Littoral 2017

Change, Naturalness and People

5th - 7th September, Liverpool Hope University

Proceedings of the 2017 Littoral conference
'Change, Naturalness and People'

EUC Coastal & Marine

Contents

Foreword

Coasts are highly dynamic systems, but how do people perceive them? Can we use natural processes to manage some of the challenges affecting coastal areas, and what does natural mean? These are some of the questions that were discussed in the 2017 Littoral conference of the Littoral conference, which focused on 'Change, Naturalness and People'.

The 2017 Littoral conference was held between 5th – 7th September 2017 and was hosted by Liverpool Hope University on behalf of the European Union Coastal Community (EUCC). The Littoral conference series commenced in Leiden in 1987, stemming from the Coastal & Marine Union (EUCC) network's mission of 'bringing together the scientific community, coastal practitioners and policy makers'. The event brought together academics and coastal managers from Australia, Belgium, Canada, Germany, Lithuania, Malta, the Netherlands, Portugal, Spain, Turkey, and the USA, as well as from several universities and agencies in the UK.

A wide range of issues which are relevant to the coast were explored at the conference through oral and poster presentations. As well as these 'open' themed sessions, four themes were given dedicated sessions. These were 'Invasive Alien Species in Coastal Dunes', 'Threats and solutions in dunes and dune slacks', 'Marine Planning: achieving progress across boundaries, theories, and sectors towards sustainability' and 'Mobile dunes and dune dynamics'

This issue collects selected proceedings from the conference highlighting the diversity and scope of the conference. The papers in these proceedings showcase current challenges faced in the coastal environment and the research being conducted to better understand these changes.

Editors

Professor Laurence Jones, UK Centre for Ecology and Hydrology

Dr Thomas Smyth, University of Huddersfield

Rev Paul Rooney, Liverpool Hope University

Group photo of the Littoral 2017 delegates on the mid-conference field trip to the Sefton Coast, England.

Effects of Periodic Lake Level Variations and Local Influences on the Ecohydrology of a Lake Michigan Coastal Dune Slack

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Suggested citation:

DeVries-Zimmerman, S.J., Fuller, J.L., Van Gorp, B.C.T., Watts, A.M., Peterson, D.C & Hansen, E.C. (2020). Effects of Periodic Lake Level Variations and Local Influences on the Ecohydrology of a Lake Michigan Coastal Dune Slack. In L. Jones, T.A.G. Smyth & P. Rooney (eds.) *Proceedings of the 2017 Littoral conference 'Change, Naturalness and People'* (pp. 5 – 23).

ABSTRACT

Interdunal wetlands or slacks are an imperiled ecosystem along the Great Lakes. We initiated an ecohydrological study of an interdunal wetland/slack in the deflation basin of a large parabolic dune ~200 m inland from Lake Michigan near Saugatuck, Michigan, USA. The slack formed where wind unevenly scoured the sand to the water table, creating a series of pools and ridges. We reviewed historic aerial photographs together with the Lake Michigan water level curve to examine the relationship between slack features and the lake's hydrology. The earliest photo, 1938, shows three pools along the northernmost edge and emergent wetland vegetation in the northeast corner and along the western edge of the slack. In subsequent photos, larger pond and emergent wetland vegetation areas occurred in years with higher water levels, while smaller pond and emergent vegetation areas occurred in years with lower water levels. Low lake levels from 1998–2014 significantly shrank the wetland areas with non-wetland/dune vegetation replacing wetland vegetation in many places. Even the northernmost pools were dry during a portion of this time. Rising lake levels (2014–present) reflooded the slack. Groundwater levels from a slack/dune monitoring well network show the slack's levels generally drop in May, June, and July due to evapotranspiration. Contrastingly, Lake Michigan's levels rise throughout the spring, peaking in July. Local rain events can temporarily raise the slack's levels, up to 30cm, while not impacting those of Lake Michigan. Hence, the slack's levels generally reflect the long-term Lake Michigan water level cycles while also experiencing short-term fluctuations due to local influences. Our vegetation quadrat sampling shows predominant wetland vegetation comprised of over 30 species throughout the slack. Almost half of these

species are sedges/rushes with *Cladium mariscoides* as both the predominant sedge and wetland species. Many of the slack's pools and depressions have zoned plant communities in response to different water depths in these areas.

INTRODUCTION

Slacks, or interdunal wetlands as they are referenced in the North American literature, occur along the shores of Lake Michigan, one of the North American Laurentian Great Lakes. Wooded dune and swale complexes, alternatively called beach-ridge or strand-plain complexes, occur in embayments or sand spits along the coast, forming in response to changing water levels in Lake Michigan. The swales are frequently occupied by wetlands, exhibiting an ecological diversity from open wetlands in the younger swales near the lake's edge to bogs and/or forested wetlands further from the lake in the older swales (Lichter, 1998; Comer and Albert, 1993). Consequently, these features have been used to construct paleo-lake-level fluctuation curves extending back to the Holocene (e.g., Baedke and Thompson, 2000; Thompson et al., 2011). Slacks can also form within coastal dune complexes where the wind scours the sand to the water table, creating a depression that fills with water and is colonized by wetland vegetation. Slacks formed by this process are termed secondary dune slacks (Liverpool Hope University, 2018). Both wetland types tend to be ecologically diverse, albeit rare in occurrence in Michigan, USA. The Michigan Natural Features Inventory (MNFI, 2008) ranks their status as G-2, meaning they are "imperiled in the state because of rarity due to very restricted range, very few occurrences (often 20 or fewer), steep declines, or other factors making it very vulnerable to extirpation from the state" (MNFI, 2008). Perhaps because of this scarcity, there have been relatively few ecohydrological studies of these ecosystems.

We initiated an ecohydrological study of a large slack near Saugatuck, Michigan, USA in May 2016, as rising water levels in Lake Michigan-Huron rewetted the slack, turning a dry depression dominated by non-wetland/dune vegetation to wetland dominated by hydrophytic vegetation. We began with a review of historic aerial photographs and the Lake Michigan-Huron water level curve to investigate the response of this feature to fluctuating lake-levels over time. We have subsequently installed monitoring/dip wells and annually perform vegetation quadrat sampling as part of a long-term project studying the effects of changing water levels on the ecohydrology of this area. It is hoped that the knowledge gained from this project will guide managers of these scarce resources in state and national parks, especially with respect to climate change. This paper presents the results of the initial phase of this study.

LOCATION AND SITE DESCRIPTION

Our study site lies on the eastern shore of Lake Michigan in the state of Michigan, USA (Figs. 1 and 2), ~200 m east or inland from Lake Michigan, ~600 m south of the mouth of the Kalamazoo River, and ~400 m west of Oxbow Lake. Large parabolic dunes reaching heights of 50 m lie along Lake Michigan's eastern shore north of the Kalamazoo River.

The studied slack is located within a low relief (10 m high) coastal dune complex preserved as the Saugatuck Harbor Natural Area (SHNA) (Fig. 2). The study site (Fig. 2) is a secondary slack, ~1.25 hectares in size, lying between the arms of a large parabolic dune where the wind scoured the sand to the water table. A number of smaller blowouts have formed within the arms of this parabolic dune. Other wetlands at SHNA range in size from ~0.25–~0.76 hectares.

A

B

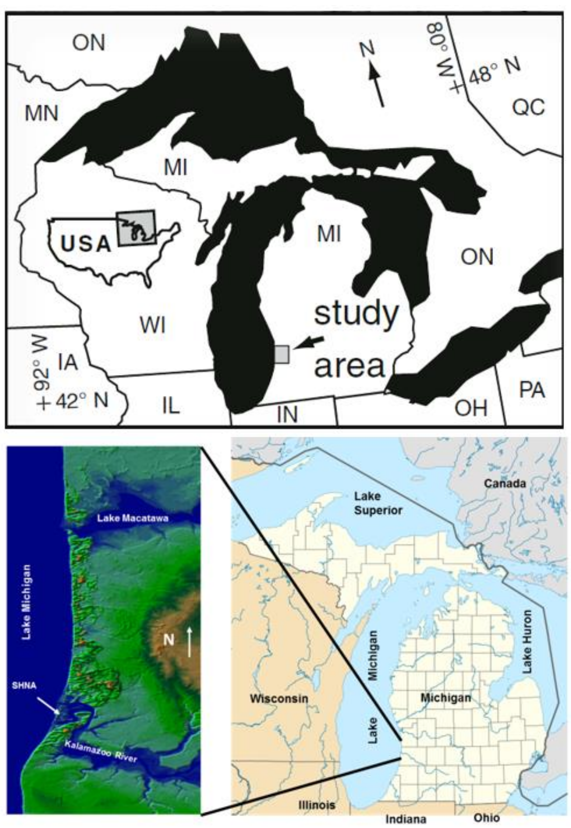

Figure 1. (A) Location map for study area, Saugatuck Harbor Natural Area (SHNA). (B) Digital elevation model (DEM) of Allegan County, Michigan (MI). DEM image generated from data obtained by the Shuttle Radar Topography Mission. IA—Iowa; IL—Illinois; IN—Indiana; MN—Minnesota; OH—Ohio; ON—Ontario; PA—Pennsylvania; QC—Quebec; WI—Wisconsin.

Figure 2. Google earth image of study area in relation to Lake Michigan (west), Kalamazoo River (north), and Oxbow Lake (east and south).

The slack has a subtle microtopography consisting of low-relief ridges and pools of varying depths (Figs. 3 and 4). The deepest pools, up to 1.4 m in depth, lie on the slack's north side. These pools are separated from the larger and shallower main wetland area by an east-west-trending ridge bordering their southern edge. Two smaller north-south trending ridges extend from the southern edge of the larger ridge almost to the arms of the parabolic dune surrounding the slack. Shallower pools up to 0.6 m in depth are located within the main body of the slack.

HISTORIC LAKE-LEVEL CURVE FOR LAKE MICHIGAN-HURON AND IMPACT ON SLACK

Lakes Michigan and Huron are considered one hydraulic basin due to their connection at the Straits of Mackinac (Rodionov, 1994; Wilcox et al., 2007). Optically Stimulated Luminescence (OSL) and radiocarbon ^{14}C studies of beach ridges and organic deposits in strand-plain complexes along the Lake Michigan-Huron shores show two quasi-periodic lake-level fluctuations extending back ~4,700 years, a shorter-term fluctuation averaging ~30 years and a longer-term fluctuation averaging ~160 years (Baedke and

Thompson, 2000). Higher lake-levels are associated with periods of heavier precipitation and less evaporation from the lake while lower lake-levels are associated with lower precipitation and higher evaporation rates (Fraser et al, 1975; Rodionov, 1994; Wilcox et al., 2007). Lake-level data collected since 1860 show the Lake Michigan-Huron basin has the greatest fluctuations, ~2 m, of the Great Lakes (Argyilan and Forman, 2003; Wilcox et al., 2007).

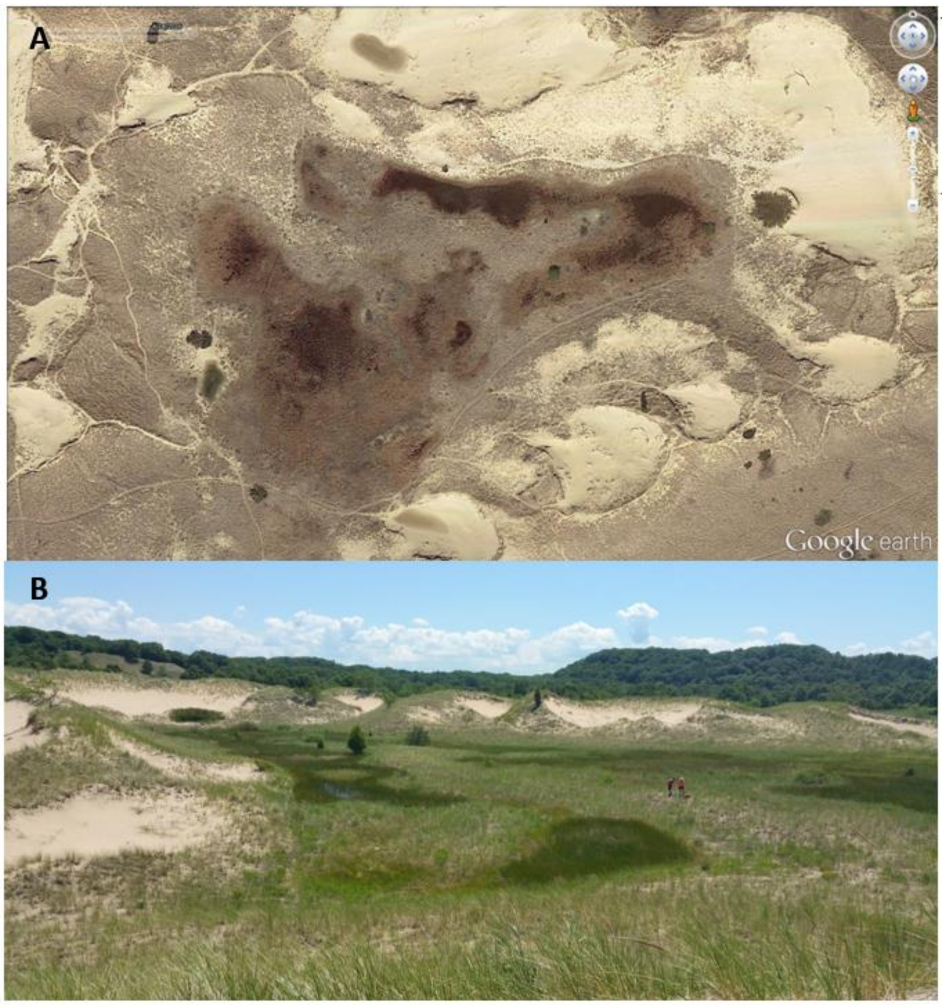

Figure 3. Google earth image of study site showing slack within large parabolic dune. Note small blowouts on southern limb and larger blowout on northern limb of the parabolic dune. (B) View of the northern portion of the slack, looking east. The slack’s deepest pools lie on the north edge, separated from a large pool in the main slack area by the east-west trending ridge on which two student researchers are standing.

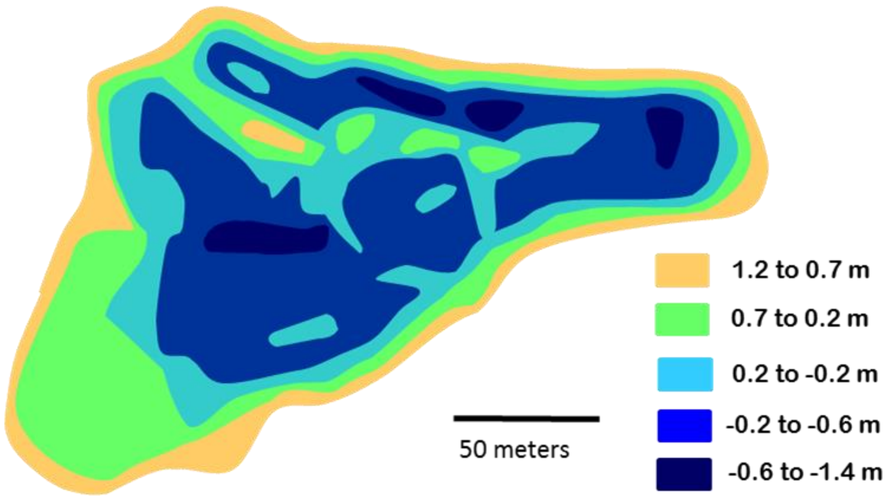

Figure 4. Topographic map of slack constructed from total station survey in July 2016. Height ranges from +1.2 to -1.4 m above datum established at site.

Conventional wisdom on the hydrologic setting of secondary slacks within Lake Michigan's coastal dune complexes states that their water levels are connected to and reflective of those in Lake Michigan-Huron (Barko et al., 1977; Albert, 2006; Hiebert et al., 1986). However, few studies have examined the hydrologic setting of secondary slacks compared to that of the strand-plain/wooded dune and swale complexes (e.g., Shedlock et al., 1993, 1994; Baedke, 2005). Hence, we wanted to examine how the slack at SHNA has responded to fluctuating water levels in Lake Michigan-Huron over time.

We collected historic aerial photographs and compared them to the Lake Michigan-Huron water level curve (GLERL, 2016). Historic aerial photographs for 1938, 1950, 1955, 1960, 1967, 1974, 1981, and 1994 were obtained from Michigan State University's Aerial Imagery Archive. Aerial photographs and satellite images dated 1997, 2011, 2013, and 2016 were obtained from Google earth, the 2005 aerial photograph was obtained from USGS EarthExplorer. The amount of open water and area of wetland vegetation were noted for each image and the date of that image was compared to the Lake Michigan-Huron water level curve (GLERL, 2016) (Fig. 5).

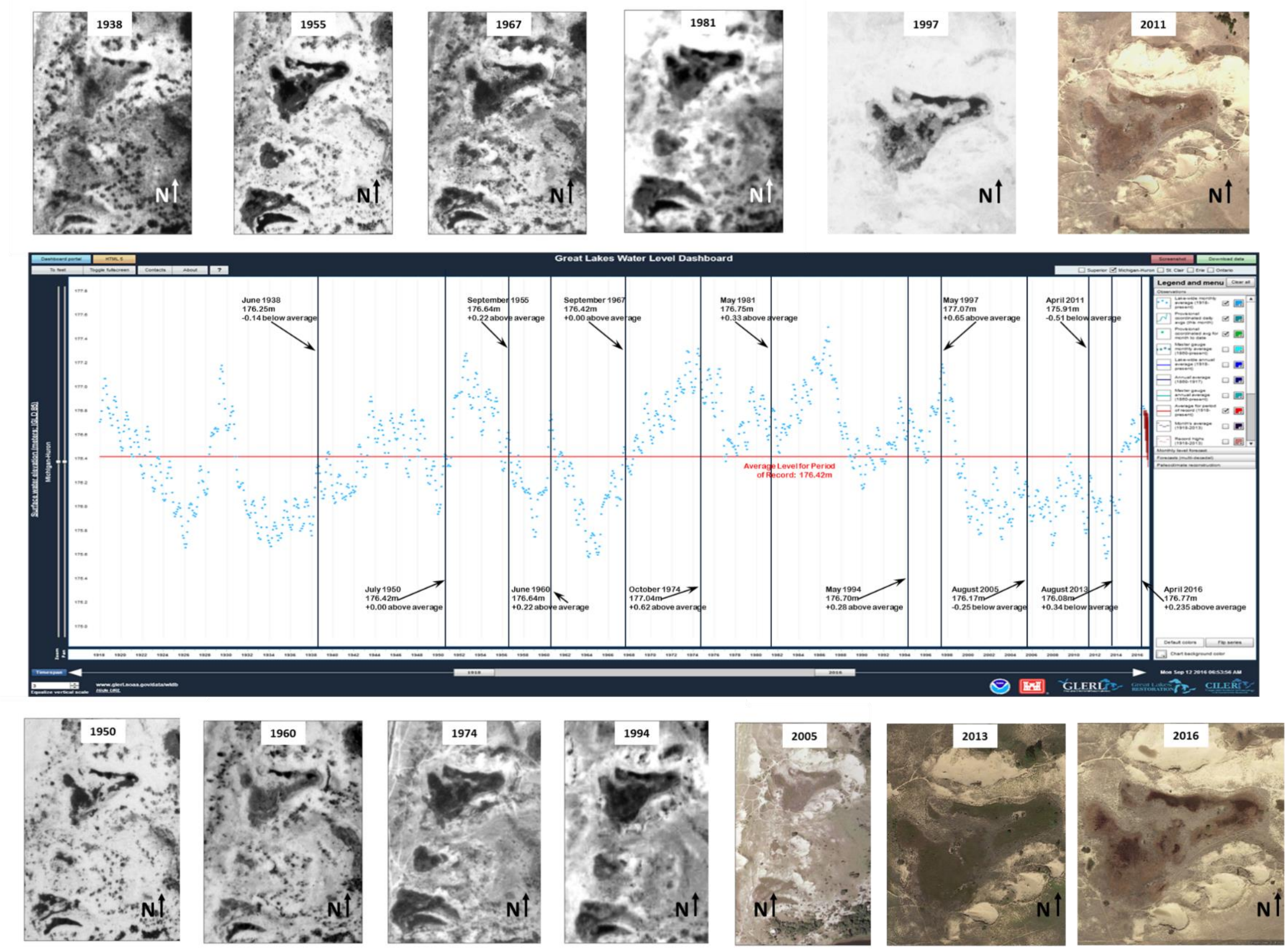

Figure 5. Historic aerial photographs and satellite images, and historic Lake Michigan-Huron water level curve. Water level curve - monthly average water level gauge data from 1918–2018 (GLERL, 2016); average lake level, 176.42 m International Great Lakes Datum 1985 (IGLD 1985).

Our oldest photo, 1938, was taken at the end of a series of droughts occurring in Michigan from 1930–1937 (Blumer, 1991; Argyilan and Forman, 2003). During the 1930s as the central plains of the U.S. experienced severe drought, becoming the “Dust Bowl,” Michigan underwent the most severe drought in its history. Lake-levels were well below average during this time (Fig. 5). By 1938 lake-levels had begun to rise, though they remained below average. The earliest photo, 1938, shows the overall configuration of the slack is similar to that seen today. Dark areas indicating standing water bodies can be noted in the slack. Three pools lie along the northern edge and areas of emergent wetland vegetation are located in the northeast corner and along the western edge. As water levels rose through the 1940s and into the 1950s, the areal extent of the northern ponds and of the wetland significantly increased. Shallow ponds developed within the emergent vegetation areas, indicating an increase in water levels. These wet areas expanded not only in our studied slack, but also in the depressions south of this slack (Fig. 5). The second longest drought on record, 1960–1965, dropped lake levels to near record lows, 175.58 m IGLD in March 1964 (Blumer, 1991). The 1960 photo shows most of the wetland ponds disappeared, leaving only three pools on the northern edge, similar to those in the 1938 photo. In 1965, water levels began to recover quickly, rising above average in 1967 and remaining mostly above average until 1998. Lake-levels were especially high in the 1980s, reaching a record high of 177.5 m (IGLD 1985) in October 1986. Correspondingly, in the 1967, 1974, 1981, 1994, and 1997 photos, large ponds and areas of emergent vegetation are noted during this time of mostly above average water levels in Lake Michigan-Huron. Water levels dropped below average in 1998 and remained there until 2014, reaching their lowest recorded level, 175.57 m (IGLD 1985) in January 2013. The 2005, 2011, and 2013 photos show emergent vegetation areas have disappeared and the northernmost (and deepest) pools are dry. In 2014 water levels rose above average, and have remained there since that time. The 2016 image shows the northernmost pools have refilled and that additional ponds appeared in the northeastern corner and main body of the slack.

