kon ik niet iets geschikts vinden. Gert van der Slikke, bedankt voor jouw hulp. Nieuwsgierig naar de omgeving van Meijendel informeerde Christopher Briggs in het bezoekerscentrum van Dunea om floravrijwilliger te worden. Ik nam Christopher graag mee in Meijendel samen met een groep nieuwe plantenvrijwilligers. Hij wilde graag een wederdienst doen. Ik ben je zeer dankbaar voor de Engelstalige correcties van bijna alle hoofstukken van dit proefschrift.

Toen Eddy van der Meijden mij vroeg Meijendel Mededelingen weer op te starten, deed ik dat graag. Dit magazine van Dunea, later Holland's Duinen, is een perfecte manier om de door amateur- en beroepsonderzoekers verzamelde kennis te etaleren. Samen met alle redacteuren en de vriendelijk overtuigende begeleiding van Eddy, was het een groot genoegen om 62 nummers te realiseren.

Op zoek naar antwoorden op bepaalde mediterrane planten, hoorde Piet Zomerdijk over mijn (overschatte) floristische kennis; ik kon hem wel wat op weg helpen. Toen ik hoorde van zijn volgende reis naar Portugal, vroeg ik of ik mee mocht. Het werden vele, vele prachtige reizen. De excursies naar Spanje en Portugal met Piet en zijn partner Hetty Koremans waren een floristisch Walhalla, en over dingen die er in het leven toe doen.

Ik dank jullie allen oprecht voor de fijne momenten die we samen hebben doorgebracht, professioneel en vriendschappelijk, en direct of indirect mij veel vreugde hebben gegeven, zowel in de verleden tijd als ongetwijfeld in de toekomst nog gaat komen.

En last but absolutely not at least, mijn lieve partner André. Iets meer dan twintig jaar geleden ontmoetten wij elkaar. Op het juiste moment kwam André in mijn leven om mijn metgezel te worden. We delen veel en een deel van onze gemeenschappelijke gronden zijn natuur en cultuurhistorie. In de vele omzwervingen in Nederland en in de vele vakanties ver daarbuiten genieten we samen van deze combinatie. In dit afsluitende jaar wacht André geduldig tot ik klaar ben met dit proefschrift, en ook met mijn werk bij Dunea! Dan is er nog meer tijd om samen aan cultuur en natuur te besteden, en om samen van ons huiskasteeltje te genieten.

Terugkijkend op dit dankwoord, realiseer ik me dat ik een van de meest bevoorrechte personen moet zijn en ook ben.

About the author

I, Harrie van der Hagen, was born in Stevensbeek in the township of Oploo c.a., the Netherlands, on the 9th of November 1957, where I grew up. In 1976, I finished secondary school at the *Boschveld College* in Venray. My drawing teacher, the class mentor in the 3rd year, advised me to choose Beta instead of my preference for Alpha. After finishing secondary school, I went to the *Katholieke Universiteit Nijmegen* (now *Radboud University*) to study genetics, fascinated by this subject from the teachings of my biology teacher. After the first year, working the rest of my life in the genetics of Drosophila did not appeal. Plant ecology took my interest, as this had always been present in my mind growing up on a farm and remembering the sounds of frogs and skylarks, when they were still there. During my Bachelor degree, field ecology became more and more attractive due to the influence of several field courses, especially the one in Austria (Kölner Haus). Logically, a major subject for my Master's degree followed in Meijendel in The Hague (Mapping the vegetation and Research on the effect of recreation on vegetation), supervised by Prof. dr. Victor Westhoff and Dr. Frank van der Meulen. A minor subject on the relationship between vegetation and soil, was supervised by Dr. L. Kempers, and also carried out in Meijendel. I hoped for a second major at the *ITC* (Faculty of Geo-Information Science and Earth Observation) in Enschede with a month field work in Africa or Asia. Prof. dr. I. Zonneveld arranged for an application to the *ITC;* sadly it all went wrong due to an administrative hitch. The alternative option for going abroad was magnificent: six months research studying the coral reef quality off the Kenyan coast of Malindi, north of Mombasa. I joined the Watamu Reef Expedition, with nine other diving ecologist, two physical geographers, two social geographers, an underwater photographer and an organizer. The research was supervised by Prof.dr. C. den Hartog. Apart from the scientific lessons, it was a major experience in international project management and dynamic group functioning. After all those positive experiences, I gained my master's degree on January 29th 1985.

During the latter part of my studies, I was able to exchange the mandatory call for military service for civic duties for almost two years. This duty was a research on the effects of released Chinese Grass Carp in drinking water extraction canals in the *Amsterdamse Waterleiding Duinen,* under supervision of Dr. G. Baeyens of the A*msterdam Drinking Water Company,* now *Waternet.* A few months before finishing the civic duties in December 1987, I was called upon by Dr. Frank van der Meulen from the *Duinwaterleiding van 's-Gravenhage* to incorporate the 1984 management plan into the Staatsbosbeheer (State Forestry Service) format, as well as finishing the Grass Carp report in the evenings. I finished both successfully in the given time. After finishing a report on the permanent plot data of Meijendel, I was offered a job at the Duinwaterleiding van ‘s-Gravenhage in 1988 and I am still working there. The company name has since changed into *Duinwaterbedrijf Zuid-Hollan*d and once more into *Dunea*. The work I perform is research into a broader context of the dune landscape to improve the natural quality of the dunes entrusted to Dunea, as well as the river water quality that is infiltrated in the coastal dunes of Solleveld, Meijendel and Berkheide.

Apart from my professional career as a dune ecologist, during eight years I was one of the editors of the nature magazine De Levende Natuur. A few years later, I joined the foundation board for four years as its secretary. Since 2006, I am the ecological adviser for the Natura 2000 aspects of the coastal sand dunes managed by the Noordwijkse Golf Club under the auspices of *“Hagenia ecologisch advies”*.

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