Therefore, it appears that there is a hydrologic connection between water levels in the slack and Lake Michigan-Huron. During times of higher water levels in Lake Michigan-Huron, we see wetter environments in the slack with ponds occurring throughout, and sometimes flooding much of it. Correspondingly, we see much drier conditions in the slack with the ponds significantly decreasing in size and sometimes disappearing all together in times of low water levels in Lake Michigan-Huron.

HYDROLOGY OF THE SLACK

The hydrology of interdunal wetlands can be complex because their water levels can be related to nearby water bodies, such as Lake Michigan-Huron, groundwater, precipitation, or a combination of these sources. A network of groundwater monitoring wells, constructed of 5 cm-diameter PVC pipe, was installed within the slack and immediately adjacent to it to study the effects of seasonal changes and precipitation events on the slack's hydrology (Fig. 6). Wells SHNA-1, 2, and 3 form an east-west transect across the slack, while wells SHNA-5, 2, and 6 trend north-south. Wells SHNA-4 and SHNA-7 are installed in incipient slacks north and southeast, respectively, of the main slack. SHNA-8 is installed on the dune west of and ~6 m above the slack. Static water levels are measured at least monthly throughout the year using a Solinst water meter and compared to the Lake Michigan-Huron daily water level gauge data (USACE, 2017) (Fig. 7).

Measured water levels in the wells and the Lake Michigan-Huron water level curve are shown in Figure 7. Lake Michigan-Huron typically has its highest water levels in July and its lowest levels in the winter, February (Wilcox et al., 2007) (Fig. 5). Water levels rise from February through July/August as water from melting winter snow enters the basin, and subsequently drop from July to low winter levels again due to evaporation (Rodionov, 1994). We noted similarities to that pattern in our monitoring well data. The slack's water levels are at their lowest point in winter (January/February) and rise through the spring. However, they begin to drop in mid-May, prior to the drop in Lake Michigan-Huron levels, at the start of the growing season. We noted a continuing drop in water levels within the slack as wetland vegetation began to appear and grow, suggesting that evapotranspiration was responsible for lowering water levels.

We have observed this pattern in both 2016 and 2017. For most of June–July 2016, water levels dropped slowly in the slack due to a minor drought in the local area. Water levels continued to drop until mid-August when a dramatic rise of ~0.3m was noted after a series of large storms with heavy rainfall. Water lines on the slack edges indicated that water levels had been even higher than those recorded on 2 September 2016 by ~10 cm. However, there was no such rise in Lake Michigan-Huron's levels during this time. In fact, the lake's water levels continued their drop from the summer high while the slack saw brief rises in its water levels. Similar short-term increases in the slack's water levels occurred in 2017 following rain events (Fig. 7). The photographs of the northern incipient slack near SHNA-4 (Fig. 8) illustrate these short-term water level fluctuations due to rain events.

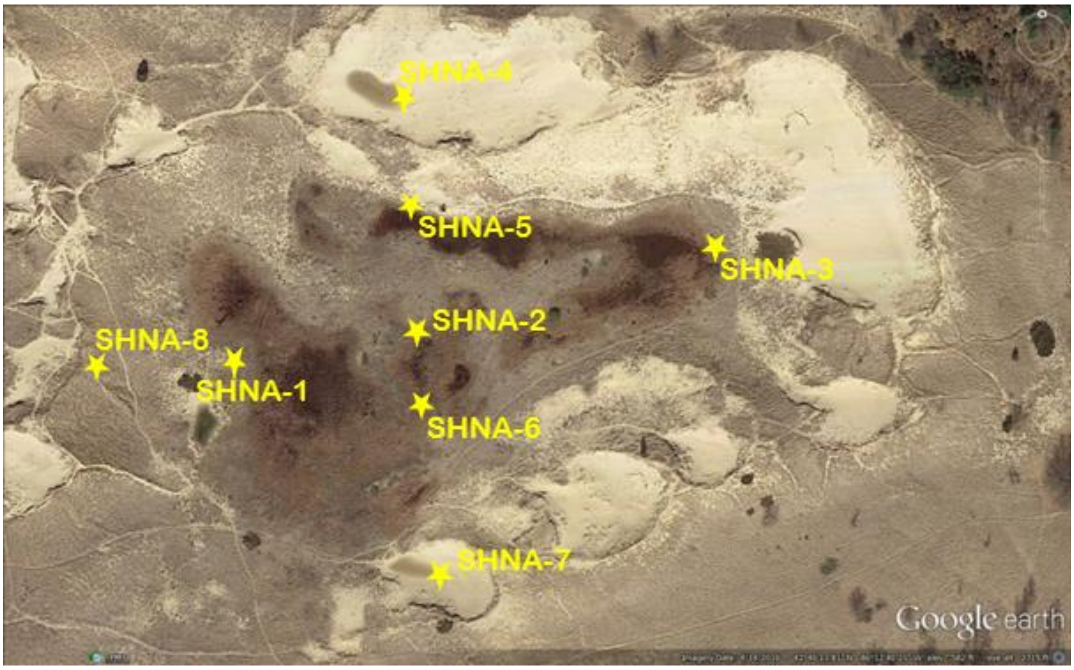

Figure 6. Map of monitoring/dip well locations.

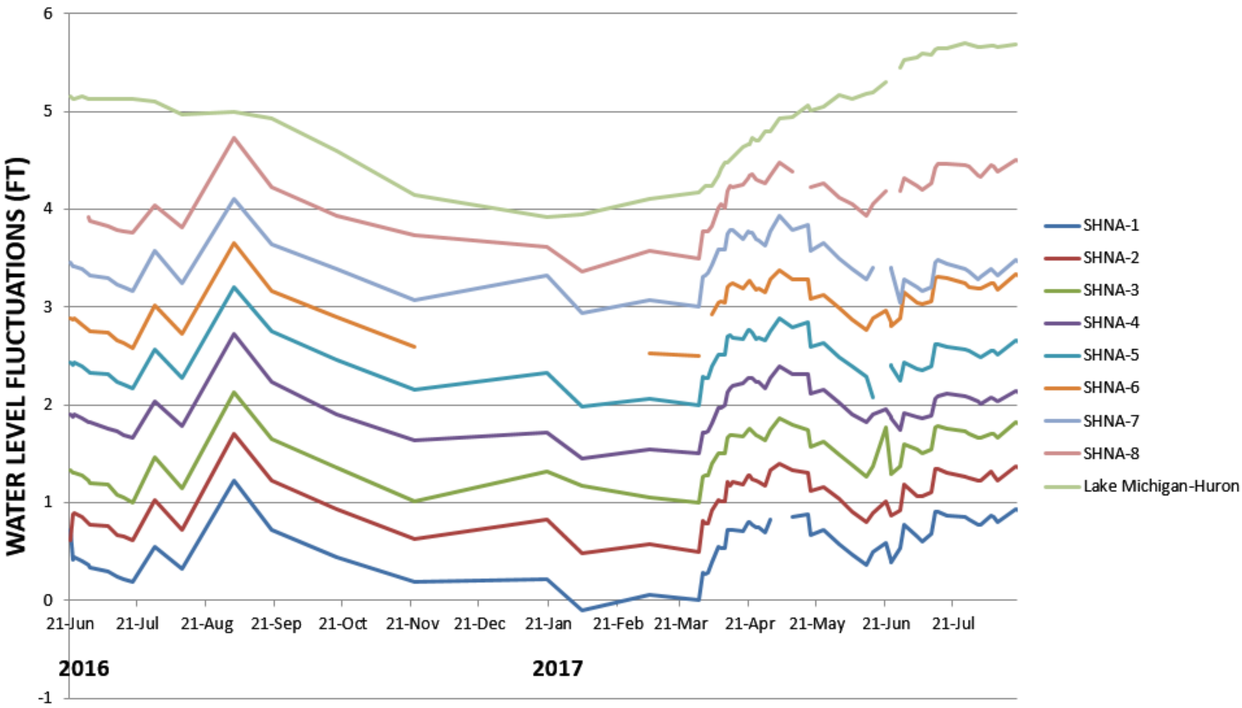

Figure 7. Water level curves for static groundwater levels in SHNA monitoring wells and for Lake Michigan-Huron. Lake Michigan-Huron water level curve created using monthly average water level gauge data from 1918–2018 (GLERL, 2016).

Figure 8. Photographs of water levels in incipient slack pool by SHNA-4 on selected dates.

Figure 9. Vegetation sampling quadrats locations.

Overall, water levels in the slack are generally reflective of those in the Lake Michigan-Huron basin, rising and falling accordingly. However, some deviations from this pattern have been noted. Water levels in Lake Michigan-Huron reflect the amount of precipitation and evaporation within the lake's watershed, an area covering over 252,000 km^2 (Schaetzl, 2016), whereas water levels within the slack are reflective of both Lake Michigan-Huron water levels and local influences. Local rain events can significantly raise the slack's water levels as its drainage basin is considerably smaller, while not significantly impacting those of Lake Michigan-Huron. Conversely, the slack's vegetation can increase the water lost to evapotranspiration, lowering the water table further, especially on hot summer days with temperatures exceeding 32˚C.

We also monitored a number of rain events in spring 2017 to determine the response time between the rain events and a rise in the static water levels in the monitoring wells. Overall, we noticed a time lag of about a day between the rain event and the rise in water levels in the monitoring wells.

ECOLOGY OF THE SLACK

Prior to beginning the ecohydrological study in 2016, we did not collect vegetation data within the slack. Great Lakes water levels were below the average level of 176.42 m (IGLD 1985) until 2014 and non-wetland vegetation, including open dune species, had expanded into many areas of the slack, especially in the slack's main area south of the large east-west trending ridge. However, we frequently traversed this area enroute to the blowout used in our wind dynamic studies (Yurk et al., 2014) and observed the vegetation growing within it. Species noted in this area included *Rubus sp., Rumex acetosella, Asclepias syriaca, Verbascum thapsus,* and the grasses *Agrostis scabra* and *Dichanthelium implicatum*. Open dune species marram grass *(Ammophila breviligulata),* sand reed grass *(Calamovilfa longifolia),* little blue stem grass (*Schizachyrium scoparium),* and horse mint *(Monarda punctata),* were also present throughout this area. Conditions in the slack were sufficiently dry so that jack pine (*Pinus banksiana),* a facultative upland species preferring dry sandy locations, grew to mature trees in some sections (Lichvar et al., 2012, 2016; University of Michigan Herbarium, 2018). Searches through this vegetation did reveal a few sedges, albeit with very short sward heights (<15 cm). However, mature flowering sedges were not noted in the main body of the slack.

A shift towards wetland vegetation occurred as Lake Michigan-Huron water levels rose, beginning in 2014, and the slack's water levels concurrently increased. By April 2016, the slack was sufficiently wet that amphibians were noted within it for the first time since wind dynamic studies began in 2010. In summer 2016 we performed our first round of vegetation quadrat sampling to identify the species present and the distribution of these species within the slack. The slack's vegetation is heterogeneous, varying with the topography and depth of water. Hence, we divided the slack into 28 1m x 1m sampling quadrats based on the site's topography, water depth, and the plant communities (Fig. 9). At each location, we identified the plant species within the quadrat, then counted the number of individuals by species, and estimated their respective coverages. These data, together with vegetation quadrat data collected during summers 2017 and 2018, are currently being used for statistical analyses.

A list of identified species is provided in Table 1. The slack vegetation is now dominated by wetland species ranging from facultative wetland to obligate wetland species (Lichvar, et al., 2016). The non-wetland/dune species in the slack have been completely replaced by wetland species and the jack pine trees have succumbed due to the flooding. The dominant species throughout the slack is twig rush, *Cladium mariscoides*. However, many other Juncaceae and Cyperaceae species are found, depending on the depth of the water. Deeper pools have *Carex aquatilis*, *Carex lacustris, Scirpus cyperinus*, and *Juncus canadensi*, while damp areas and shallow pools (<2 cm deep) have *Eleocharis elliptica* and *Carex viridula*, amongst other species. The shrub, Kalm's St. John's-wort, *Hypericum kalmianum*, rings the slack's edges where conditions are moist but not inundated, while steeplebush, *Spiraea tomentosa*, grows throughout much of the slack. Hence, we see zonation of those species which we believe is due to water depth and the degree of moisture (Fig. 10). Statistical analyses to examine the species' distribution with respect to water depth are also being performed using the 2016–2018 vegetation data.

IMPLICATIONS FOR MANAGEMENT

Secondary dune slacks have been little studied along the Lake Michigan shoreline. Hence, much remains to be understood about these systems, including the relationships between water levels, surface water/groundwater chemistry, and species composition. In contrast, many aspects of European slacks have been studied, such as hydrologic and geochemical influences (e.g., Grootjans et al., 1991; Adema et al., 2002; Jones et al 2006), nitrogen deposition (e.g., Jones et al., 2004; Rhymes et al., 2014), management strategies (e.g., van Dijk and Grootjans, 1993; Jones and Fovet 2014;), and dune stabilization impacts (Provoost et al., 2011).

Table 1. List of vegetation species identified in 2016 vegetation sampling quadrats. Nomenclature follows Voss (University of Michigan, 2018). Wetness index based on State of Michigan 2016 Wetland Plant List (Lichvar et al., 2012, 2016). FAC – Facultative plants, equally likely to occur in wetlands and non-wetlands (34–66%); FACW – Facultative wetland species, usually occur in wetlands (67–99%), but occasionally found in non-wetlands; OBL – Obligate wetland species, almost always (99%) occur in wetlands under natural conditions.

Table 1.

Scientific Name	Common Name	Wetness Index
Agrostis scabra	ticklegrass	FAC
Carex aquatilis	sedge	OBL
Carex lacustris	sedge	OBL
Carex viridula	sedge	OBL
Cephalanthus occidentalis	buttonbush	OBL
Cladium mariscoides	twig-rush	OBL
Cyperus bipartitus	brook nut sedge	FACW
Eleocharis elliptica	golden-seeded spike rush	OBL
Hypericum kalmianum	Kalm's St. John's wort	FACW
Juncus alpinoarticulatus	rush	OBL
Juncus balticus	Baltic rush	OBL
Juncus brachycephalus	rush	OBL
Juncus canadensis	Canadian rush	OBL
Juncus dudleyi	Dudley's rush	FACW
Juncus effusus	soft-stemmed rush	OBL
Lobelia kalmii	Kalm's lobelia	OBL
Osmunda regalis	royal fern	OBL
Rosa palustris	swamp rose	OBL
Schoenoplectus pungens	threesquare bulrush	OBL
Schoenoplectus tabernaemontani	softstem bulrush	OBL
Scirpus cyperinus	wool-grass	OBL
Spiraea tomentosa	steeplebush	FACW
Thelypteris palustris	marsh fern	FACW

Unfortunately, similar to European dune systems, Great Lakes dunes and the slacks therein are under threat from multiple sources. Because of their dynamic nature, the open dune ecosystem is typically a multiseral community, meaning different areas of the dune complex are concurrently in different stages or seres of ecological succession. Slacks naturally form in blowouts as the wind scours them to the water table, essentially 'chasing the water table.' However, development by its very nature stabilizes the dunes, thus precluding this process. Development has also destroyed dune slacks, especially when they are drier due to low lake levels and not recognized as wetlands. Dune stabilization practices, beginning in the 1930s and continuing to some degree today, also threaten the natural dune dynamics needed to sustain this ecosystem. Climate changes are anticipated to have significant impacts on Michigan's ecosystems (e.g., Kling et al., 2003). Predicted changes include higher summer temperatures and lower precipitation rates, causing a drop in Great Lakes water levels (e.g., Kling et al., 2003), and subsequently drying slack areas.

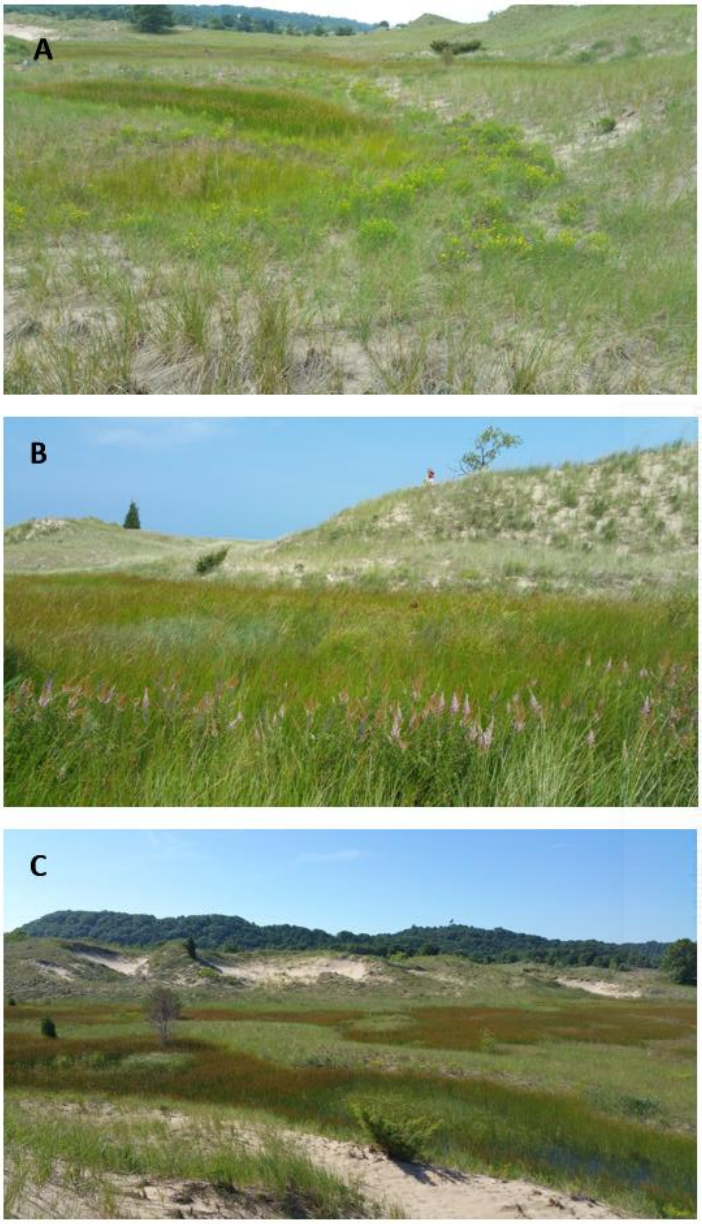

Figure 10. (A) Northwest corner of slack showing *Hypericum kalmianum* on margin of wet area and *Eleocharis elliptica*, *Juncus dudleyi*, and *Carex viridula* in depression with <2 cm standing water. (B) *Cladium mariscoides* and *Spiraea tomentosa* in shallow/damp slack areas while *Scirpus cyperinus* and *Carex aquatilis* occur in deeper pool. (C) Deep pools on north edge of slack with *Cladium mariscoides* along pool edges and *Carex lacustris* and *Carex aquatilis* in the deeper pool.

CONCLUSIONS

The slack appears to have formed in a large parabolic dune where wind scoured the sand to the water table, creating a secondary slack. Water levels in the slack are generally reflective of those in the Lake

Michigan-Huron basin as fluctuations in the areal extent of the ponds correspond to changes in the lake's water level. Larger pond/slack areas are noted in years with higher water levels, smaller pond/slack areas are noted in years with lower water levels. However, local rain events can significantly raise the slack's water levels while not significantly impacting those of Lake Michigan-Huron due to the size difference of their respective drainage basins. In addition, the slack's vegetation increases the water lost to evapotranspiration, lowering the water table further within the slack, while not affecting Lake Michigan-Huron water levels. Vegetation quadrat sampling shows dominant wetland species throughout the slack, including areas where non-wetland/dune species were noted as the dominant species in the past. The slacks face multiple management issues, including development pressures, dune stabilization, and climate change.

ACKNOWLEDGEMENTS

Thank you to the summer 2016 survey crew, Hope College students: Clay Sanders, Elijah Riggens, and William Zimmerman, and summer 2017 Hope College research students, Kathleen Fast and Kaitlyn Caltrider. Justin Heslinga, Stewardship Director, Land Conservancy of West Michigan (LCWM), provided invaluable help with Cyperaceae and Juncaceae identification. April Scholtz, Land Protection Director, LCWM, and the City of Saugatuck provided access to SHNA.

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Prunus serotina invades Dutch coastal dunes; management experience from the Amsterdam Water Supply Dunes

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Suggested citation:

Geelen, L.H.W.T. and Oosterbaan, B. (2020) Prunus serotina invades Dutch coastal dunes; management experience from the Amsterdam Water Supply Dunes. In L. Jones, T.A.G. Smyth & P. Rooney (eds.) *Proceedings of the 2017 Littoral conference 'Change, Naturalness and People'* (pp. 24 – 35).

ABSTRACT

Black Cherry (*Prunus serotina*) is an invasive exotic species in the Netherlands, which has expanded enormously in the Dutch dunes in the last 20 years. Expansion has been particularly rapid in deteriorated sea buckthorn thickets (H2160) and open dunes. Due to its rapid growth, Black Cherry is displaces dune vegetation and has formed a serious threat to the conservation objectives of the Natura 2000 area South-Kennemerland. Especially the habitat types H2160 (buckthorn thickets), and H2130A and H2130B (calcareous and decalcified dune grasslands). In 2004 the first complete mapping of Black Cherry in the 3400 ha of the Amsterdam Water Supply Dunes (AWD) was conducted and a management plan started in 2005. Waternet performed a great management effort over the years. Larger trees were cut and pulled down, areas mown, sod cutting applied and grazing with sheep and cattle employed on an extensive scale to combat Black Cherry. No herbicides were used. In 2008, 2012 and 2016 further surveys of the area were done to monitor the spread of the invasive species and to monitor effects of management. This paper aims to give an overview of the development of the distribution and abundance of Black Cherry in the AWD. The comparison with previous mappings is analysed to see whether the management has been effective. A wider management overview and recommendations are presented at the end.

BACKGROUND OF THE INVASION

In the first half of the 20th century, Black Cherry (*Prunus serotina)* was introduced in many (dune) areas as a useful soil conditioner in the undergrowth of planted pine forests. Also, Black Cherry was frequently planted as an ornamental species near buildings and engineering works in the dunes with water abstraction. First attempts to control Black Cherry in the Amsterdam Water Supply Dunes (AWD) (Figure 1) began in 1975, but only locally in the pine plantations. At the end of the 1980s, thinning in pine forests with the objective to get more mixed deciduous and pine forests, were stopped to keep the forest floor shaded and to give no further chance to the Black Cherry in the undergrowth. This approach seemed to work, plants remained relatively small and did not produce seeds. Black Cherry was therefore tolerated in (dune) forests, and not seen as potentially threatening to the open dune landscapes. Moreover, many conservationists in that period supported the idea that intervention should be kept to a minimum, they had great faith in the natural regulation mechanisms in large ecosystems.

In the early 1990's attention to fighting Black Cherry in the AWD declined. Many shrubs started to produce seeds in a period that coincided with a low density of rabbits. Since that time, the spatial extent of Black Cherry gradually has expanded. This expansion outside the woods, happened especially in (slightly) decalcified middle and inner dunes of calcareous dunes along the Dutch mainland coast, and in the acid dunes near Bergen and Schoorl. In the dunes of Zeeland, the South Holland islands and on the Wadden islands, local high-density patches of Black Cherry started to appear.

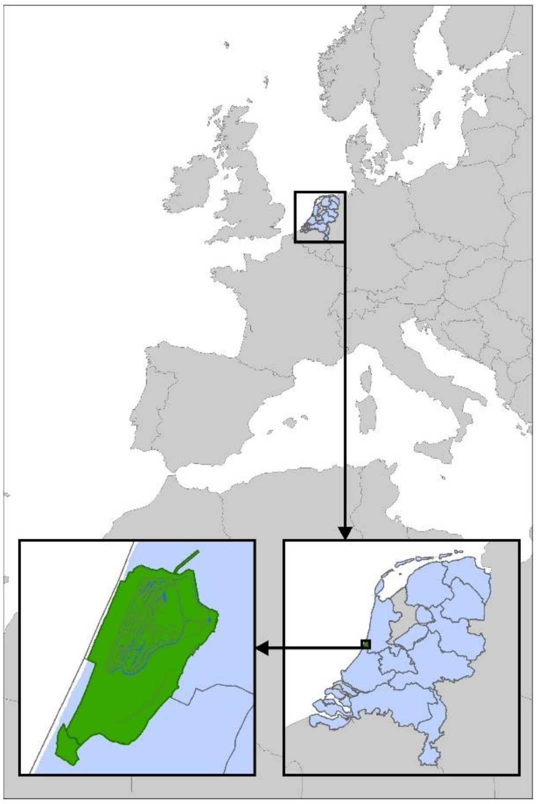

Figure 1 Amsterdam Water Supply Dunes (AWD) in the central part of the Dutch mainland coast

There was a parallel with the situation in Dutch inland forests. Black Cherry became invasive after its introduction and has already been termed a “wood pest”. The inland Black Cherry expansion beyond the forests, e.g., on heaths, was quickly noted and relatively easy to control by sod cutting, mowing, grazing and pulling with the help of volunteers. In a hilly dune landscape with dense sea buckthorn thickets the initial expansion of Black Cherry was difficult to detect and appeared much harder to address with mowing, sod stabbing or volunteer work. On the other hand, the combination of persevering cutting of Black Cherry and the pulling of young individuals over many years from the 1980’s onward proved to be effective to control expanding of Black Cherry in Meijendel dunes and Zwanenwater dunes (Ehrenburg et al., 2008). Here managers continued their early intervention management successfully.

INVASIVE BEHAVIOUR OF BLACK CHERRY

The combination of species properties, local environmental conditions and management history explain the successful colonisation of Black Cherry in the Dutch dunes. Important features that aided its colonisation are that Black Cherry has a large genetic variability (Pairon et al., 2006) and the species can reproduce rapidly at an early age by producing large quantities of seed. The authors found that a single tree can produce up to 8,940 fruits, but flower and fruit production were highly variable between years and among individuals.

Seeds effectively distribute in time and space. Birds, and foxes are not to be an underestimated diffusion mechanism (Ehrenburg et al., 2008). Seeds without pulp (passed through a bird's stomach) are more viable than those with pulp (Pairon et al., 2006). Seeds in the soil can remain viable up to five years and plants respond to cutting by resprouting. The survival of seedlings was low but once older than four years, the survival of young plants is large (Pairon et al., 2006). A high growth rate gives Black Cherry a great competitiveness. Due to its rapid growth, Black Cherry can dominate a dune grassland or dune thicket within a few years. Dune grassland disappears, and Sea Buckthorn dies by the lack of light. Favourable (local) conditions like slightly acidic soils, high temperatures, excessive moisture and the absence of soil pathogens promote the rapid growth of Black Cherry. Soil pathogens of Black Cherry in the region of origin in the United States are missing in the Netherlands (Reinhart et al., 2005). Furthermore, low grazing by rabbits, because of the outbreak of rabbit hemorrhagic disease (RHD), and the lack of active management of exotic species in that period, favoured Black Cherry growth.

This combination of factors caused a chain of favourable conditions for Black Cherry and continuous vegetation succession with many dense grass and shrubs means more shelter and a moisturised soil. This leads to superficial soil acidification and as a result to more favourable micro-climate conditions for germinating Black Cherry. Once established the species promotes its own habitat and expandability allowing a rapid colonisation.

MAPPING OF BLACK CHERRY EXPANSION AND MANAGEMENT RESULTS IN AWD

Black Cherry mapping, with a coverage estimation during field work in an acre-grid, was conducted in the years 2004, 2008, 2012 and 2016. A Vegetation map of 1989 was translated in the same format (Ehrenburg, 2005). The results give an impression of the rapid and extensive spatial expansion of Black Cherry in the AWD from the late 1980s, especially in dune scrublands and grasslands (Ehrenburg, 2005, Oosterbaan et al, 2004). Black Cherry struggled to establish in calcareous foredunes where higher rabbit densities and a more extreme climate, less rainfall and more salt spray occurs. Easier settlement occurred in the slightly decalcified middle and inner dune area. The middle dune area is also the area where the heaviest grass encroachment occurred with *Calamagrostis epigejos* and *Carex arenaria* (Remke et al., 2009). This encroachment was reflected in the Black Cherry coverage of the map of 2004 (Figure 2). The coverings of each acre block are also used to calculate how much surface Black Cherry covers in total, and this was also estimated for vegetation maps of 1988, 1996 and 2011.

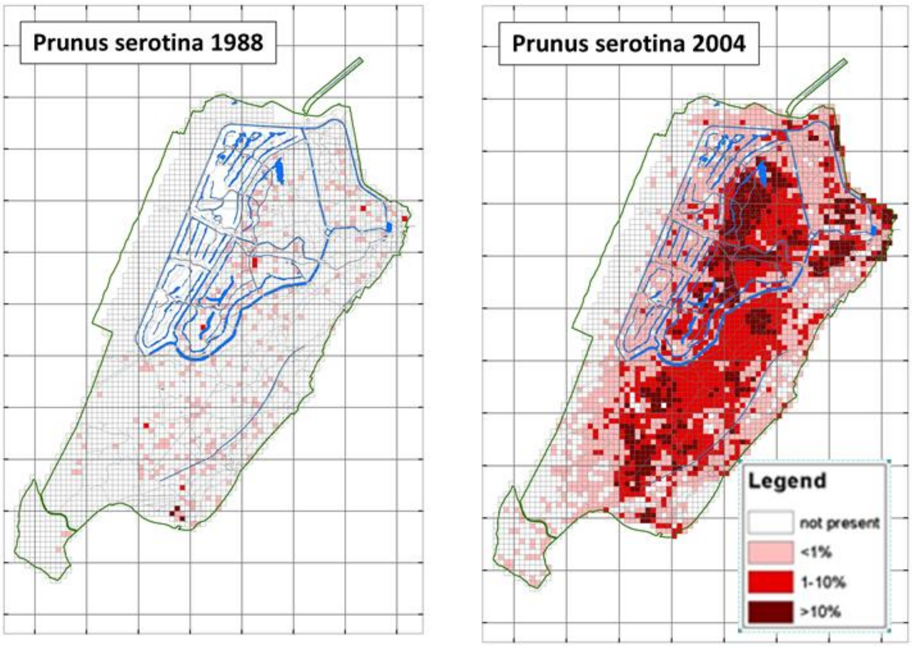

Figure 2 Coverage of *Prunus serotina* in acre blocks in 1988 and 2004 : white = not present; pink <1%; red 1-10%; dark red >10%.

When it became clear by the mapping results of 2004 that Black Cherry was threatening the entire dune area, Waternet, the management administration of the AWD, conducted phased and structural control from 2005 onward. This control consisted mainly of cutting or completely removing large cherry bushes, and long term follow-up management with sheep and cattle grazing. This management was intense, radical and expensive because the expansion of Black Cherry had already advanced.

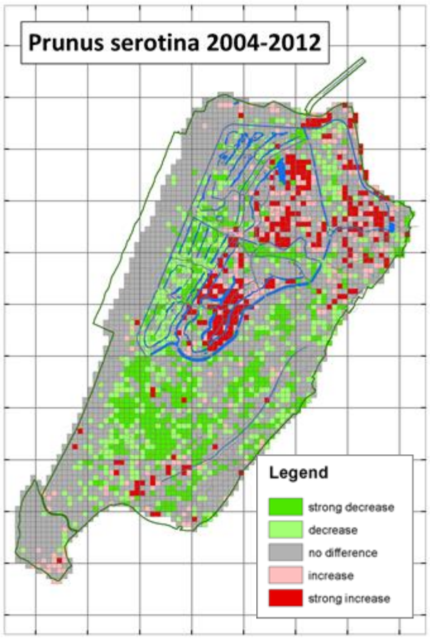

Figure 3. Change in coverage between 2004-2012 in acre blocks. The map indicates a clear difference between managed and non-managed sites. Managed: (dark)green (strong) decline, Not managed: grey no difference and (dark)red (strong) increase.

When comparing the map of 2004 with the one of 2008 and 2012 (Oosterbaan et al, 2004;2008;2012) (Figure 3), it is possible to distinguish areas with and without management. Till 2012 there was no cutting and grazing in the central part of the AWD, and Black Cherry could still increase in these areas. In the north-eastern part of the AWD, the increase of Black Cherry was taking place in the Pine forests. In the southern part where the management to control Black Cherry started in 2005, there was a strong decline, although Black Cherry was still present but on a much smaller scale. Overall, efforts to control Black Cherry have been successful. Since 2010 more Black Cherry has been eradicated than the annual growth, so a net decrease by management has been achieved (Oosterbaan, 2012). The total coverage of Black Cherry has dropped from ca.197 hectares in 2008 to 149 hectares in 2012, (Figures 4 and 5). Without management total coverage was expected to increase to almost 300 hectares (Oosterbaan e.a., 2008 & 2012). It was estimated that when continuing the then present management efforts, in five more years all the seed-bearing Black Cherries could disappear from the AWD. However, in places without management and only few (natural) grazers, there still was a slight increase of Black Cherry coverage. Therefore, Waternet decided to speed up the process with help of

EU an Provincial subsidies. Within the LIFE+ project “Amsterdam Dunes – Source for Nature” Waternet cleared all the remaining Black cherry from the central part of the dune area. In the densest thickets the soil was also removed to ensure that no seeds of black cherry were left behind. Mapping in 2016 (Oosterbaan, 2016) shows the invasion is in control (Figures 4 and 5).

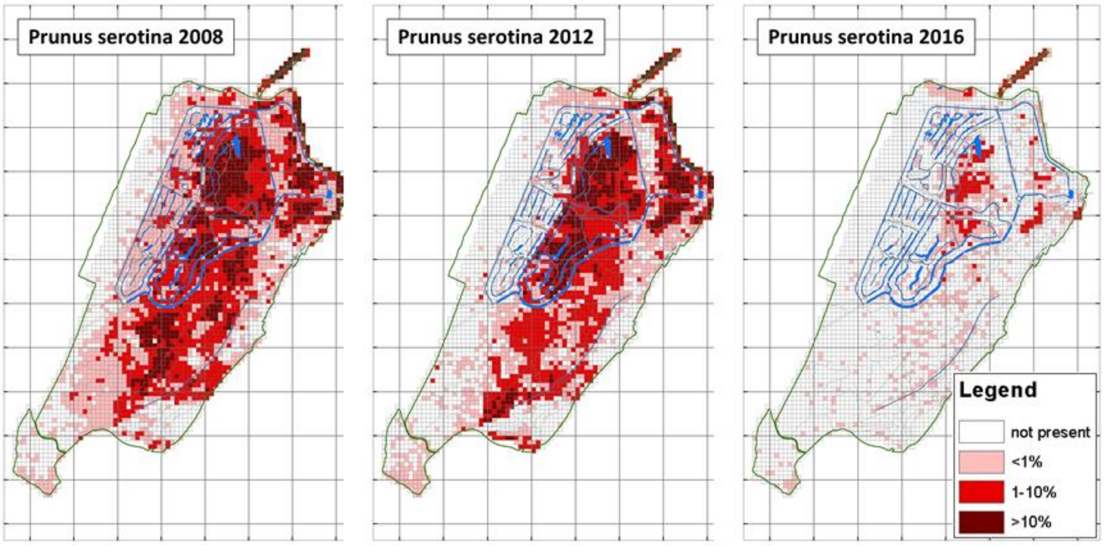

Figure 4. Coverage of *Prunus serotina* in acre blocks in 2008, 2012 and 2016: light grey = not present; pink <1%; red 1-10%; dark red >10%.

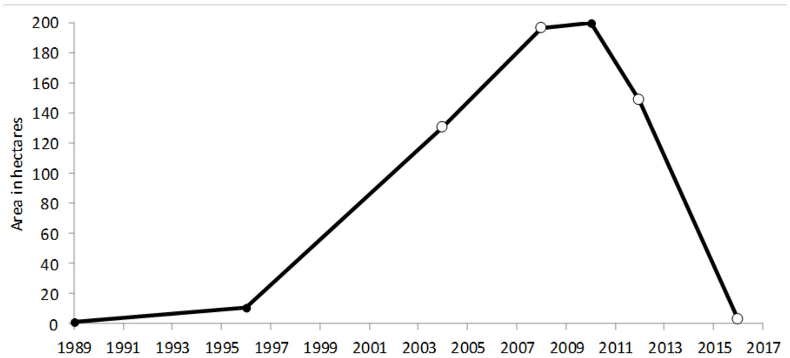

Figure 5. Area of the AWD (total surface = 3400ha) covered by *Prunus serotina*. Open bullets present actual invasive species mapping in 100x100m blocks. Closed bullets are estimates from general vegetation mapping

OVERVIEW OF MANAGEMENT OPTIONS FOR PRUNUS SEROTINA

Control of an invasive alien species is not easy, and this is especially true for Black Cherry. Experiences of others (Brehm, 2004; Straatsma & Jansen, 2005; Starfinger & Kowarik, 2007) and our own experiences from the different Dutch dune areas are helpful in making management decisions. There is not one single, one size fits all solution. Since many of the problematic stands result directly from plantation. The further use of the species should be restricted in the future, by (inter)national or regional regulation (T'ai et al., 2019). Large scale planting and planting in the vicinity of vulnerable Natura 2000 sites should be no longer conducted (Starfinger, 2010).

Sawing and girdling

Felling Black Cherry is ineffective when no further action is taken, because resprouts occur on 100% of the treated trees and biomass increment is not reduced in the long term. Sawing and the succeeding use of glyphosate works on the sawed stumps very effectively, especially when it is performed in dry periods in September / October. However, glyphosate cannot be applied in the Amsterdam Water Supply Dunes due to its drinking water abstraction function. Therefore, sawing and an aftercare grazing regime was used. The advantage is that the higher bushes can also be addressed. Grazing should be continued for several years (at least five). The effectiveness of girdling or ring-sawing varies, it is necessary to repeat it several times, but it is especially applicable in inaccessible terrain with solitary adult specimens, and it does not result in wood waste. It can be used by trunk diameter 1-20 cm by chain saw or machete. Girdling can be done by 2 rings with double chains or with a 15-20 cm wide girdle. A limitation of this method however is that the lower trunk part can survive.

Grubbing up method

Grubbing up is the extraction of whole trees with a small machine (Figure 6). Mechanical control is feasible but labour and cost intensive. In Black Cherry stands succeeding management by intense grazing is necessary, because of mass sprouting of seeds. In suitable (i.e. not too hilly) terrain with tightly packed young seedlings, mowing can be a useful method of control. Also, local sod cutting may be considered to counteract germination and re-establishment, but this is costly.

Figure 6. Large-scale grubbing up

Grazing

Grazing to reduce Black Cherry is used in several Dutch dunes (sheep, cows, goats). Sheep and goats in higher densities appear to be particularly effective (Kivit & van Diepen, 2007). The targeted use of a shepherd led herd also can achieve effective grazing. Sheep eat mostly (older) seedlings and new shoots from sawed stumps. Black Cherry contains a compound what can break down into hydrogen cyanide when ingested. All types of animals can be poisoned by ingesting leaves and twigs so it’s very important that grazers not only eat Black Cherry but also get enough grass. Cattle don’t seek the Black Cherry but graze it passing by. In the autumn cows seek the berries of Black Cherry, sometimes, breaking many branches and opening shrubs. Many seeds that have gone through a cow's digestives no longer germinate (in contrast to the seeds eaten by birds), so cow grazing is helpful in limiting the spread of Black Cherry, but germination in cow droppings has been observed. However, on locations with dense Cherry shrubs extensive grazing is not effective enough. But extensive grazing is complicating the establishment and rapid expansion of the Black Cherry so that it can be helpful in the case of a low density of Black Cherry.

Burning

Burning of Black Cherry is possibly a (temporary) efficient method, but there are few experiences available from the dunes. The fire should affect the complete root system, otherwise, Black Cherry will resprout from the roots in several years. Scaling up of management will lead to possible adverse effects on the characteristics of dune grasslands, such as breeding birds and butterflies, and should be weighed against the reduction of Black Cherry. Obviously, it is not the intention that years of intensive and large-scale combatting of Black Cherry will result in a monotonous dune grassland without breeding birds or butterflies. On the other hand, non-intervention will lead to a homogeneous cherry thicket for the next few decades, and the priority dune habitats will be lost. Increased litter input of Black Cherry may also affect the dune soils. These processes may be irreversible and should be better investigated (Tietema, 2008).

In all management methods, it is important to avoid new trees starting to spread seeds, to prevent the spreading of new seedlings. The achievement of all these forms of management in the long term is not yet known. A controlled study experiment on the efficiency of different control measures has not been carried out up to now. The effects of intensive grazing on different components of the dune ecosystem, such as butterflies, breeding birds, grasshoppers and vegetation, have so far only generally or locally been mapped (Mourik & Ehrenburg, 2007).

CONCLUSIONS AND RECOMMENDATIONS

Black Cherry (*Prunus serotina*) is an invasive exotic species in the Dutch dunes. In the last 20 years it has posed a serious threat to the Natura 2000 conservation objectives of habitat types H2130, H2160 and H2190. To avoid the spread of invasive species, the best thing to do is to start an early warning system and a systematic approach to non-native species specific for NATURA2000 sites. If non-native plant species occur in a dune area, it is easier, cheaper and more effective to remove them on a small scale. It is wise to eradicate them early, even if these species seem to cause no problems in the present ecosystem and a rapid spatial expansion seems unlikely. Changing environmental conditions or changes in natural grazing pressure may accelerate the rate of spatial expansion.

A control effort should start with monitoring and assessment of the actual impact of the specific situation. Control measures should not be undertaken without making sure that an appropriate method is available and that funding is sufficient to continue the work for five years and to preclude reinvasion. As proven in the AWD, a mechanical control program can be successful in combination with a grazing regime.

Other species are also becoming a pest in the dunes. *Rosa rugosa* is the most aggressive as it can overgrow large areas of grey dunes (Isermann, 2008, Kollmann, 2009, Weidema, 2006.). In the dunes near The Hague, *Rosa rugosa* is already spreading on a large scale, and it takes considerable effort and cost to remove it. *Berberis aquifolium* , *Cotoneaster spec*. and *Symphoricarpos albus* are increasing in the undergrowth of forests. It is recommended to eradicate these species while it is still possible. In the Natura 2000 site Kennemerland-Zuid, we succeeded to incorporate a list of potentially invasive alien species which should be monitored and managed (Table 1). We recommend working on national or regional blacklists in addition to the European Invasive Alien Species (IAS) list.

Table 1. Main invasive alien species (IAS) in Natura 2000 area Kennemerland-Zuid (not exhaustive list**)**

SPECIES
Prunus serotina
Rosa rugosa
Cotoneaster spp.
Berberis aquifolium (Mahonia aquifolium)
Symphoricarpos albus
Ailanthus altisissima
Heracleum mantegazzianum
Fallopia spp.
Impatiens glandulifera
Datura stramonium
Crassula helmsii
Ambrosia artemissifolia

In dune areas where Black Cherry occurs management to control it should be sustained for a long time, to maintain the typical grey dunes and dune thickets in a favourable conservation status as intended by Natura 2000. We also advocate for the provision of adequate funds for conservation purposes in the framework of Natura 2000. Otherwise, it will be increasingly difficult to meet obligations of the Habitats Directive. A controlled experiment to study the effectiveness of various management measures including burning should be carried out to optimize the control efforts. More research is needed into the possible effects of increased litter input of Black Cherry and intensive long-term (after-care) grazing on soil and other components of the dune ecosystem.

ACKNOWLEDGMENTS
We want to thank Thomas Smyth and Laurence Jones for their comments to improve this paper.

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Conservation of dune habitats in the Atlantic Biogeographic Region: the Dune Roadmap for knowledge exchange and networking 2016-2020

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Suggested citation:

Houston, J. (2020) Conservation of dune habitats in the Atlantic Biogeographic Region: the Dune Roadmap for knowledge exchange and networking 2016-2020. In L. Jones, T.A.G. Smyth & P. Rooney (eds.) *Proceedings of the 2017 Littoral conference 'Change, Naturalness and People'* (pp. 36 – 53).

INTRODUCTION

The European Union Biodiversity Strategy aims to halt the loss of biodiversity in the EU by 2020 (EC, 2011). The full implementation of the Birds Directive (EC, 2009a) and Habitats Directive (EEC, 1992) is one of the six targets adopted in the strategy. As work to develop the Natura 2000 network of European protected sites designated under these nature directives nears completion attention has turned to the management of the network with a focus on reaching favourable conservation status of all habitats and species of European importance. To support this aim the European Commission established the new Biogeographical Process in 2012 to promote the sharing of experience, good practice and cross-border collaboration on the management of sites. The Biogeographical Process provides a mechanism for member states, nature conservation organisations, NGOs and academic and research bodies to develop and support conservation measures for European habitats and species.

The Biogeographical Process is structured on the nine biogeographical regions within the territory of the EU28. The Atlantic Biogeographical Region is one region and includes a range of sand dune habitat types (EC, 2009b). In relation to northern European coasts there are also significant extents of dune habitats in the Continental and Boreal biogeographical regions associated with the western North Sea and Baltic Sea. Habitat Directive targets for favourable conservation status apply both at member state and at biogeographical region levels. Thus, the need for cooperation between member states is implicit in the legislation. For each region there is a member states' Steering Group and seminars are held, on average, every four years supported by the European Commission (EC), the European Environment Agency (EEA) and the European Topic Centre on Biological Diversity (ETC-BD).

THE FIRST ATLANTIC BIOGEOGRAPHIC SEMINAR 2012

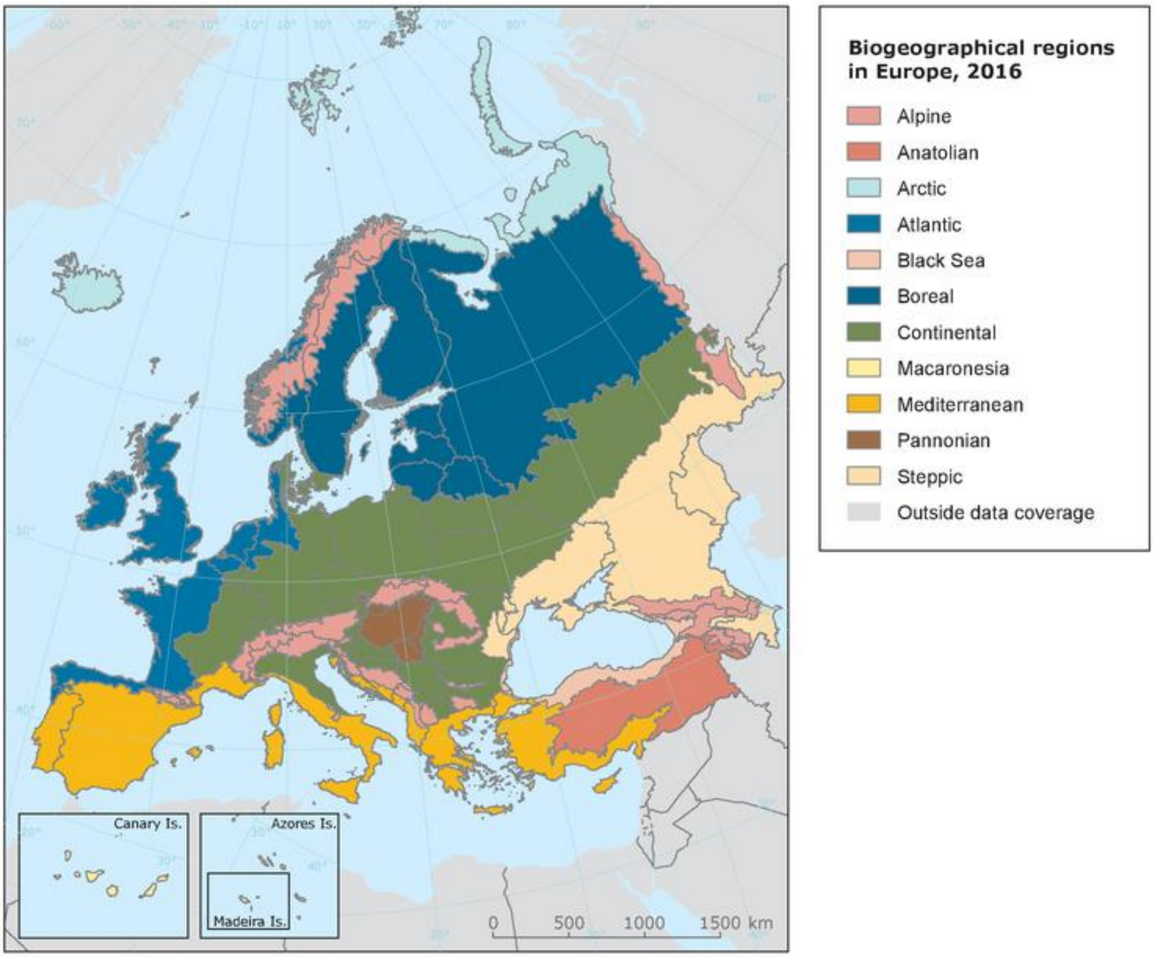

Figure 1. European biographical regions (Source: European Environment Agency)

The Atlantic biogeographical region includes nine member states: Ireland, United Kingdom, Portugal, Spain, France, Belgium, the Netherlands, Germany and Denmark (Figure 1). The first seminar for the Atlantic biogeographical region was held in 2012. A pre-scoping report was prepared by ETC-BD and from this the Steering Committee of the nine member states in the Atlantic region identified 20 priority habitats across four habitat groups (ECNC, 2012a). Included in the coastal and dunes habitat group were three Habitats Directive habitats as described in the EU Interpretation Manual (EC, 2013): 2120 Shifting dunes along the shoreline with *Ammophila arenaria* (white dunes), 2130 *Fixed coastal dunes with herbaceous vegetation (grey dunes) and 2190 Humid dune slacks.

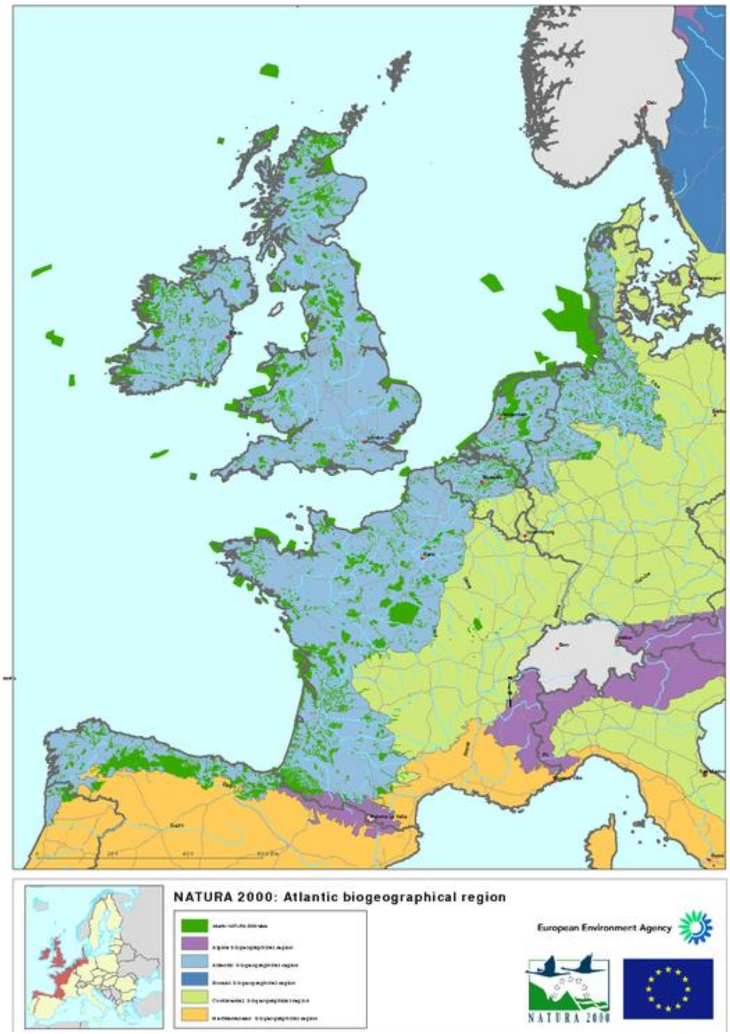

Figure 2. Natura 2000: Atlantic biogeographical region

The significance of this is that a rigorous assessment of priority habitats identifies sand dune habitats as characteristic features and priorities for conservation in the Atlantic region. The Atlantic region holds 44% of mobile dunes (2120), 57% of fixed dunes (2130) and 58% of dune slacks (2190) in the EU. It gives an invitation to the Atlantic region 'dune community' to engage with the process: this paper outlines how this could be done.

Following preparation of background notes on the selected habitats, including national expert input, the second step was a preparatory workshop led by national experts held in The Hague, The Netherlands in June 2012. The workshop report (ECNC, 2012b) was then taken forward to the more formal Atlantic seminar held in Bergen, The Netherlands in December 2012. The report of the seminar includes the results of discussions at both meetings and identifies a number of key actions (ECNC, 2013).

The first Atlantic seminar identified the key issues affecting the conservation status of coastal dune habitats and made recommendations for networking actions such as further guidance on the way in which natural dynamics can be incorporated into definitions of European habitats. The main issues for dunes were reported as:

- Large scale loss of natural habitat
- Interference with natural dynamics
- Lack of an integrated approach
- Invasive alien species
- Public communication
- Connectivity

Cross-cutting issues included policy integration, knowledge transfer, stakeholder involvement and communication and cross-boundary issues.

The intention in the report of the seminar was for member states to take the lead in establishing habitat working groups and to use a number of tools such as the Natura 2000 Communication Platform for developing habitat networks. However, in these areas very little progress was made in the period between the first seminar in 2012 and the second in 2016. The intention to create "an expert-network of governmental agencies that are competent for the conservation policy and the management of coastal dune sites in all member states of the EU" (ECNC, 2013 pp.15, 18, 20) has not been met. As a consequence the process had little drive and was not well known outside the work of the members of the Habitats Committee.

PRIORITISED ACTION FRAMEWORKS

The establishment of the Natura 2000 network is the cornerstone of EU action for nature. By 2018 it covered over 18% of the terrestrial area of the EU28 (EC, 2018, pp. 8-9). Establishing the network, coordinated by the European Commission, has been a political process involving dialogue with individual member states, technical support of the EEA and publication of lists of sites by biogeographical region. Insufficiencies in the lists are discussed in biogeographic seminars or bilateral meetings with a view to updating the lists.

As the terrestrial network became substantially complete the Commission turned its attention to funding the conservation measures required to address the pressures and threats to habitats and species within the network and the wider EU. Prioritised Action Frameworks (PAFs) were introduced as a tool for member states to assess the needs for EU co-financing to help meet their obligations in relation to Natura 2000, especially those habitats and species for which the member state had a special responsibility (Figure 2).

PAFs are living documents and will be updated for the next multiannual financial framework 2021-2027. The process of preparing PAFs has already proved to be useful in terms of securing EU LIFE co-financing for priority projects. Both England and Wales made use of the LIFE programme to help develop their national PAFs (JNCC, 2016; Natural Resources Wales, 2015) and a direct output of this process has been two successful applications for LIFE projects for coastal dunes in 2017. The projects are LIFE17NAT/UK/000023 *Sands of LIFE* and LIFE17NAT/UK/000570 *Dynamic Dunescapes*.

NETWORKING ACTIVITY 2012-2016- DEVELOPMENT OF THE ROADMAP FOR KNOWLEDGE EXCHANGE

In the absence of a coordinated approach by member states or a specific lead being taken by a member state in relation to dunes in the period between biogeographical seminars, the momentum has been maintained by LIFE projects and national networks.

The most significant of the LIFE project meetings was the 'Dynamic Dunes 2015' meeting organised by Waternet, PWN and Natuurmonumenten in Zandvoort, The Netherlands in October 2015 (Waternet, 2015). Major issues discussed were dynamics in dunes and coasts, multi-functionality and ecosystem services of Natura 2000 areas, nitrogen overload and invasive alien species. The conclusions of the meeting (Waternet, 2015 p. 5) were:

1. It is clear that the overall target of favourable conservation status can only be achieved by concerted efforts. 75% of the area of dune habitat across the region should be in favourable conservation status to meet the targets. Because of their worrying state, dune habitats should be higher on the political agenda of the European Commission.

2. Dunes should also be higher on the European research agenda (e.g. in Horizon 2020). European research priorities to reach favourable conservation status of all dune habitats must be assessed and agreed upon between the dune habitat expert community and government agencies.

3. The experience connected to the positive trend with regard to dune habitats, management and restoration in the Netherlands should be disseminated to the whole Atlantic region. This can be done *by the European Dune Network and the EUCC in cooperation with the Dutch water companies and other nature management organisations like Natuurmonumenten.*

Taking up the third point in the conclusions, a LIFE Platform Meeting and thematic seminar of the biogeographic process was organised in association with these same Dutch LIFE projects LIFE11NAT/NL/000776 *Amsterdam Dunes- Source for Nature* and LIFE09NAT/NL/000418 *Dutch Dune Revival* in June 2016. The output of the LIFE Platform meeting, attended by representatives of all Atlantic member states and others, was the preparation of a first version of the Dune Roadmap for knowledge exchange as a contribution to the biogeographical process.

THE SECOND ATLANTIC BIOGEOGRAPHIC SEMINAR 2016

The LIFE Platform Meeting revisited the issues discussed in the first Atlantic seminar (ECNC, 2013), confirmed that they remain valid and added several new issues. As the Platform Meeting was a contribution to the biogeographical process, its results were presented at the second Atlantic biogeographical seminar held in Ennistymon, Ireland in October 2016. The first version of the Dune Roadmap was discussed in a coastal habitats workshop. One of the reasons for making the effort to connect the work of dune managers to the biogeographical process was a concern that if no action was taken, or little interest shown in the process, there would be no voice present to champion dune habitats and the priorities may shift elsewhere.

There is clearly a political element to the biogeographic process. The most recent assessment of progress with the EU Biodiversity Strategy shows that whilst there is some progress, much greater effort is required. Progress towards favourable conservation status of the habitats and species of the Habitats Directive is assessed by member states every six years as required by Article 17 of the Directive: the first assessment was completed in 2007 (EC, 2009), the second in 2013 (EC, 2015) and work is underway for the third in 2019 covering the period 2013-2018. These Article 17 national reports are collated to produce a snapshot of the state of nature in the EU (EEA, 2015).

DEVELOPING THE DUNE ROADMAP FOR KNOWLEDGE EXCHANGE

The 2015 state of nature report (EEA, 2015) showed that across the EU dune habitats were the group with the least percentage of favourable reports, and that there were few signs of improving trends. The need to significantly improve the status of dune habitats across Europe has been stressed by both scientists and managers through evidence and practice. What is now required is a gearing up of work from projects to national programmes. This is where LIFE projects, the biogeographical process and the national PAFs should be able to work together to share best practice and support cross-border programmes. The Dune Roadmap (Anon, 2018) suggests that such programmes of work would be assisted by the explicit commitment of member states to work together, and through resources to support national networks and a European Dune Network. Strengthening cooperation and networking in the Atlantic region would also help to develop links across all biogeographic regions. What is required is a sustained and coordinated, transnational approach.

A set of dune habitats, listed in Annex 1 of the Habitats Directive (EC, 1992) and described in the Interpretation Manual (EC, 2013), characterize the Atlantic biogeographical region.

- 2110 Embryonic shifting dunes
- 2120 Shifting dunes along the shoreline with *Ammophila arenaria* (white dunes)
- 2130* Fixed coastal dunes with herbaceous vegetation (grey dunes)
- 2140* Decalcified fixed dunes with *Empetrum nigrum*
- 2150* Atlantic de-calcified fixed dunes (*Calluno-Ulicetea*)
- 2160 Dunes with *Hippophae rhamnoides*
- 2170 Dunes with *Salix repens* ssp. *argentea (Salicion arenariea)*
- 2180 Wooded dunes of the Atlantic, Continental and Boreal region
- 2190 Humid dune slacks
- 21A0 Machairs (* in Ireland)

Habitats marked with * are priority habitats (i.e. habitat types in danger of disappearance and whose natural range mainly falls within the territory of the European Union). Some EU habitat types, such as embryonic shifting dunes and the fixed coastal dunes, occur in all nine member states of the Atlantic region whereas others, such as machair or wooded dunes, occur in fewer member states. A proportion of the habitats in each member state are protected through the designation of Special Areas of Conservation (SAC) as part of the Natura 2000 network, but in some cases significant proportions of the habitats lie outside SAC designations. Conservation measures are required for all coastal dune habitats to address the known pressures and threats. This approach forms the basis of LIFE projects and national programmes.

The Dune Roadmap is an outcome of discussions at two biogeographical seminars, workshops at Dynamic Dunes 2015 and the LIFE Platform meeting 2016, national workshops and input from dune experts from across the region. The Dune Roadmap was updated following discussions at the Coastal & Marine Union (EUCC) Littoral 2017 conference in held in Liverpool in September 2017, and was presented at the *LIFE+ FLANDRE* international workshop on management of coastal dunes and sandy beaches held in Dunkirk in June 2018 (Houston, 2018). It represents the views of dune experts and has been adopted as a tool by EUCC and other dune networks. It is published as part of the report of the second Atlantic Natura 2000 seminar (ECNC, 2016). It therefore carries some weight by recording what member state experts and others see as actions that would help member states make progress towards achieving favourable conservation status for the dune habitats in the Atlantic region. The current Dune Roadmap, updated following the *LIFE+ FLANDRE* workshop, covers the period 2016-2020 between the second and third Atlantic seminars.

Discussions at the above workshops highlight the following common problems:

- Continued large scale loss of dune habitat
- Interference with natural dynamics
- The lack of an integrated approach
- Spread of invasive alien species
- Predicted impacts of climate change
- Need for intra- and inter-sector communication
- Impacts of more intensive agricultural land use
- Long-term impact of nitrogen deposition
- The need to involve and engage the public

The specific objectives of the Natura 2000 Biogeographical Process include collecting information on threats and priority conservation needs, exchanging experiences, case studies and best practices, identifying common objectives, priorities and management actions, developing new management insights, stakeholder's cooperation frameworks and specialist networks, enhancing trans-boundary networking and strengthening recognition for management that contributes to socio-economic objectives (ECNC, 2014).

National experts, including scientists, practitioners and policy officers, have contributed to the process and have supported the assembly of a Dune Roadmap to help set out what should be done to share knowledge and best practice, to promote research and to encourage member states to develop national programmes using the PAFs as a tool for setting priorities.

The Dune Roadmap:

- Identifies actions for guidelines, interpretation and studies
- Includes habitat inside and outside Natura 2000 sites
- Highlights the role of LIFE projects and other projects
- Reiterates the recommendation for the establishment of an expert-network of governmental agencies
- Sets out the need for a European Dune Network
- Includes a record of activity as a measure of effort

The Dune Roadmap is a live document which, since the LIFE Platform meeting in 2016, has been updated by the Neemo LIFE Team with input from experts attending the series of meetings listed above. Its aim is to highlight issues, and constraints, in relation to the overall target of reaching favourable conservation status for all dune habitats in the Atlantic biogeographical region. It is designed to encourage key actors to take the lead on actions identified as being important for making progress towards targets, or for improving understanding of habitat requirements at the biogeographical level. It suggests added value actions which, across the region, will assist member states in meeting their objectives.

The Dune Roadmap concerns habitats and species both inside and outside the Natura 2000 protected area network and highlights actions where it is important to work with sectors such as coast defence authorities, forestry and agriculture. It repeats the recommendation from the first Atlantic seminar in 2012 (ECNC, 2013) for the establishment of an expert-network of governmental agencies to develop a joint biogeographic conservation and restoration strategy, and seeks to re-invigorate a European Dune Network by establishing a central resource linked to national nodes.

The Dune Roadmap is presented as a table (Table 1) which, in the version of March 2019 (Houston, 2019), elaborates information on eight actions, includes a section on communication and networking and maintains a record of conferences, workshops, events, outcome of submitted bids and key publications from information provided by the experts noted above.

Table 1. Dune roadmap as published in Houston (2019)

1	Guidelines on how to incorporate dynamics into the interpretation of Favourable Conservation Status
2	Addressing dynamic coastal change with attention to sandy beaches and the formation of strandline vegetation
3	Interpretation, mapping and management guidelines for EU habitat types
4	Restore ecological connectivity in fragmented dune belts along strongly urbanised coasts
5	Addressing protection and management of 2130* fixed coastal dunes
6	Further studies on 'low hanging fruit' habitats: habitats which in the view of experts at ETC-BC could be targeted by member states to effect an improvement in conservation status
7	Developing and promoting research programmes with relevance across the biogeographical region, such as studies on the impact of N-deposition and on the monitoring of habitat restoration projects
8	An early warning system for invasive alien species and the sharing of practical control methods with costs

The proposal at the second Atlantic biogeographical seminar in September 2016 to consider 'low hanging fruits' reflects the political drive behind the process. For the EU Biodiversity Strategy to meet its targets there must be visible and substantiated progress towards Favourable Conservation Status for habitats and species. A paper on the low hanging fruits methodology (Richard et al, 2016) was included in the second Atlantic seminar Input Document (ECNC, 2016a). For dune habitats it was proposed that significant progress could be made to improve the conservation status of *2140 Decalcified fixed dunes with *Empetrum nigrum* and 2180 Wooded dunes of the Atlantic, Continental and Boreal region mainly through actions in Denmark and France respectively. Whilst representatives of member states at the second Atlantic seminar had reservations about the 'low hanging fruit' approach (ECNC, 2016b), it gives an indication of how precise targeting, e.g. through a LIFE project, can have an impact on conservation status or trends in conservation status. The Dune Roadmap does not dismiss the rationale for 'low hanging fruits' and suggests that further studies would be useful.

KEY ACTIONS DESCRIBED IN THE DUNE ROADMAP

The four examples below highlight a range of networking opportunities from actions which can only really be taken at the Commission or member state level, to actions where national experts could contribute to knowledge, to self-help actions led by practitioners and to actions which require an Atlantic regional overview.

1. Guidelines on how to incorporate dynamics into the interpretation of Favourable Conservation Status

For most dune habitats the definition of favourable conservation status should include the presence of bare sand and active processes of erosion and accretion at varying scales. This is not explicit in the interpretation of EU habitat types. Without a wider understanding of the role of abiotic processes in dune systems it could lead to conflicts in setting conservation objectives, or to stabilisation of mobile dunes where this is detrimental to the overall health of the dune system measured by its biodiversity. Interference with natural dynamics, by artificial stabilisation or sea defence structures, was the top issue raised in the 2012 Atlantic Biogeographical Seminar (ECNC, 2012b).

Field discussions, such as at the EUCC-France meeting in Merlimont in 2014 and the work of several LIFE projects, have shown that the exchange of sediment between beaches and dunes and the recycling of sediment within the dune system are essential components of structure and function. However, there is prevalence in some regions and by some authorities to favour artificial sea defences and to stabilise inland sand drift. Also there can be a concern that by increasing the area of one habitat type there may be a consequent decrease in another, both of which are of conservation value.

The Dune Roadmap proposes that the European Commission and member states could support a science and practice review of the rationale for creating and maintaining bare sand and dune mobility in all dune habitats. Target values can be set in conservation objectives for bare sand and dynamics in dune habitats. Several authorities, the UK conservation agencies for example, recommend a figure of at least 10% bare sand across the dune system and others, such as the *SandLIFE* project in Sweden LIFE11NAT/SE/000849, recommended much higher percentages. The scale of dynamics is also important with a balance between large mobile features, smaller blowouts, sand patches and scrapes.

The value of bare sand and mobility within dune systems is not universally accepted despite substantial scientific evidence and the results from projects across Europe. It is important, therefore, for the European Commission, with member states, to support the dissemination of these approaches in the nature conservation sector and in other relevant sectors such as coast protection, agriculture, forestry and tourism. Alongside this work should be broad public awareness campaigns to explain why bare sand matters.

2. Interpretation, mapping and management guidelines for EU coastal dune habitat types

The reporting of conservation status across a biogeographical region tends to assume that each member state is measuring the same parameters and that the assessments can be combined to give a single report on status. There is no evidence to confirm that this is the case. If there are different interpretations of habitat types and condition then it may be difficult to be certain that favourable conservation status is achieved at the biogeographical level.

For some habitat types, such as 2160 dunes with *Hippophae rhamnoides*, the Interpretation Manual (EC, 2013) has little guidance and for others, such as 2170 dunes with *Salix repens* ssp. *argentea* and 2190 humid dune slacks it leaves room for different interpretations. In an email dated 23 September 2016 Graham Weaver, the national coastal ecologist for England showed that he was considering merging 2170 dunes with *Salix repens* ssp. *argentea* and 2190 humid dune slacks into one for objective setting and condition monitoring as it is difficult to distinguish between the habitat types.

The Dune Roadmap identifies three habitats which may cause confusion: 2170 dunes with *Salix repens* ssp. *argentea*, 2160 dunes with *Hippophae rhamnoides* and 2180 wooded dunes. The table of actions in the Dune Roadmap suggests that the national agencies for Belgium, The Netherlands, United Kingdom and France could take a lead on this task using the expertise of their national scientific bodies. There is a precedent for this work: two Atlantic dune habitats are already covered in the management models for fixed dunes and humid dune slacks already published by the Commission (Houston 2008a, 2008b). Outputs from expert meetings in a similar format would improve understanding of the habitat types across the Atlantic region and provide advice on management and monitoring. These would be low cost and could provide useful reviews of the management of these habitats even where, in the case of 2160 dunes with *Hippophae rhamnoides*, the status is generally favourable.

3. An early warning system for Invasive Alien Species and the sharing of practical control methods and costs

At the LIFE Platform meeting in 2016 Maike Isermann in a presentation explained that coastal dunes, due to their naturally open and dynamic habitats, are particularly susceptible to colonisation by alien species. In the habitat assessments compiled as part of the Habitats Directive reporting process for the period 2007-2012 Invasive Alien Species (IAS) are identified as highly important threats for dune habitats 2120 shifting dunes, 2130 fixed dunes and 2190 humid dune slacks and the most significant pressure and threat to 2130 fixed dunes (EEA, 2014). LIFE projects across the Atlantic region are addressing the consequences with particular attention given to the control of Japanese Rose *Rosa rugosa* and Black Cherry *Prunus serotina*. There is however a common list of other species including Long-leafed wattle *Acacia longifolia*, Pampas grass *Cortaderia selloana*, Hottentot-fig *Carpobrotus* *edulis*, Oregon grape *Mahonia aquifolium* and Swamp stonecrop *Crassula helmsii* which should be added to a 'black list' of invasive alien species of conservation concern for the Atlantic dune habitats.

It is suggested that the compilation of a black list would primarily be a bottom up, self-help initiative using the knowledge of dune networks to identify the most problematic species and to share the experience of spread and control. The EU Regulation on Invasive Alien Species (EC 2014) can provide a context, but the vigilance, knowledge exchange and actions required to address invasive alien species are best addressed through member states and project to project networking. In a contribution to the Dune Roadmap (Albrechtsen, D., 2018) proposed the need for a platform meeting on best practice in the fight against *Rosa rugosa*. This could be hosted either by a LIFE project or a national agency.

In the period 2016 to 2020 information will be collated and published on the control of *Rosa rugosa* by Maike Isermann taking lessons from LIFE projects in northwest Europe. The exchange of knowledge on the control of *Rosa rugosa* is one example where there should be communication across the Atlantic, Boreal and Continental regions. According to the European Delivering Alien Species in Europe (DAISIE) project *Rosa rugosa* in one of the 100 worst alien species in Europe and is widespread along the coasts of the North Sea, Baltic Sea and northwest-European Atlantic coasts (Essl, 2006)

*4. Protection and management of fixed coastal dunes (priority habitat *2130)*

*2130 fixed coastal dunes with herbaceous vegetation is a priority habitat occurring in all Atlantic member states. As it is a priority habitat it can be expected that conservation measures are included in each of the national PAFs.

*2130 is by far the largest dune habitat type by area but only 40% of the c. 110,000 ha in the Atlantic biogeographical region is within the Natura 2000 network according to analysis of EEA data derived from the reports of member states (EEA, 2014). In France only 20% of the total area of fixed dune *2130 is within the Natura 2000 network. In the UK the figure is 44%, whereas in The Netherlands it is 95% and in Belgium 100%. As much of the available EU co-financing for nature is focused on the Natura 2000 network there is a risk that habitat loss and deterioration continues outside the protected sites.

There seems to be no information readily available on the distribution of *2130 outside Natura 2000, yet concerns have been raised by representatives of statutory nature conservation agencies at the two Atlantic biogeographical seminars about loss of habitat, intensification of agricultural use, eutrophication and changes in land use. The Dune Roadmap recommends that there should be a joint focus on *2130 by the member states and this in itself could be a catalyst for setting up the cooperative expert group as proposed at the first seminar.

Through the Action Plan for nature, people and the economy (EC, 2017) the Commission and member states are supporting the development of Habitat Action Plans for two threatened habitat types, 6210 semi-natural dry grasslands and 4030 European dry heaths. If the pilot work in 2019 is successful then the approach could be extended to other habitats. The Dune Roadmap proposes that a European overview of 2130 *fixed coastal dunes, a habitat occurring in all coastal regions could help to focus attention on the threats to the habitat outside the Natura 2000 network.

NEXT STEPS FOR THE ROADMAP FOR KNOWLEDGE EXCHANGE AND NETWORKING

The LIFE Platform Meeting, development of the Dune Roadmap and the second Atlantic biogeographic seminar in 2016 have connected the current informal network of dune scientists and practitioners with the European Commission's interests in securing favourable conservation status for European habitats and species listed in the Habitats Directive.

The Dune Roadmap is a tool owned by a group of stakeholders from all member states in the Atlantic biogeographical region. It has developed bottom up through the sharing of knowledge between practitioners and scientists through informal dune networks. It is supported by the Coastal & Marine Union (EUCC), by national coastal and dune networks, and by LIFE and other EU co-financed projects. The Dune Roadmap can help support applications for EU co-financing. The LIFE Application Guide 2018 includes in the list of thematic priorities for LIFE Nature projects "activities in support of the Natura 2000 network biogeographical seminars" (EC, 2018 p.20).

All stakeholders in the Natura 2000 Biogeographical Process can propose networking events through the Natura 2000 Communication Platform coordinated by the European Commission if the event addresses a theme already identified as a common priority and shared interest from the biogeographic seminars and networking events. The Dune Roadmap, and its updates, provides the basis for future applications for networking events. LIFE projects, with their requirement for networking, and inbuilt flexibility, are well placed to take the lead on a number of actions in the Dune Roadmap.

The European Commission in publishing the Action Plan for Nature in 2017 (EC, 2017) reaffirmed its commitment to support the Natura 2000 biogeographic process. It proposes to refocus the Natura 2000 Biogeographical Process to enable it to better contribute to conservation systems for the Natura 2000 network, to develop biogeographical-level roadmaps, to support thematic events and to further develop the Natura 2000 Communication Platform to make it more effective.

From the perspective of the interest in conservation of dune habitats it is vital that the community of interest described above organises itself in such a way that it can contribute positively and effectively to the Natura 2000 Biogeographical Process. Some resources from LIFE projects, including the more strategic LIFE Integrated Projects should be directed to this goal. LIFE projects are intimately linked to the Habitats Directive, PAFs and the Biogeographic Process and can work together through their networking activities to address some of the actions highlighted in the Dune Roadmap.

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Identifying The Drivers Of Long-Term Vegetation Change In Scottish Sand Dunes

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Suggested citation:

Pakeman, R.J. (2020) Identifying The Drivers Of Long-Term Vegetation Change In Scottish Sand Dunes. In L. Jones, T.A.G. Smyth & P. Rooney (eds.) *Proceedings of the 2017 Littoral conference 'Change, Naturalness and People'* (pp. 54 – 67).

ABSTRACT

Coastal ecosystems provide valuable ecosystem services and host many specialised species and habitats. Using a resurvey approach, we assessed how vegetation composition and diversity had been affected by climate, pollution and land use change between 1975-77 and 2009-13. Climate had minimal impact, though the analysis did reveal a number of sites where succession by woody species had caused significant vegetation change. Nitrogen pollution impacts were higher in the east, and particularly south east, of Scotland, with significant changes in species composition but no declines in diversity. Sulphur deposition and reduced grazing reduced species richness, and reduced grazing allowed the spread of taller, nutrient demanding species at the expense of species characteristic of short turf. Grazing could be re-introduced to east coast sites to improve their condition and, potentially, to counteract the impact of nitrogen deposition. Dune and machair habitats on the west coast and islands are generally in better condition, but these are at risk from the impacts of long-term demographic shifts in these isolated areas compromising the success of current management at maintaining their conservation interest.

Keywords: Climate change, coastal vegetation, grazing, land use change, machair, nitrogen deposition

INTRODUCTION

Coastal ecosystems deliver highly valuable ecosystem services that are far more important to society than the limited area they cover would suggest (Jones et al. 2011). In particular, their value for coastal defence, tourism and recreation are high. They also contain spatially restricted habitats, which in turn contain many specialised and rare species. Also, coastal systems, in particular sand dunes and machair (a species-rich habitat complex found on shell sands on exposed coasts in Scotland and Ireland), are inherently fragile and subject to changes driven by sea level rise, increased storminess, changes in sediment supply, development, changing land use, climate change and pollution (Jones et al. 2011). Geomorphological changes and development result in habitat loss but climate change (Parmesan & Yohe 2003), continued atmospheric deposition (Jones et al. 2004; Remke et al. 2009) and land use changes (Brunbjerg et al. 2014; Millett & Edmondson 2013) impact more on the composition of vegetation and its ability to respond to changing environments.

In order to manage these fragile and valuable systems for a sustainable delivery of key ecosystem services it is necessary to understand their dynamics, and in particular the dynamics of individual plant species and the vegetation that covers these habitats. If species' trends and their functional characteristics can be assessed, then it offers the potential to understand both what is driving the dynamics of the system and the potential impacts of those species' trends on the rest of the system based on the functional traits or attributes of the species changing and their environmental preferences (Smart et al. 2003).

A resurvey approach was taken using species composition data to address the following questions: have changes in (1) climate, (2) atmospheric pollution and/or (3) land use caused changes in vegetation composition, individual species' abundance and species diversity in Scottish sand dunes?

METHODS

Survey data

Species composition data were collected during two vegetation surveys of Scottish dune and machair sites (Shaw et al. 1983; Pakeman et al. 2015). Survey one was carried out from 1975 to 1977 and survey two from 2009 to 2013, with 89 sites revisited and 2532 quadrats repeated. During the second survey, quadrats were selected at random within sites to avoid bias. The surveys used the same methods and were made by the visual cover estimation of all higher plant species, as well as composite categories for bryophytes and lichens, litter and bare ground within 5 m x 5 m plots. Survey two used GPS to relocate quadrat positions digitised from original 1:10 000 maps. This relocation approach has been shown to be robust and effective for re-visitation surveys of non-permanent quadrats (Kopecký & Macek, 2015; Ross et al. 2010). Composition data were summarised as richness and Shannon diversity per quadrat.

Measures of land use and vegetation structure were also collected during both the surveys. Grazing was assessed into four categories: heavy = 3; moderate = 2; light = 1; and no grazing = 0 (Pakeman et al. 2017a). The presence and absence of livestock species (cattle, horses, and sheep) or their dung was noted; in the analysis this was converted to presence/absence of Livestock (1/0). Vegetation structure was used as a proxy for the intensity of past management or land use; this was scored for forbs, grasses, shrubs and trees in a similar four-point scale; dense cover = 3, moderate cover = 2, light cover = 1, absent = 0 in different height classes. For analysis this data was aggregated into the following derived variables: Woody – the sum of structure scores for shrubs 50 – 200, shrubs 200 – 500 and trees > 500 cm (scale 0 – 9); Openness – the sum of grass 0 - 20 and herb 0 – 20 cm rescaled so that 0 represented closed ground vegetation and 3 open sand (i.e. 3 minus the sum of cover); and Density - the sum of all herbaceous and short shrub layers (0 - 20, 20-50, 50 – 200) with a maximum of 3 per layer (scale 0 - 9). The cover of bare ground and litter from the quadrat survey were also used as descriptors of vegetation structure. A final land use driver was whether the site had been in the Environmentally Sensitive Area (ESA) scheme, an agri-environment scheme that was geographically restricted, started in 1987 and closed in 2000 (though some agreements ran up to 2009, Department of Agriculture and Fisheries for Scotland 1989). With respect to this analysis, this scheme covered quadrats in the Inner Hebrides, the southern half of the Outer Hebrides and the Shetland Islands.

Plant attribute and trait data

The PLANTATT database (Hill et al. 2004) provided mean climate values for species based on the mean climate of the 10 km squares where they occur in Britain, Ireland and the Channel Islands based on their distribution records in the New Atlas of the British and Irish Flora (Preston et al. 2002). The values used were TJan - January mean temperature (°C), TJul - July mean temperature (°C) and Prec - Annual precipitation (mm). The database also provided Ellenberg indicator values (EIV, Ellenberg 1988) recalculated for the UK; values for N and R were used in the analysis. For each combination of quadrat and year a community weighted mean attribute score for the three climate variables and two indicator values was calculated to assess an estimate of change at the assemblage level. In addition, data on species' status were added to the analysis: the number of occupied 10 km squares in Great Britain to assess if trends were linked to the commonness of species and the change index (a measure of change in 10 km square occupancy between the two editions of the Atlas of the British Flora, Perring & Walters, 1962; Preston et al. 2002; Telfer et al. 2002).

Data on key functional traits for all vascular plants were assembled from two sources: BiolFlor (Klotz et al. 2002) for canopy structure, life-span and vegetative spread method and LEDA (Kleyer et al. 2008) for canopy height, leaf dry matter content (LDMC), leaf size and specific leaf area (SLA), with life span, canopy structure and vegetative spread assessed as separate attributes. The traits were selected as they have been shown to be key response traits (Garnier et al. 2007; Pakeman 2011).

Environmental data

Climate data were assembled from the UKCP09 5 km x 5 km gridded data (Perry & Hollis 2005) for 1960 to 2009. To reduce the number of potential (and highly correlated) explanatory variables available for analysis, the monthly data were averaged (temperature) or summed (precipitation) to give yearly values and relevant seasonal values for each year: Winter – December, January, February (for analysis of TJan); Summer – June, July, August (for analysis of TJul and Prec). Finally, to account for changing climate, averages of these seasonal and annual values for the 15 years prior to each survey period were calculated (1961 to 1975 for 1976, 1995 to 2009 for 2010).

Data on cumulative total nitrogen and sulphur deposition on a 5 km x 5 km grid for the period between the surveys (1976 to 2010) was obtained from the CBED-model (Smith et al. 2000) using historical scaling factors (Fowler et al. 2004) on a base year of 2005. 2010 deposition estimates for nitrogen ranged from 2.96 to 12.36 kg ha^{-1} yr^{-1} for total nitrogen and 0.89 to 6.57 kg ha^{-1} yr^{-1} for sulphur.

Statistical analysis

Changes in the community weighted climate attributes, EIVs, species richness and Shannon diversity were tested with a linear mixed model, with the fixed factor Year, and the random factor of Quadrat nested within Site. Analysis used the nlme package (Pinheiro et al. 2010) in R 3.2.0 (R Development Core Team 2015). To identify potential drivers, the change in weighted attributes, EIVs, Richness and Diversity were regressed against their respective putative drivers, climate or pollution. The changes were analysed with a linear mixed model with Site as a random factor using nlme (Pinheiro et al. 2010) within R.

Trends for individual species were assessed by using a linear mixed model after logit transformation (Warton & Hui 2011) to model their abundance as a function of the fixed term of Year and a random term of Quadrat nested within Site to account for the repeated measures nature of the data and the potential for site-based changes in management to differ between sites. Mixed modelling was carried out in lme4 (Bates et al. 2014) in R. To identify response traits, modelled slopes of the species responses were correlated with trait values; each trait was tested separately as the fixed factor (Bowler et al. 2015). Again, this used a mixed modelling approach in lme4 (Bates et al. 2014) with each species weighted to ensure that the results were not dominated by the dynamics of a few rare species. Weights were calculated as the inverse of the coefficient of variation from each species' trend model; the best fitting models had the highest weight in the analysis. To control for relatedness between species we included genus nested within family nested within order as the random model (Blackburn & Duncan, 2001).

To identify the drivers of changes in species richness, the data were analysed separately for non-mobile (i.e. fixed) habitats (2151 quadrats) and mobile habitats (257) as strandline and mobile dunes will show increased species richness as a result of succession following dune stabilisation. Potential environmental drivers examined were of three types: the change in the level of a parameter between the two survey dates, cumulative values for the deposition data or a single value for the parameter. The latter group was made up of values that were fixed, e.g. in the ESA scheme area, or were available at only one date. The data were subject to multi-model inference approach to investigate the weight of evidence surrounding individual drivers (Burnham & Anderson 2002). Models were fitted with residual maximum likelihood with the potential environmental drivers as fixed effects and site as a random effect. The best supported models identified with the bias-corrected form of Akaike's Information Criteria (AICc) and multi-model inference carried out using MuMIn (http://CRAN.R-project.org/package=MuMIn) within R. Models within a ΔAICc < 4 were compared using model weights and model averaging carried out using the zero method - where a parameter estimate of zero is used in models where that parameter is absent in averaging over all models in the top model set so as to decrease the effect sizes of predictors that do not occur in all models (Burnham & Anderson 2002). The intention was to compare the importance of different drivers (Nakagawa & Freckleton 2010) rather than to select the single best performing model.

RESULTS

Vegetation functional composition

There was little change in the weighted mean climate attributes between the two surveys (Table 1), except for a slight, but significant decline in that for TJan. This reduction was concentrated in a small number of sites along the east coast of Scotland. However, there was evidence that the weighted mean value for TJul increased more in areas where changes in annual mean temperature had been highest (t = 2.172, p = 0.030).

In contrast there was an overall substantial increase in EIV-N for Scotland of c. 0.15 units (Table 1). Again, there was regional variation, with site level changes ranging from -0.45 for Dornoch in the Moray Firth and +1.27 for Barry Links in Angus. In fact, four sites had an increase in EIV-N greater than 1, all for sites in south-east Scotland. Changes in EIV-N were correlated with cumulative nitrogen deposition between the surveys (t = 3.182, p = 0.002).

Table 1. Shifts in community weighted climate attributes, Ellenberg indicator values (EIV) and diversity measures between 1976 and 2010. TJan - January mean temperature (°C), TJul - July mean temperature (°C) and Prec - Annual precipitation (mm), N – nitrogen, R –reaction, df =2409.

	1976	2010	Δ	t	p
TJan	3.65	3.62	-0.03	4.559	<0.001
TJul	14.40	14.41	+0.01	1.457	0.145
Prec	1114.3	1113.6	+0.70	0.537	0.591
EIV-N	3.922	4.071	+0.149	7.788	<0.001
EIV-R	5.512	5.530	+0.018	1.358	0.175
Richness	18.71	20.14	+1.436	7.695	<0.001
Shannon	3.358	3.434	+0.076	3.796	<0.001

Individual species' trends

The list of increasing species was dominated by monocotyledonous species from mesotrophic or even somewhat eutrophic habitats (Table 2), the latter including *Arrhenatherum elatius* which showed the largest total increase in cover between the two surveys. The list of the decreasing species was dominated by low growing forbs of typically infertile habitats, though it was the common grass *Festuca ovina* that saw the largest overall reduction in cover.

Table 2. The mean cover (%) of the top ten increasing and decreasing species in 1976 and 2010 from the quadrats identified as fixed habitats in 1976 ranked by their weighting in the analysis. Species shown only if weights > 1.

Rank		1976	2010
	Increasing		
1	*Holcus lanatus*	3.30	6.93
2	*Carex flacca*	1.95	4.64
3	*Agrostis stolonifera*	4.92	5.29
4	*Trifolium pratense*	1.50	2.87
5	*Arrhenatherum elatius*	3.86	11.1
6	*Helictotrichon pubescens*	1.30	4.51
7	*Carex arenaria*	2.87	3.17
8	*Agrostis capillaris*	5.07	6.81
9	*Poa trivialis*	0.94	1.83
10	*Rumex acetosa*	0.58	0.94
	Decreasing		
10	*Euphrasia officinalis*	1.01	0.96
9	*Achillea millefolium*	1.23	1.17
8	*Cerastium diffusus*	1.33	0.26
7	*Thymus polytrichus*	3.37	2.74
6	*Danthonia decumbens*	3.09	0.22
5	*Carex nigra*	6.91	5.79
4	*Festuca ovina*	10.7	5.04
3	*Lotus corniculatus*	2.59	1.90
2	*Bellis perennis*	3.56	1.92
1	*Poa pratensis*	3.83	2.29

This impression from changes in the cover of individual species was confirmed by analysis of the traits of the increasing and decreasing species (Table 3). Increasing species in fixed habitats tended to be taller, have larger leaves, have high EIV-N scores, were abundant across GB and were getting commoner at a national level. Decreasing species tended to have a rosette or hemi-rosette growth habit, were rhizomatous and have a high EIV-R score. The picture for mobile habitats, where change is largely driven by succession, was different with increases in Specific Leaf Area and rhizomatous growth and decline in annual life history as a strategy. Increasing species were also those more common across GB and were increasing across GB.

Table 3. Significant regressions between species trends (response) and traits (predictors) for fixed and mobile habitats for overall, occupancy and abundance trends. + represents a positive relationship and – a negative one. +/- 0.05 ≥ p > 0.01, ++/-- 0.01 ≥ p > 0.001, +++/--- 0.001 ≥ p.

	Fixed habitats (n=505)	Mobile dune (n=160)
Vegetative traits		
Canopy height	++	
Canopy structure - erosulate		
Canopy structure - hemi-rosette	-	
Canopy structure - rosette	---	
Leaf size	+	
Leaf Dry Matter Content		
Life-span - annual		---
Specific Leaf Area		+++
Vegetative spread - rhizome	-	+++
Vegetative spread - stolon		
Environmental preferences		
Ellenberg N	++	
Ellenberg R	---	
Status		
Change index	+++	+++
GB abundance	++	+++

Species diversity

Across the two surveys species richness and Shannon diversity increased significantly, richness by an average of 1.4 species per quadrat (Table 1). The changes in species richness were inversely correlated to cumulative sulphur deposition ($t = 2.690$, $p = 0.007$), but not to cumulative nitrogen deposition ($t = 0.156$, $p = 0.876$). Shannon diversity changes were not correlated to either driver.

The more detailed multi-model inference approach, however, picked out land use drivers as the main influences on species richness (Table 4). Species richness declined where there had been disturbances such as large-scale blowouts that had occurred since the first survey (ΔBare, ΔOpenness, Openness), or where there is evidence of succession (ΔLitter, ΔWoody, Woody). However, it is promoted by grazing or increases in grazing (ΔGrazing, ΔLivestock, Grazing) as well as the previous presence of an Environmentally Sensitive Area (ESA).

Table 4. Summarised model averaging results for the multi-model inference of species richness and the movement of quadrats in ordination space for the Full data set. Estimates of parameter slopes are shown along with importance scores (sum of the Akaike weights over all of the models in which the term appears).

	Species richness	
	Estimate	Importance
Intercept	-0.810	
ΔLitter	-0.067	1
ΔBare	-0.096	1
ΔOpenness	-1.537	1
ESA	5.434	1
Mean Temp	0.090	1
ΔWoody	-0.077	0.14
ΔDensity	0.032	0.15
ΔGrazing	1.074	1
ΔLivestock	1.267	1
Grazing	0.853	1
Density	-0.199	0.71
Woody	-0.463	0.27
Openness	-0.040	0.07

DISCUSSION

Climate

The impact of increasing temperatures and rainfall appear to have had little impact on the coastal vegetation in this study. Whilst there is some evidence that the climate preference TJul of the vegetation increased more where temperature had risen most, the overall pattern is that of little change and, in fact, a reduction in the weighted temperature preference TJan. Detailed investigation at the site and quadrat level indicated this has been driven by succession dominated by inland species with low TJan scores such as *Pinus sylvestris* (Pakeman et al. 2015). Similarly, there was no evidence for a northward shift in species' ranges (Pakeman et al. 2015).

Atmospheric deposition

The significant overall increase in the Ellenberg Nitrogen score shows that there has been an overall eutrophication of coastal habitats between the two surveys (Table 1). The increase in EIV-N of 0.15 units is higher than the 0.02 units for "open countryside" quadrats in Countryside Survey for a similar time frame (1978 to 2007), but similar to the 0.15 for grassland habitats (acid, calcareous and neutral) in that survey (Carey et al. 2008). As these coastal habitats are rarely subject to agricultural inputs, it appears that atmospheric deposition of nitrogen is leading to an overall eutrophication of these habitats, especially as changes in EIV-N are correlated with nitrogen deposition over the period between the surveys. A consequence of this is that sites in eastern Scotland show higher impacts of eutrophication (mean change in EIV-N of +0.384, Pakeman et al. 2016) than those on the west coast, north coast and islands (mean change +0.062).

The nitrogen impacts on the east coast may have been exacerbated by the lack of grazing management of many east coast sites (Pakeman et al. 2017a, b), as grazing can mitigate the impact of experimentally added nitrogen to dune systems (Plassmann et al. 2009). Increased grazing of these impacted sites may be an option to reduce the impact of nitrogen deposition.

Land use change

For the fixed habitats land use change appears to have had dramatic impacts on both species richness (Pakeman et al. 2017a) and the functional characteristics of the species present (Pakeman et al. 2017b). Species richness has been maintained or even increased in areas where grazing livestock are still present, the west coast and islands, whilst it has declined on the east coast, especially where sulphur deposition has been high. On top of these richness losses, there has been a change in species dominance towards species characteristic of less disturbed habitats; namely taller, larger-leaved species with higher nutrient demands. Decreasing species tended to be those of short-turf and with a preference for more calcareous substrates. In addition, the species that increased were those already abundant across Great Britain and becoming commoner, suggesting a homogenisation of coastal vegetation with that of inland areas.

Implications for management and conservation

The drivers of change for coastal vegetation cross a range of scales. Whilst climate change impacts on composition appear small, these habitats are vulnerable to erosion caused by rising sea levels and increased storminess. Action, however, has to be taken at all scales from local to international. Considerable pollution impacts are evident across the period of the surveys. Action, primarily at a national level, is ongoing to reduce sulphur pollution (UK peak in 1968, Fowler et al. 2004), though its impacts were still evident on species richness. Similarly, nitrogen deposition peaked in 1990 (Fowler et al. 2004), but levels are still high enough to exceed critical levels for these nutrient poor ecosystems (Remke et al. 2009). However, local actions are likely to have the biggest impacts on conservation. The maintenance of diversity in the habitats of the west coast and islands is a consequence of their continued usefulness for grazing livestock. The absence of livestock from sites on the east coast is a consequence of neighbouring farms concentrating on intensive livestock rearing and cereals, and hence they don't need the poorer quality grazing offered by dune vegetation. However, as local action can have an effect, schemes to encourage farmers to put livestock back on to dune systems could be included in future agri-environment schemes to benefit biodiversity and to prevent succession to woody species that would require more labour-intensive control. The former ESA scheme may well have benefited vegetation species richness through direct support of appropriate land management and awareness raising of the importance of agricultural management for biodiversity.

However, the west coast and island systems are mainly managed by crofters – small-scale, part-time farmers. The current demographic trends in these relatively isolated areas suggest that populations will continue decline (Hopkins & Copus 2018) and this will have knock on effects on agricultural activity. Over the period of the survey it was clear that the number of active crofters had declined (Pakeman et al. 2011) and there will come a point where activity drops to a level which impacts on the conservation of these important habitats. The decline in activity has already impacted on the use of common grazing on neighbouring hill land. Without intervention, it is possible that the currently "healthy" coastal habitats on the west coast and islands may see the same loss of diversity evident on the east coast if grazing declines or is used inappropriately to manage these systems.

ACKNOWLEDGEMENTS

The resurvey would not have been possible without the many landowners/managers who gave their access permission. It depended on the hard work of the original survey team and the many people who helped with the resurvey: Jim Alexander, Joan Beaton, Rob Brooker, Roger Cummins, Antonia Eastwood, Debbie Fielding, Julia Fisher, Sarah Gore, Richard Hewison, Russell Hooper, Sally Huband, Antoinette Kriel, Jack Lennon, Rob Lewis, Ruth Mitchell, Emily Moore, Andrew Nolan, Katy Orford, Clare Pemberton, Dave Riach, Dave Sim, Jenni Stockan and Clare Trinder. The research was funded by the Esmée Fairbairn Foundation and the Scottish Government's Rural and Environmental Science and Analytical Services Division.

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Conservation or Preservation; the challenge of aligning scientific, public and policy understanding of dune ecosystems to deliver Favourable Conservation Status.

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Suggested Citation:

Ratcliffe, J., Rees, S., Bosanquet, S., Creer, J., Howe, M. and Litt, E. (2020). Conservation or Preservation; the challenge of aligning scientific, public and policy understanding of dune ecosystems to deliver Favourable Conservation Status. In L. Jones, T.A.G. Smyth & P. Rooney (eds.) *Proceedings of the 2017 Littoral conference 'Change, Naturalness and People'* (pp. 68 – 90).

ABSTRACT

Coastal sand dunes in England and Wales are failing to achieve Favourable Conservation Status. The history of dune management has been about stabilisation but the scientific basis for dune management policy has changed as a result of new evidence. A new paradigm of dune conservation places emphasis on bare sand, early successional stages and dynamic change. We illustrate this with examples of problems that traditional dune conservation management has created or exacerbated and compare this with recent work which challenges long-held conventions and now informs future dune restoration plans. The need for public understanding of the science, management and beauty of dynamic dunes is emphasized.

INTRODUCTION

European coastal sand dune Annex I habitats are not achieving Favourable Conservation Status (EEA 2015), with many 'Red List' habitat types vulnerable or near-threatened (Jansen et al 2016). In England and Wales, concerns about the long-term prospects for rare and specialised dune species such as natterjack toad *Epidalea calamita*, the dune form of fen orchid *Liparis loeselii* and assemblages of invertebrates and bryophytes have identified dunes as a conservation priority. The history of dune management has been characterised by the assumption that stability is the desire state but the scientific basis for that has changed as a result of new evidence and understanding of the pressures driving change, which result in over-stabilisation, in recent decades. We are beginning to understand that deliberate stabilisation has interacted with other pressures that cause declines in quality and condition. Shifts in approach are essential to ensure that legal drivers for conservation of habitats and species recognise that management practices and application of the Habitats Directive to sand dunes and other coastal environments must reflect their inherently dynamic nature. But new policy and management approaches will progress slowly without public support, and resistance to change also must be addressed in parallel with science-based shifts that also have to be embraced by the wider conservation community.

NATURAL DUNE RESOURCES: CURRENT STATE AND PAST LOSSES

Sand dunes are geomorphological systems which underpin diverse biological communities adapted to the challenging environments of shifting dry sand, topographic variation, seasonally wet slacks, low nutrients and salt spray. Their potential area is largely restricted to the coastal fringe where appropriate shoreline morphology, sediment supply, tidal and aeolian transport coincide (May & Hansom 2003). But such areas and locations have also been attractive for human development and have suffered disproportionate losses to agriculture, forestry, infrastructure, urban and recreational developments. For instance, in Wales, of an underlying 15,065ha of "blown sand" substrate 6, 867ha (46%) has been permanently lost to urban, industrial, military and agricultural development leaving only 8,198ha of dune, of which a further 1,610ha (20%) was lost to conifer afforestation (Blackstock et al 2010) (Table 1 and Fig. 1). In England, national data from the Sand Dune Survey of Great Britain (Radley 1994) indicates 11,897ha of recognisable sand dunes (of which 372ha are now planted with conifers and 375ha managed as fairways on golf courses). On the largest English dune system at Sefton (Merseyside) there is an underlying circa 3,000ha of blown sand (Pye 1990). Extensive dune systems were present here from around 4000BP but coastal change combined with losses to housing, agriculture, forestry, golf courses, airfields, roads and other developments has reduced the sand dune habitat to 1521ha (51%) (Natural England, 2014). These direct losses are compounded by indirect threats; coastal defences and navigation channel training walls endanger sediment supply and movement, invasive species smother natural habitats, nutrient pollution impoverishes the flora, water abstraction unbalances the delicate hydrological system, but most of all stabilization, whether deliberate or as a consequence of other factors, replaces these challenging dynamic environments with stable successional phases leading to the loss of the biota adapted to pioneer dune communities and other functional services of healthy dune systems (Jones et al 2011).

Table 1. Land cover of Welsh dune sand.

Welsh "Blown Sand" resource	15,065 ha
Sand dune habitat	6,200 ha
Conifer plantation	1,610 ha
Scrub	378 ha
Dune heath	10 ha
"Lost dunes"	6,867 ha

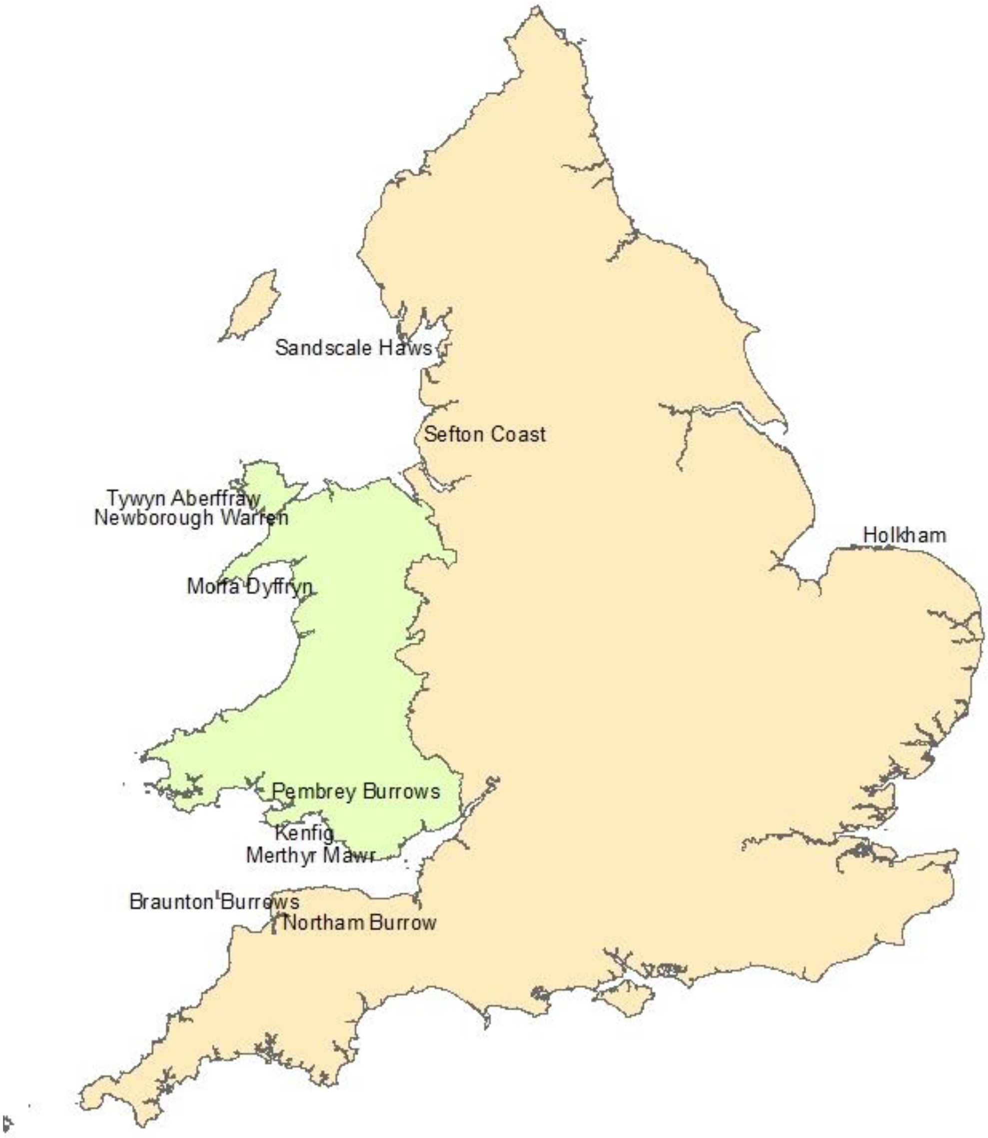

Figure 1. Dune locations referred to in text

HISTORICAL PERSPECTIVE

For centuries people have battled mobile sand and enforcing stability has been the objective, both for the dune surfaces and the shoreline.

In Wales, legends abound of land lost to the sand, such as the storms of 1331 at Kenfig and Newborough (where the erodibility of the sand may be linked with the arrival of Welsh refugees evicted from Beaumaris by Edward I in 1294, causing overexploitation of the land). Elizabethan laws forbade the cutting of marram grass lest the land be overrun again.

Expanses of bare sand evident at Newborough even 100 years ago, were compared to "*the deserts of Soudain*" [Sudan] (Greenly 1919) (Fig. 2) and described in classic ecological research from 1950-53 (Ranwell 1955) (Fig. 3). Local memories of roads blocked with sand live on in these communities today.

Figure 2. Newborough 1911 (Greenly E 1919)

Figure 3. Newborough 1950 (Ranwell D S 1955)

These are the landscapes our forebears knew, that ecologists and foresters considered as eroding, unstable and therefore undesirable and did all in their power to stabilise (Fig. 4). Doody (1985), provides a wide range of information about the basis of dune function and conservation value, but a specific quote given in the context of trampling damage stands out from the chapter on the conservation of sand dunes in Great Britain '..*the loss of mature dune vegetation cannot be replaced except in the very long term and the prevention of damage must be the first priority*', this chapter also concludes that the specialist plants that create them '*are vulnerable to forces which initiate instability. The resulting erosion not only threatens the survival of the biological interest of the system, but also the system itself*'. Despite other sections of the same report providing a foundation for dune management, it is the emphasis on stability and prevention of change that seems to have persisted in the context of conservation management. We were not alone in this thinking; throughout western Europe and beyond, ecologists and foresters advocated various means to stop erosion. They were successful; there are many examples but at Ranwell's research site, Newborough Warren, afforestation of over half of the 1300ha system from 1947 to 1965 to supply timber, along with marram planting and fencing of mobile dunes was typical management to prevent sand blow or erosion. On English dune sites, conifer planting was initiated earlier to stop sand movement onto residential land, such as at Sefton (Merseyside), or reclaimed farmland, as at Holkham (Norfolk).

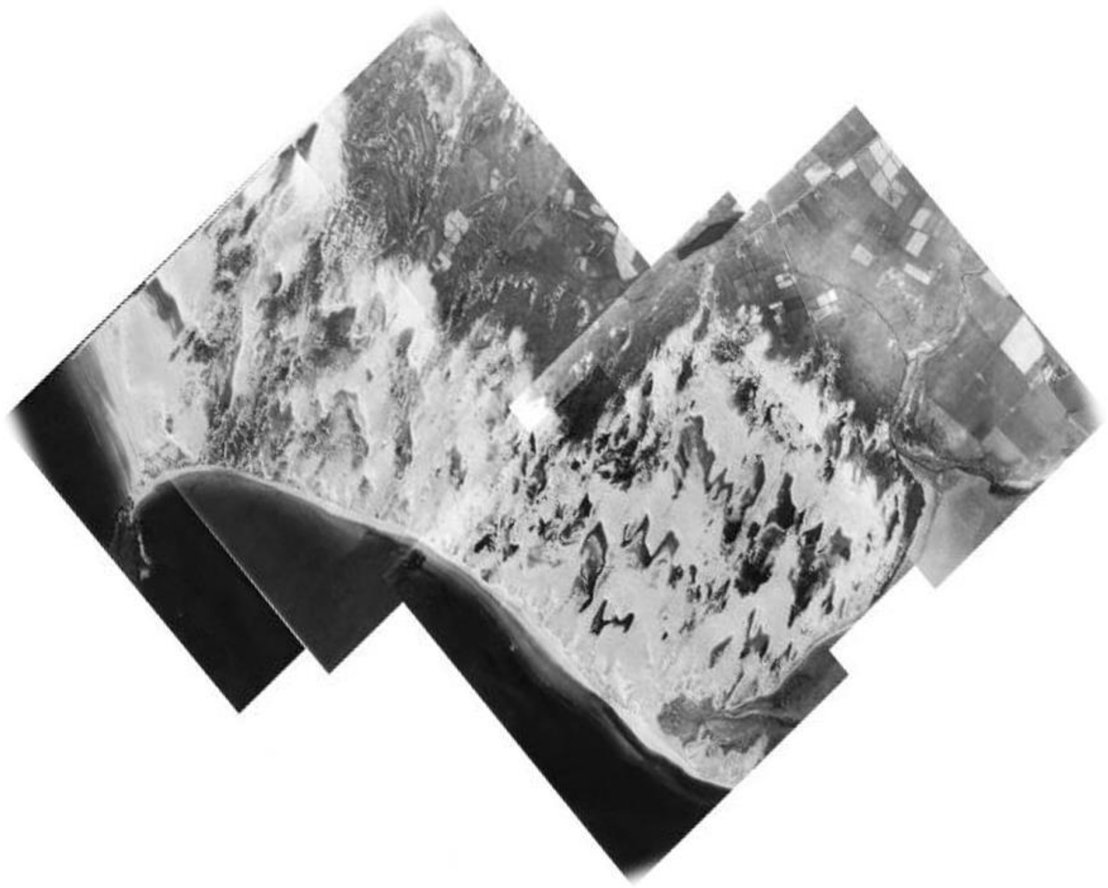

Figure 4 Aerial image Newborough dunes 1951, showing 50.6% bare sand

Figure 5 Aerial image Newborough dunes 2009 showing afforestation and 2.8% bare sand on remaining open dunes. (Getmapping plc and Bluesky International Ltd 2009).

What is notable however, is that it was not just under the pines that the sand was immobilised; the open dunes were also stabilising without such intervention (Fig. 5). We now know that there are many contributing factors to this stabilisation, which has occurred not just at Newborough, but across North-west Europe (Provoost et al. 2011). These include: decline in traditional management practices, atmospheric nitrogen deposition, subtle shifts in weather and climate, and the rapid decline in rabbit populations in 1954 due to myxomatosis. While the latter is often considered a major factor, research into the timings of vegetation change at Newborough has shown that the onset of stabilisation predated myxomatosis (Jones et al. 2010).

There is an old saying; "Be careful what you wish for!". Now that we have achieved stability, evidence shows that much of the ecological value of sand dunes lies in their dynamic, constantly changing nature, with early successional stages being particularly species-rich (Howe et al 2010). But people abhor change, especially unpredictable change, so there is a deeply rooted psychological resistance to dynamism.

PROBLEMS

The UK's report (JNCC 2013) on the condition of the sand dune resource, compiled under the 6-yearly Habitats Directive Article 17, notes a number of pressures and threats resulting in the overall Unfavourable assessment.

- Invasive species, such as sea buckthorn *Hippophae rhamnoides* and garden escapes such as Japanese rose *Rosa rugosa*.
- Nutrient enrichment, often from atmospheric nitrogen deposition but also from groundwater contamination.
- Lack of grazing, either by domestic stock or rabbits
- Hydrological change, resulting from drainage, afforestation and possibly exacerbated by climate change
- Scrub encroachment, often linked to lack of grazing
- Coastal defence measures, sometimes directly on site, sometimes elsewhere in the sediment cells, which reduce sediment supply
- Development on dunes; which is contributing to continuing loss of habitat, especially on non-designated sites.
- Loss of species associated with mobile sand and loss of diversity of vegetation types present

Many of these factors are linked. Atmospheric nitrogen deposition encourages vegetation growth, the stabilisation of bare sand and decline in species diversity (Jones et al. 2004). Similarly, nutrient inputs from groundwater cause changes in dune slack plant communities, even at relatively low levels of nitrogen (Rhymes et al. 2014). Drying out of slacks causes 'internal eutrophication' where shorter periods of winter inundation leads, via faster decomposition of soil organic matter, to increased soil nutrients and vegetation change (Stratford et al. 2014). Where such changes are not offset by increased grazing, scrub will develop (Hodgkin 1984) and invasive species take hold (Houston et al. 2001). But grazing alone does not create significant areas of bare sand, does not overcome the decline in pioneer habitats, and does not remove accumulated nitrogen from dunes (Jones et al. 2017).

IMPACTS OF OVERSTABILISATION ON BIODIVERSITY

Howe et al (2010) showed that in Wales, 680 red data book and nationally scarce invertebrates have been recorded from dunes. But of the 424 such invertebrate species specifically associated with dunes, 295 (70%) are dependent on early successional habitats; strandline, beach flora, marram, bare or sparsely-vegetated sand and pioneer slacks (Table 2). Species which were once widely distributed across these landscapes now cling to a narrow band of such pioneer habitat or have not been recorded on many sites in recent times. For example, the ground beetle *Broscus cephalotes* was once widespread across the Newborough Warren system but is now restricted to the strandline. The 34 species associated with pioneer slacks (Howe *et al*., 2010) have been particularly affected as this habitat has become scarce or even lost on some systems.

Table 2. Dune specialist invertebrate habitat associations in Wales (Howe et al 2010)

Habitat	**Associated invertebrate species**
Strandline & Driftwood	26
Beach Flora (*Cakile, Beta, Agropyron*)	7
Marram	35
Bare & Sparsely-vegetated Sand	194
Dune Slacks	51
Dune Grassland	65
Dung & Fungi	24
Ruderals & Bramble	7
Scrub & Carr	15
TOTAL	424

A similar fate has befallen bryophytes. For instance, Tywyn Aberffraw on Anglesey boasted 17 nationally rare or scarce notable species, more than any other Welsh dune system. Several of these, including blunt bryum, *Bryum calophyllum*, broad-nerved hump-moss *Meesia uliginosa* and golf-club moss *Catoscopium nigritum* are now presumed extinct in Wales while sea bryum *Bryum warneum* hangs on in one slack. These are species of bare damp base-rich sand with low, open, early-successional vegetation which is now rare on this site, in common with other dune systems. This picture of decline as a result of stabilisation is repeated at all of Wales' bryophyte-rich dune systems: Newborough Warren retains only 9 of its 16 recorded Nationally Rare and Scarce bryophyte species, Morfa Dyffryn 8 of 14, Kenfig 8 of 12 and Pembrey Burrows just 5 of 11.

The fen orchid *Liparis loeselii*, one of the most threatened plants in northern Europe, occupies winter-flooded, open dune slacks. In England this species was last recorded at Braunton Burrows in the 1980s. It is now considered extinct from the site, having only been recorded for the first time in 1966 (Willis 1985). Historically recorded from 8 sites in Wales supporting 90% of the UK resource, with populations of tens of thousands, fen orchid had declined by 2014 to just 44 plants at Kenfig Burrows. Changes to the associated vegetation density were considered to be a factor in its decline.

Webb et al (2010) set out habitat requirements of the listed species of principal importance in England, published under section 41 of the Natural Environment and Rural Communities (NERC) Act 2006. Coastal sand dunes support 72 of the species. Some of these are now restricted to dunes with one species, fen orchid, as described above not seen on English dunes in the last 30 years. Habitat requirements for these species were analysed (Fig 6), and for over 60% of these bare ground was identified as an important niche, highlighting the complexities of this habitat and the risk to species from excessive dune stabilisation.

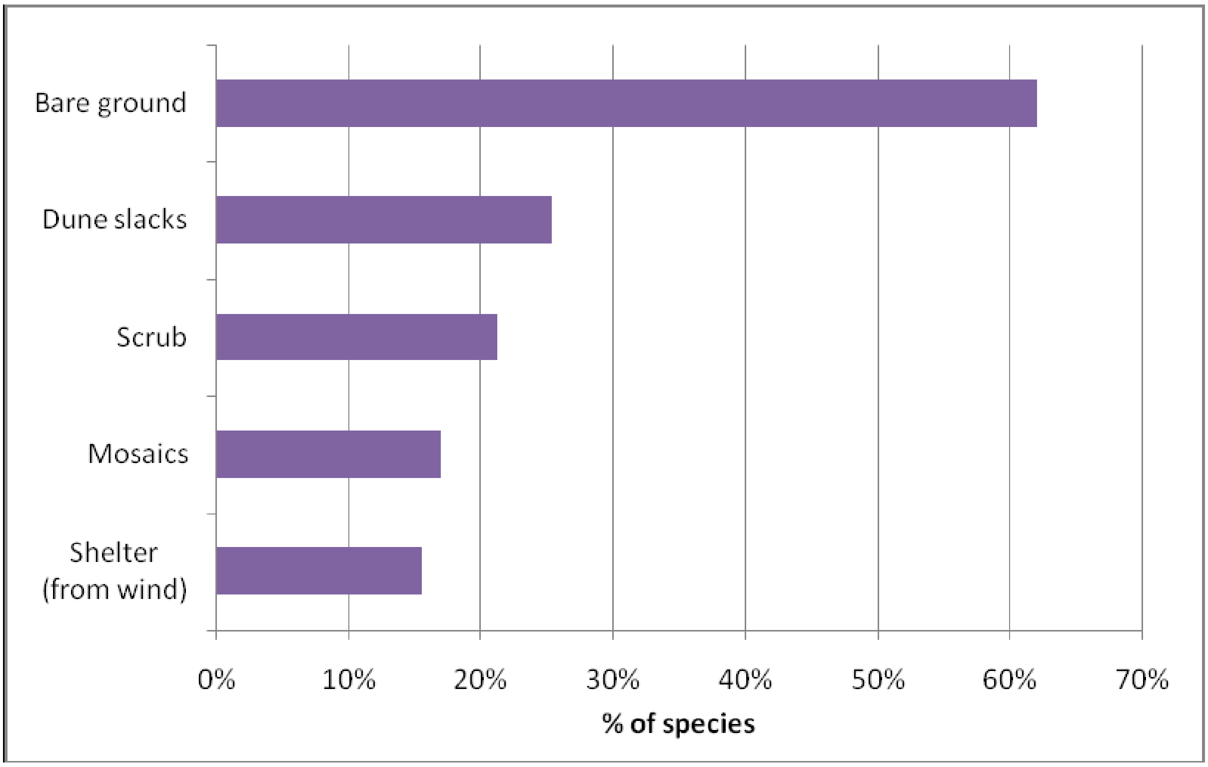

Figure 6. Habitat/niche requirements of Section 41 species associated with coastal dunes (Webb et al 2010).

In a challenge to conservation managers, Howe et al (2010) suggested that a healthy dune system for invertebrates should include 30% pioneer habitats of which 10% should be bare sand. Such standards would not seem incompatible with the requirements for other specialist dune species. In reviewing this and other information, Natural England has suggested that ‘fixed dunes’ in good condition could have up to 25% bare sand rather than the 10% bare sand initially recommended in the Common Standards Monitoring guidance for sand dunes (JNCC 2004). The guidance needs reviewing based on the increasing knowledge of how species are now known to use dune habitat niches. Some of the numbers make a compelling case to support a higher level of openness in our dunes.

Management measures to counter over-stabilisation, nutrient enrichment, hydrological change and invasive species issues all need integrating with use of dunes by the public and maintaining other functions such as flood risk management to achieve and sustain improvement in habitat and species condition. But the evidence about ecological requirements of sand dune species and habitats is increasingly at odds with management advice which promotes dune stabilisation.

SUCCESSES AND SUPPORTING EVIDENCE

There is an increasing body of evidence geared towards improving dune conservation management which is influencing the wider issues of awareness and practice. Collaboration between academics and practitioners has led to some important lessons and examples to draw from. It is known from monitoring of exclosures set up 50 years ago at Sandscale Haws in Cumbria, that lack of any intervention leads to initially open vegetation in slacks turning into scrub and trees. Fenced plots, established in 1967 to exclude sheep and cattle, but not rabbits, were monitored by Brathay Field Study Centre from 1968 to 1974 (National Trust, Personal Communication). An unpublished 1975 report highlighted changes in both unfenced and fenced plots, but the latter had more extensive vegetation cover, loss of light-demanding short species, more litter, a lower rate of new plant colonisation and increased vigour of *Salix repens*, *Festuca rubra* and *Holcus lanatus*. Grazed plots retained *Euphrasia nemorosa*, *Cerastium* sp., *Linum catharticum*, *Luzula campestris*, *Sagina maritima* and *Trifolium repens*. Three of the fenced plots have been maintained and in 2017, apart from the wettest location, these were dominated by tall trees and shrubs in contrast to the shorter surrounding areas (N Forbes, *pers comm*).

Experimental dune management at several sites in Wales has shown that this decline in biodiversity is reversible. Guided by an appraisal of their future under climate change and sea-level rise scenarios (Saye & Pye 2007) and detailed geomorphological appraisal (Pye & Blott 2012), Natural Resources Wales (NRW) embarked on a programme; first in avoiding active stabilisation of dunes, then in actively intervening to re-mobilising them. Various methods of remobilisation were considered including creation of scrapes and turf stripping; breaches (notches) in the frontal dunes, removal of conifers, realignment of roads and restoration of rabbit warrens.

NRW selected three sand dune complexes for trial rejuvenation works; Kenfig Burrows and Merthyr Mawr Warren (both part of Kenfig SAC) and Newborough Warren (part of Abermenai to Aberffraw Dunes SAC). Mechanical intervention was undertaken, consisting of; excavation of notches in frontal dunes, new deflation basin and troughs; stripping of rank vegetation in dune slacks and dry dunes, localised placement of excavated sand, and removal of some planted conifers from frontal dunes. Table 3 lists the sites and total bare sand created during the works. Additional gains have been made by subsequent aeolian movement of sand.

Table 3. Pilot dune remobilisation projects in Wales

Sand dune site	Bare sand (ha)					
	1940s-50s	2009 (% site)	Created *via* rejuvenation	2015 (% site)	% change 2009-2015	Aeolian gain by 2016
Kenfig Burrows	154 (18%)	4 (0.5%)	10	14 (1.5%)	+250%	1.02
Merthyr Mawr	218 (39%)	20 (3%)	8.5	28.5 (5%)	+42.5%	0.91
Newborough	691 (51%)	40 (3%)	14	54 (4%)	+35%	4.37

Radical turf stripping at Kenfig, where fen orchid was on the verge of extinction, has successfully rejuvenated critical slacks and from a low of just 44 plants in 2014, 1012 plants were recorded in 2017[1]. The nationally scarce short-toothed hump-moss *Amblyodon dealbatus*, has also reappeared in similar turf-stripped areas at Pembrey and Kenfig. Examination of the soil indicated that this bryophyte forms a long-lived diaspore bank which could be germinated in the laboratory (i.e. long after the species has not been seen at a site it may still be present, sitting dormant below ground). Most viable spores are within the upper 15 cm of soil. (Callaghan 2017). Similar sand scrapes at Braunton Burrows and other sites in Devon have shown how other plant species such as Sea stock *Matthiola sinuata* and Water germander *Teucrium scordium* respond to this treatment. At Northam Burrows Country Park in Devon, where scraping began in winter 2014/15, Water germander was recorded for the first time in many years in the following summer.

Removal of conifers and rejuvenation of mobile dunes and slacks at Newborough Warren has also resulted in a rapid response from vegetation and invertebrates of open dunes. Removal of conifers was conducted as an experiment, with carefully designed replication of 'treatments' which aimed to test which restoration approaches worked best (e.g. removal of trees + stumps + litter, removal of trees only, removal of trees where there was some remnant dune vegetation, and control areas with no tree removal). In all treatments, the recolonising plant communities are much closer to mobile dune vegetation types than the controls (Wallace & Jones 2017), showing the benefit of structured evaluation and monitoring. In 2013/14 turf was stripped from three old slacks and subsequent annual vegetation monitoring shows a rapid return of early successional plant species, while maintaining a high percentage of bare sand (Jones et al. 2015). Monitoring of invertebrates in these restored slacks using pitfall traps and visual searches demonstrated that nine of the 16 beetle species specialists recorded on this dune system had quickly colonised the damp, exposed sand; *Bembidion pallidipenne,*

[1] 1572 plants of *Liparis loesellii* were recorded there.in 2018

Bledius longulus, *B. subniger, B. fuscipes*, *B. longulus, Dyschirius politus, Dyschirius nitidulus, Gabrius osseticus* and *Heterocerus flexuosus*, some of them in very large numbers. The invertebrate communities of artificially-created slacks are very similar to those on natural pioneer slacks found on Morfa Dyffryn (Loxton, 2018), the most dynamic dune system in Wales which contains large areas of pioneer slack. Colonisation of exposed sand can happen within months of the completion of the management work with specialist bees and wasps in particular exploiting areas of newly-created bare sand for nesting and foraging on ruderal plants on disturbed substrates. The Vernal Bee *Colletes cunicularius* has been able to colonise such excavations, nesting in sand banks on Newborough Warren and Kenfig Burrows.

These successes are based on a new paradigm of dune management. While many British dune conservationists continued to favour stability of dune ecosystems, other European countries have been exploring the concepts of dynamic, heterogenous systems for some time (van Zoest 1992). Meetings of the European Union for Dune Conservation / European Union for Coastal Conservation EUDC/ EUCC and the Littoral conferences have encouraged this debate enabling researchers and practitioners to "think the unthinkable", and then test these thoughts for real (Arens & Geelen 2006). These developments paralleled similar ideas in woodland ecology in the UK, perhaps heightened by the "Great Storm" of 1987 which 'devastated' apparently timeless woodlands in the south of England and led to an appreciation of extreme events as major drivers of dynamism in woodland ecology. Throughout the 1990s, the role of destabilising events in driving dune ecosystems also came to be more appreciated. It was discovered that rather than a steady-state stable ecosystem, dunes went through cycles of stability and change (Bailey & Bristow 2004).

LEGAL DRIVERS

We differentiate between simple <u>preservation</u> and the active <u>conservation</u> of ecosystems; the former is static, the latter is dynamic. Conservation bodies, especially statutory bodies, have legally defined duties, powers and responsibilities. In the UK, these duties include:

1. National Parks and Access to the Countryside Act 1949 power to designate national Nature Reserves and to manage them primarily for conservation, research & education and secondly for recreation that does not compromise their primary function.
2. Wildlife & Countryside Act 1981 duty to notify all sites which are of special interest for flora, fauna, geological or physiographic features, includes a duty "to have regard to ecological change". Selection of biological SSSIs is guided by selection guidelines: a recent revision of the

Part 1 principles (Bainbridge et al 2013) strongly emphasises the need for individual chapters to enable sites selection to take account of dynamic change, and structure and function.

3. The EU Habitats Directive (1992) and the Conservation (Habitats and Species) Regulations 2017 duties to designate Special Areas of Conservation, to avoid deterioration to habitat and species features listed in the Annexes, maintain the coherence of the Natura 2000 network (SACs and SPAs) and to manage appropriately to achieve Favourable Conservation Status.
4. Town & Country Planning Acts and policy to protect designated sites, habitats and species.
5. Natural Environment and Rural Communities Act 2006 s40 duty to conserve biodiversity
6. Environment (Wales) Act 2016 s6 duty on all statutory bodies "*to maintain and enhance biodiversity*"

There are also non-statutory drivers and policies which inform management approaches. These include

7. EU Biodiversity Strategy to 2020: Target 2 requirement for member states to restore 15% of degraded habitats.
8. UK Shoreline Management Plans
9. UK Biodiversity (Habitat) Action Plans
10. Biodiversity 2020: A strategy for England's wildlife and ecosystem services
11. The Nature Recovery Plan for Wales (2016)

Key amongst these statutes is the EU Habitats Directive, itself a derivative of the Bern Convention on the Conservation of European Wildlife and Natural Habitats (1979) (to which Britain is directly a signatory) which defines favourable conservation status of a habitat when:

1. its natural range and areas it covers within that range are stable or increasing, and
2. the specific structure and functions which are necessary for its long-term maintenance exist and are likely to continue to exist for the foreseeable future, and
3. the conservation status of its typical species is favourable

The first of these requirements has been interpreted as requiring no net loss of any habitat area; but for sand dunes fluctuating losses and gains are an inherent feature of dynamic change. Thus the second factor, the conservation of structure and function, is imperative. It recognises that certain habitats may change from one to another and initiate succession in order to be sustainable in the long term. Dynamic habitats naturally fluctuate over time; for instance, in recent years dune grasslands have increased in extent, reducing the areas of more dynamic stages. To reduce the impacts of human-induced pressures, we should be seeking management which ensures the continuity of early successional stages within fixed dune grassland and creates new dune slacks as well as restoring movement to 'mobile' dune zones. In this context it's better to consider cycles of management that work with climatic and coastal processes. For example, to re-excavate ponds that are then kept open by winter flooding or summer winds to sustain their quality and support typical species.

Arguably, the original subdivision of the overall dune system habitat into fine habitat divisions (fore-dune / yellow dune / slacks / dune grassland / heath etc.) in the Directive, as set out in the EU Interpretation Manual (European Commission 2013) may be at the heart of the issue. Management needs to consider these fine habitats within an overarching dune habitat class which allows natural internal variation and dynamism. An action arising from the workshop on dunes and estuaries at the 2nd EU Atlantic Biogeographic Seminar, 25-27 October 2016 (Anon. 2017; Houston, this volume) is to '*incorporate dynamics into the interpretation of Favourable Conservation Status*'. This may help to address the need to consider dunes as a complete system. We need to gather and share evidence to support a better understanding of how dune processes create sustainable improvements in conservation status.

The Habitats Directive requires Member States to put in place "*the necessary measures corresponding to the ecological requirements of the features*" of Natura 2000 sites. Ecological requirements for fixed dunes and dune slacks have been set out on the Natura models (Houston 2008a, Houston 2008b) Targets and management must secure the "*specific <u>structure and function</u> which are necessary"* for the conservation of the dunes; the *structure* being the full representation of the typical dynamic dune zones from beach to hinterland, the *function* being the movement of sediments and the change associated with this. At a LIFE Platform event in 2016, a range of LIFE-funded projects since 2009 from The Netherlands, Belgium, France, Italy, Spain, Latvia, Sweden, Denmark and Ireland showed how, at a site level, this could be successfully achieved. Of note however was the very limited number of LIFE-funded projects on UK dunes, so the challenge now is to apply this learning to dunes in England and Wales. A priority is to use new evidence about how to address the impacts of Nitrogen deposition which have been clearly shown to be a major driver in decline in quality of dune vegetation (Jones et al. 2004; Remke et al. 2009).

PERCEPTIONS ABOUT DUNE STABILITY AND CONSERVATION

For hundreds of years (at least since the time of Elizabeth I) stabilising dunes has been the primary societal objective. People have planted pines on them, repaired them with marram grass, chided children for running down them, guided people on the path and told them "keep off the grass!". Many of the conservation professionals of today began their careers planting marram grass, often as volunteers, and the prime organisation for conservation volunteers is the British Trust for Conservation Volunteers (BTCV), now "The Conservation Volunteers". Their dune management handbook (Brooks 1979, Brooks and Agate 2005) has long been the standard text for how to stabilise dunes. A practical manual, it is now somewhat dated as it fails to recognise the importance of dynamic systems or of bare sand in the biology of dunes. Similarly, the Institute of Terrestrial Ecology (ITE) Coastal Dune Management Guide (Ranwell & Boar 1986) presumed that erosion is undesirable, and that vegetation cover should be maintained wherever possible. It too is available on the web and has been downloaded thousands of times; so it would appear that the next generation of conservation managers are being trained to repeat these lessons. Given this background literature, it is no wonder that conservationists and the public are confused about the new paradigm of dune conservation. Indeed, many conservation practitioners have taken some convincing of the need for change[2]. Even to the present day, conservation managers still consider control of visitors to be a key management objective on sand dunes, rather than a tool to achieve other objectives.

The UK Sand Dune and Shingle Network worked with Natural England in 2013 to collate published material on dune dynamics as part of a staff 'toolkit' (Natural England unpublished report). This highlights the importance of dynamic processes for both dune biodiversity and geomorphology, the latter being relevant to the role of dunes in flood risk management.[3]

The public is also understandably confused about the conservation of dunes. There are tensions between our current knowledge and former practice and advice. Deterioration of habitats is often slow and long term; nobody sees the grass growing and the bare sand shrinking. It is only when old photographs are examined that the reality and magnitude of change is apparent. Dynamic dune processes are difficult to predict and to explain, and there is a natural human conservatism and resistance to change, perhaps summed up in the expression of Hilaire Belloc *"Always keep a hold of nurse for fear of finding something worse*"! This is compounded by the fact that while specialist dune species need open conditions, management to create those conditions often seems destructive (figure 7). And if the public want advice on dune conservation, there is no shortage of erudite literature and

[2] Fortunately, a revision of the guidance for dune managers has now begun.

[3] In 2018, the Environment Agency reviewed the evidence base to raise knowledge of how dunes should be managed to help manage flood risk in a way that works with natural processes (WWNP). WWNP involves implementing measures that help to protect, restore and emulate the natural functions of catchments, floodplains, rivers and the coast.

management guidance reflecting a legacy of studies about stabilisation which can support conflicting views (Ranwell & Boar 1986).

Figure 7. Dune slack turf stripping, Newborough Warren, Anglesey

There is a need for a concerted information campaign to recast the public's understanding of coastal processes and dune habitats. Public understanding of plastic pollution has been galvanised by compelling images; memorable images of dune issues need to be established with key players including local residents and influential decision makers. Dialogue across the board is vital, and a range of people need to be involved in communications and engagement work at both national and local scales.

Different conservation specialisms also have different perspectives. Change requires a robust assessment of the costs and benefits and sometimes a longer time perspective for assessment. Many conservationists (and the public) are nervous of the short-term destruction apparent in remobilisation or rejuvenation of dunes for open habitat. For instance, the creation of better sand lizard habitat (yellow and semi-fixed dunes) may involve risk to individual animals but should be assessed against overall population gains.

FUTURE PLANS

In England and Wales there is an urgent need to do more active conservation, and at larger scales, to achieve more dynamic dunes and to embed this approach as an accepted paradigm of dune management in policy and in public minds. Projects are being developed by the country conservation agencies (NRW and NE) in association with the National Trust, Ministry of Defence, Plantlife, The Wildlife Trusts, private landowners and local authorities along with other interested organisations. Project bids were made in 2016 and 2017 to UK and European funding streams for managing key sand dune complexes in England and Wales[4]. The work will be a partnership of organisations to deliver effective habitat management supported by public engagement work and citizen science, at a scale that can result in a big impact, providing transferable learning across all dune sites. Injection of such funding is essential to enable large scale, dedicated management projects, to inform and stimulate longer-term sustainable benefits. We hope that the planned work programme from 2018 to 2023 will inspire and engage dune managers and the public, rejuvenate a key suite of dunes and restore important habitats for species.

IMPLICATIONS FOR MANAGEMENT: CHALLENGES, OPPORTUNITIES AND LESSONS LEARNT

Dune management should therefore be based on some key principles:

- Geomorphology is the key to dunes; the landforms determine the biota
- Structure and Function = zonation and active processes
- System management requires a holistic approach and long-term perspective
- Joint planning and design of restoration measures by practitioners and academics
- Structured monitoring of restoration actions both before and after, to help understand reasons for success or failure some years down the line.
- Taking the public with you by informing and educating

Better dune management requires a policy review, and public understanding and acceptance of change that is compatible with legal obligations for dune conservation.

Dune management today is challenged by our historic focus on sand stabilisation. By building on the pioneering dune rejuvenation work in Welsh and English sites that are beginning to show results, we will improve managers' knowledge and promote wider public understanding of a more dynamic

[4] The Sands of LIFE (SoLIFE) project in Wales was initiated in September 2018 and DuneLIFE in England in the same year.

management approach to benefit dunes. The new Coast Paths in England and Wales offer increased access to many dune areas and opportunities to engage with significant numbers of people. Current scientific knowledge should develop further, by closer working between practitioners and academics; each have a lot to learn from the other. Public engagement activities can further support this, for example by making more use of citizen science linked to academic studies and monitoring, which can bring multiple benefits to all parties involved. We emphasise the importance of having effective partnerships and promoting learning more widely. What is vital in this is public buy-in. That will only come from engaging the public by helping them appreciate the beauty and importance of our dunes, the latest scientific understanding of how dunes function, and the need for management to achieve favourable conservation status.

ACKNOWLEDGEMENTS

We have benefited from discussions with numerous colleagues across Europe. The work of site managers in trialling new management techniques, often in challenging conditions, has been invaluable. Dr Laurence Jones (CEH) offered valuable comments on an earlier draft.

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

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Suggested citation:

van der Hagen, H.G.J.M., van Rooijen, N. & Schaminée, J.H.J (2020) Forty years of rabbit influence on vegetation development in the coastal dunes of Meijendel, the Netherland. In L. Jones, T.A.G. Smyth & P. Rooney (eds.) *Proceedings of the 2017 Littoral conference 'Change, Naturalness and People'* (pp. 90 – 116).

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 J*acobaea 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., 2020). 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

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).

INTRODUCTION

In 1975, eight exclosures were installed with rabbit proof fence in the Meijendel (52º7'N; 4º20'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.

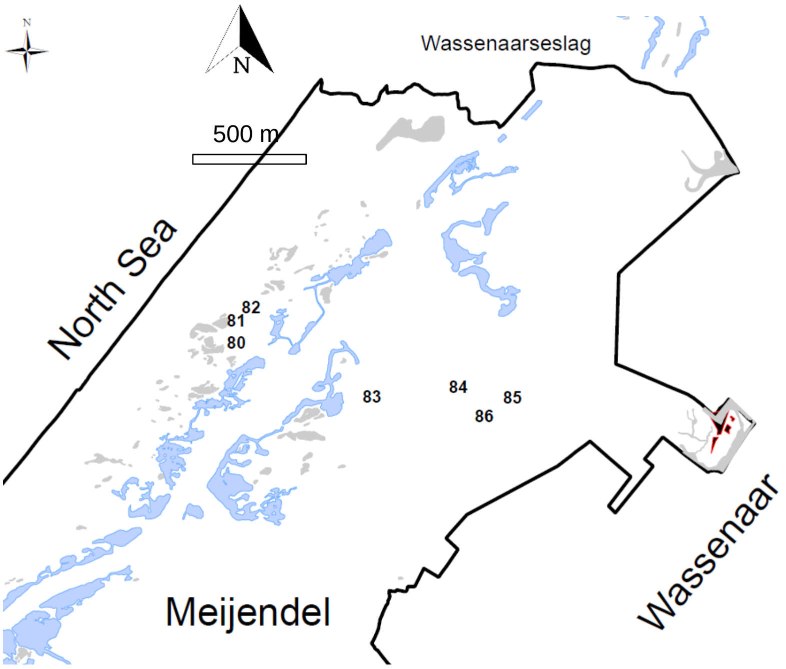

Fig. 1. Locations of the exclosure and reference plots within the outline boundaries of Meijendel (west-east distance 3 km). Blue shades: infiltration ponds; grey shades: dune slacks. 80, 81= Phleo-Tortuletem; 82= Anthyllido-Silenetum; 83= Hippophao-Ligustretum; 84, 85, 86= Basal Community Calamagrostis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

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?

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 60ºC (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.**		**H.L.**		**BC-C**	
	Excl.	Ref.	Excl.	Ref.	Excl.	Ref.	Excl.	Ref.
Plot number	80 & 81	80 & 81	82	82	83	83	84, 85 & 86	84 ,85 & 86
Plot size	5x5	5x5	4x10	6.5x10	5x5	5x5	5x5	5x5
Lollipop images	☼ 	☼ 						
Number of sites	2	2	1	1	1	1	3	3
General features								
Cover (%)								
Total	**91.5**	**45**	**90**	**50**	95	90	95	85
Tree	**-**	**-**	**-**	**-**	-	-	**50**	**3**
Shrub	**8.5**	**23**	**70**	**3**	70	70	**23.3**	**3.7**
Herb	**55.0**	**11.5**	**30**	**45**	40	50	40	30
Moss	**65**	**27.5**	**0**	**30**	**40**	**20**	**20.7**	**61.7**
Height								
(High) shrub (m)	0.8	0.5	**1.5**	**0.8**	3	2	**3**	**1.3**
Low shrub (m)	0.2	0	**0.5**	**0**	1,5	1.5	0.5	0
(High) herb (cm)	20	15	**30**	**10**	40	30	**50**	**26.7**
Low herb (cm)	7.5	7.5	5	5	10	10	**20**	**6.7**
Average number								
species	**27.0**	**20.5**	**37**	**49**	**14**	**15**	**14.3**	**20.7**
tree/shrub species	**1.5**	**1**	**6**	**2**	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. 2). 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%; 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 (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.3). They became dominant in 2015 (Fig. 3). 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 3). 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; appendix Table 1b). *Cirsium vulgare* expresses a ruderal aspect indicating a higher nutrient level in the exclosure (Table 2).

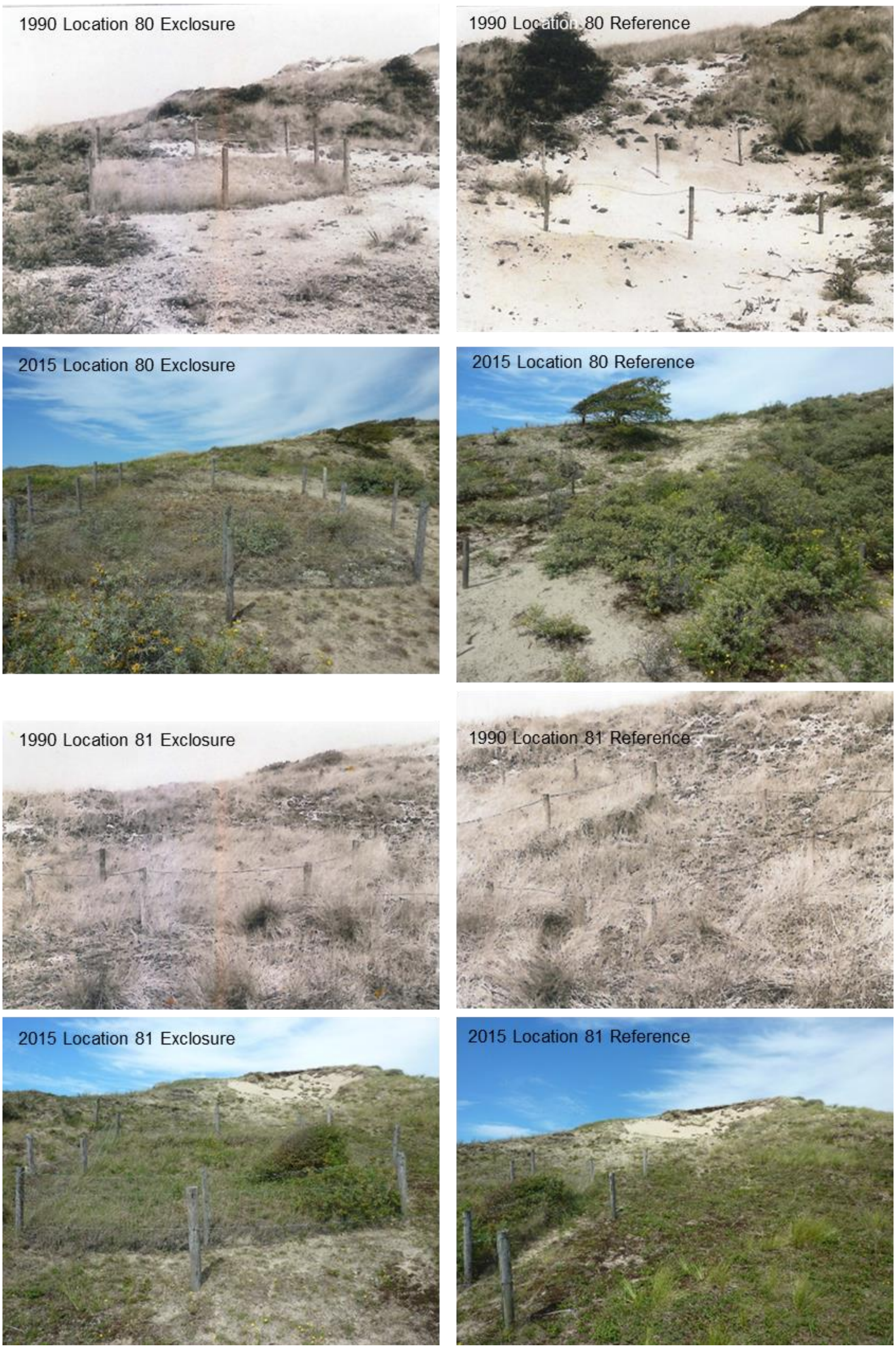

Figure 2. Photographs of the exclosure and reference plots 80 and 81 with southern exposition with a Phleo-Tortuletum plant community in 1990 and 2015.

Figure 3. Photographs of the exclosure and reference plots 82 on the northern slope with the Anthyllido-Silenetum.

LOCATION 83: GRASSLAND – HIPPOPHAE SHRUBLAND

In 1990, lateral ingrowth of *Hippophae rhamnoides* has occurred in both the exclosure and reference plot (Fig. 4). Also in 1990 derived from the photograph (Fig. 4), 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; appendix Table 1c) indicating disturbance of the soil.

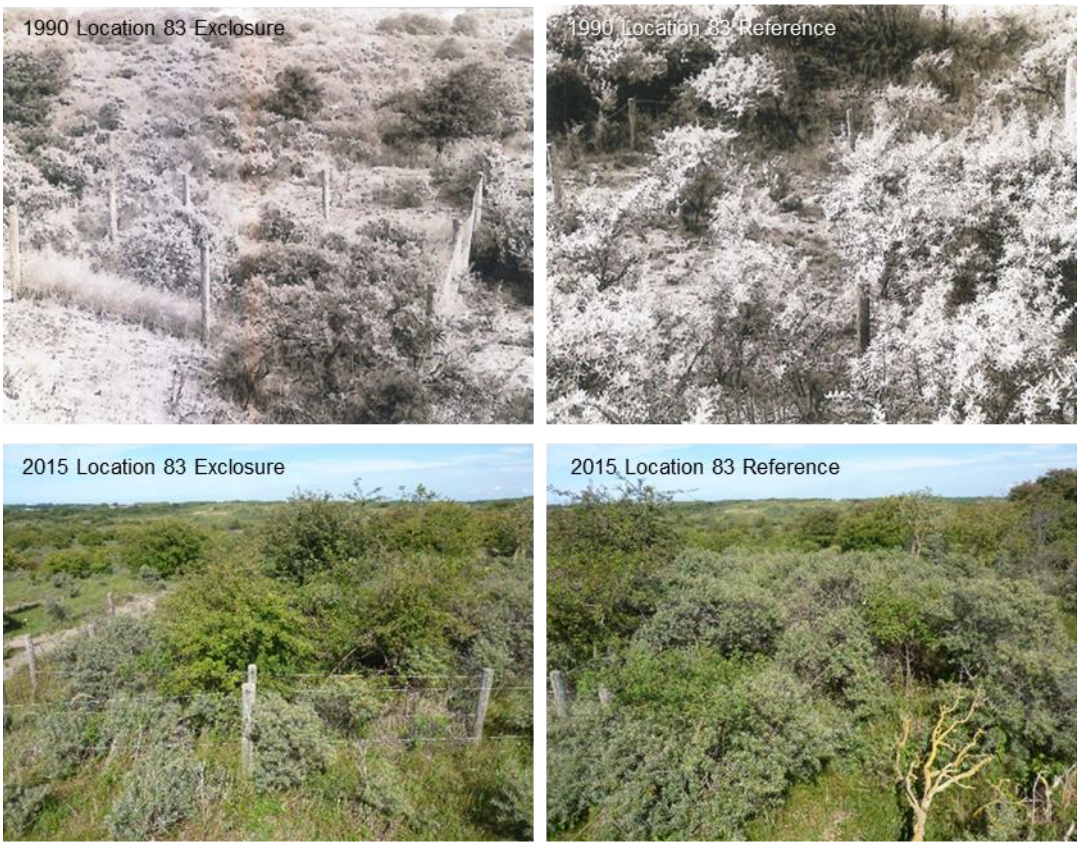

Figure 4. Photographs of the exclosure and reference plots of 83 *Hippophae rhamnoides* shrubland (Hippophao-Ligustretum) in 1990 and 2015.

LOCATIONS 84, 85, 86: DECALCIFIED DUNE GRASSLAND – FOREST

In 1990, the vegetation in locations 84 and 86 (Fig. 5) 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. 5); 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. 5). 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; 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.

Figure 5. Photographs of the exclosure and reference plots of 83 *Hippophae rhamnoides* shrubland (Hippophao-Ligustretum) in 1990 and 2015.

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 = Gentina cruciate; 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.curtisii = 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.		**A.S.**		**H.L.**		**BC-C**	
	Excl.	Ref.	Excl.	Ref.	Excl.	Ref.	Excl.	Ref.
Plot number	80 & 81	80 & 81	82	82	83	83	84, 85 & 86	84, 85 & 86
Number of sites	2	2	1	1	1	1	3	3
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						
Shrub species			C.mono L.vulga S.repen Q.robur R.catha	C.mono L.vulga				
Grass cover (%)					10	36		
Shrub cover excluding Hipp. rhamnoides (%)					40	2		
Ruderal indicator [a] Disturbance indicator [b]			Cirsium vulgare[a]	-	-	Cyno off[b] Sen jac[b]		
(High) tree layer (m)							8	2*
Anthyllido-Silenetum specific features								
# typical species			11	19				
Species presence (typical examples)			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				
# Viola species			0	4				
Species presence				V.canina V.hirta V.rupest V.curtisii				

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. 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., 2020), 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 60ºC (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. 2 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; 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. 4). 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., 2020).

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. 5). After the introduction of livestock in autumn 1990, the amount of (dead) biomass was reduced significantly resulting in the short grazed 2015 situation (Fig. 5; 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. 5).

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 Figs. 2 - 5). Fig. 6 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).

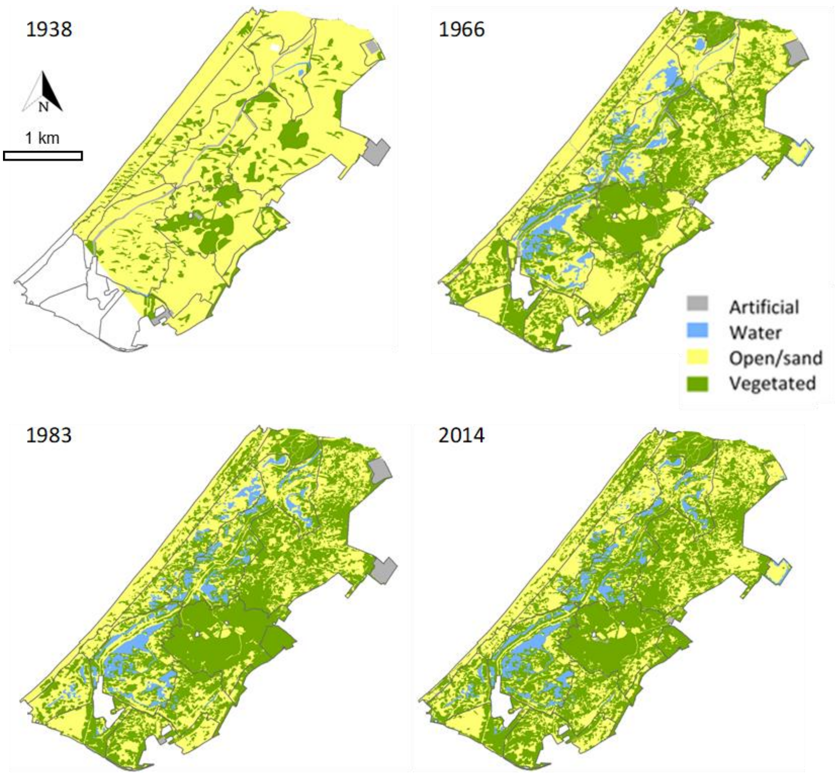

Figure 6. Development of the open/sandy vegetation versus shrubland/forests in Meijendel (± 2.000 ha) in 1938, 1966, 1983 and 2014 based on aerial photographs. The myxomatosis outbreak was in 1954; the Rabbit Viral Hemorrhagic Disease outbreak was in 1989.

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 herewith 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 et al., 2019) for the Meijendel area alone. Other dune areas in north-western Europe will most probably face the same situation.

ACKNOWLEDGEMENTS

First of all we thank Dunea duin & water for financing this study and Georgette Leltz in particular for stimulating innovative research. The organizers of the 2017 Littoral conference in Liverpool (UK), in particular Paul Rooney and Laurence Jones, are gratefully acknowledged for the opportunity to present this paper. We thank Maarten Breedveld for the images of figure 6.

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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 (m2)	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	
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 caryophyllacaea		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 (m2)	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**	
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
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 (m2)	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
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.
Date (year/month/day)	20150701	20150701	20150701	20150706	20150706	20150706
Area (m2)	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
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
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