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Changes in landscape and vegetation of coastal dunes in northwest Europe: a review

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Abstract In coastal dunes, landscape changes are a rule, rather than an exception. This paper gives an overview of changes in landscape and vegetation with a focus on the past century. The history of dunes is characterised by phases of sand drift, alternated with geomorphological stability. The historical development of dune woodland during these stable phases has been documented for sites all over Europe. Vegetation reconstructions of historical open dune habitats however is very difficult due to limited preservation of fossil remains. People have drastically altered coastal dune landscapes through centuries of exploitation and more recently development of the coast. Historical land use has generally pushed vegetation back into a semi-natural state. During roughly the past century a tendency of increasing fixation and succession is observed on coastal dunes throughout northwest Europe. Six causes of change are discussed. 1) Changes in land use, mainly abandonment of agricultural practices, have led to the development of late successional stages such as scrub and woodland. 2) Crashing rabbit populations due to myxomatosis in the 1950s caused vigorous grass growth and probably stimulated scrub development. 3) A general tendency of landscape fixation is observed due to both natural and anthropogenic factors. 4) Eutrophication, mainly due to atmospheric nitrogen deposition is clearly linked to grass encroachment on acidic but also on some calcareous dunes. 5) The impact of climate change on vegetation is still unclear but probably lengthening of growing season and maybe enhanced CO_2 concentrations have led to an acceleration of succession. 6) A general anthropogenisation of the landscape occurs with rapid spread of non-native species as an important consequence. The reconstruction of a natural reference landscape is considered largely unattainable because of irreversible changes and the long tradition of human impact, in many cases since the development of the dunes. Two contradictory elements need reconciliation. First, the general acceleration of succession and scrub and woodland development in particular is partly caused by a decreased anthropogenic interference in the landscape and deserves more appreciation. Second, most biodiversity values are largely linked to open, early succession dune habitats and are threatened by the same tendency. Apart from internal nature management, in which grazing plays an important part, re-mobilisation of stable, senescent dunes is an important challenge for dune management.

Keywords Coastal dunes · Dune formation · Landscape change · Sand drift · Dune fixation · Vegetation succession · Grass encroachment · Scrub encroachment · Land use · Nitrogen deposition · Nature management

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Introduction

Changes in landscape and species communities are a reason for nature protection and management measures, often aiming at the restoration of former values. This negative perception of change evokes questions about reference landscapes; what was the situation before the change? However, the potential for reconstruction of former landscapes is limited, not only due to lack of information but also because irreversible change might have occurred. Within a large timescale, for instance the post-glacial, these changes are mostly natural and seem of little relevance for nature conservation but rather subject to academic debate. However, this is the timescale of evolutionary processes, the very subject of biological diversity. Long term conservation thinking should consider this and provide opportunities for evolutionary processes to occur in a context as natural as possible. Short term changes are mostly due to human interference. These changes are often irreversible and force managers to adjust the reference image in view of attainable goals. Understanding the processes driving these changes is important in order to decide upon appropriate management measures.

This paper gives an overview of changes in landscape and vegetation in the coastal dunes of northwest Europe and considers both the large and small time frame. First, changes are considered within a postglacial context. This includes dune formation and an attempt to reconstruct landscapes before the dominant impact of man. Human impact is a second point of interest, linking the historical aspects of change with the recent developments, which is our main issue. Next, a range of explanations of change is presented and the paper concludes with implications for management.

Plant nomenclature according to Stace (2001).

Coastal dunes in a Holocene context

Landscape and dune formation

Sedimentary coastal landscapes are relatively unstable. Coastal dunes can be built up or washed away by the sea in less than a century (Pye and Neal 1994). Over a longer time frame, the coastal zone is ever changing, its position swinging back and forth as a result of macroclimatological oscillations and isostatic rebound. During the climax of the last ice age, about 18,000 years ago, the North Sea level was situated 100–120 m below its present level. During postglacial time, up to about 7,000 years ago, the sea level rose substantially and in Western Europe, the coast approached its actual position (Mörner 1995; Lambeck 1995). This was the starting point for dune formation along the present coastline. In general, older dune systems were situated more seaward and have been eroded by the progressing sea. Only in Northern Europe, where the isostatic uplift kept pace with the rising sea, can older dunes be found (Lambeck 1995). Gilbertson et al. (1999) for example, describes dune deposits dating up to 8,700 years B.P. on the Southern Isles of the Outer Hebrides of Scotland. Probably these are the oldest Holocene coastal dune deposits found in Europe.

Dune formation has been episodic. In geological profiles, phases of dune building and stability arise as layers of mineral sand, alternated by fossil soil layers. The occurrence of pollen or other fossil remains in these buried soils can provide information on the vegetation during phases of stability, the organic material can be used for radiocarbon dating and the layers of mineral sand can be subject to optical dating techniques (optically stimulated luminescence). In addition ground penetrating radar (GPR) can produce images of entire lithological cross sections. Figure 1 summarises some of the studies using these techniques in order to reconstruct chronologies of dune sites or regions within northwest Europe. The profiles do not necessarily reflect the entire sedimentary history because of methodological constraints or because certain layers may have been eroded before the deposition of new sediments. Furthermore, the distance to the sea of the records needs to be considered. Dune formation can be initiated at a certain time but it can take several centuries before an inland location is reached by the mobile sand.

In spite of the heterogeneity in the starting point and duration of aeolian dynamics in these coastal dune sites, many authors agree on the importance of climatic variables as a driving force. In particular, many studies recognise the climatic deterioration during the Little Ice Age (see Fig. 1) as an important catalyst for dune formation: e.g. in Denmark (Clemmensen et al. 1996; Clemmensen et al. 2001a, b; Szkornik et al. 2008), UK (Pye and Neal 1993; Wilson et al. 2001; Sommerville et al. 2007), Ireland (Wilson and Braley 1997) and France (Clarke et al. 2002), the significant increase in storminess apparently being the major causal factor (see Clarke and Rendell 2009 for a review). Figure 1 also suggests some correspondence between the four earlier periods of climatic deterioration in the northeast Atlantic region (1700–1100, about 2400–3100, 4000–4300 and 5700–6200 BP) and dune formation, especially for the 2400–3100 BP period (Wilson et al. 2004). However, in several studies this relationship is not apparent. Gilbertson et al. (1999) for example found evidence for relatively widespread soil formation, indicating dune stability on the Outer Hebrides (Scotland) between 400 years and 100 years ago, essentially within the period of increased storminess associated with the Little Ice Age.

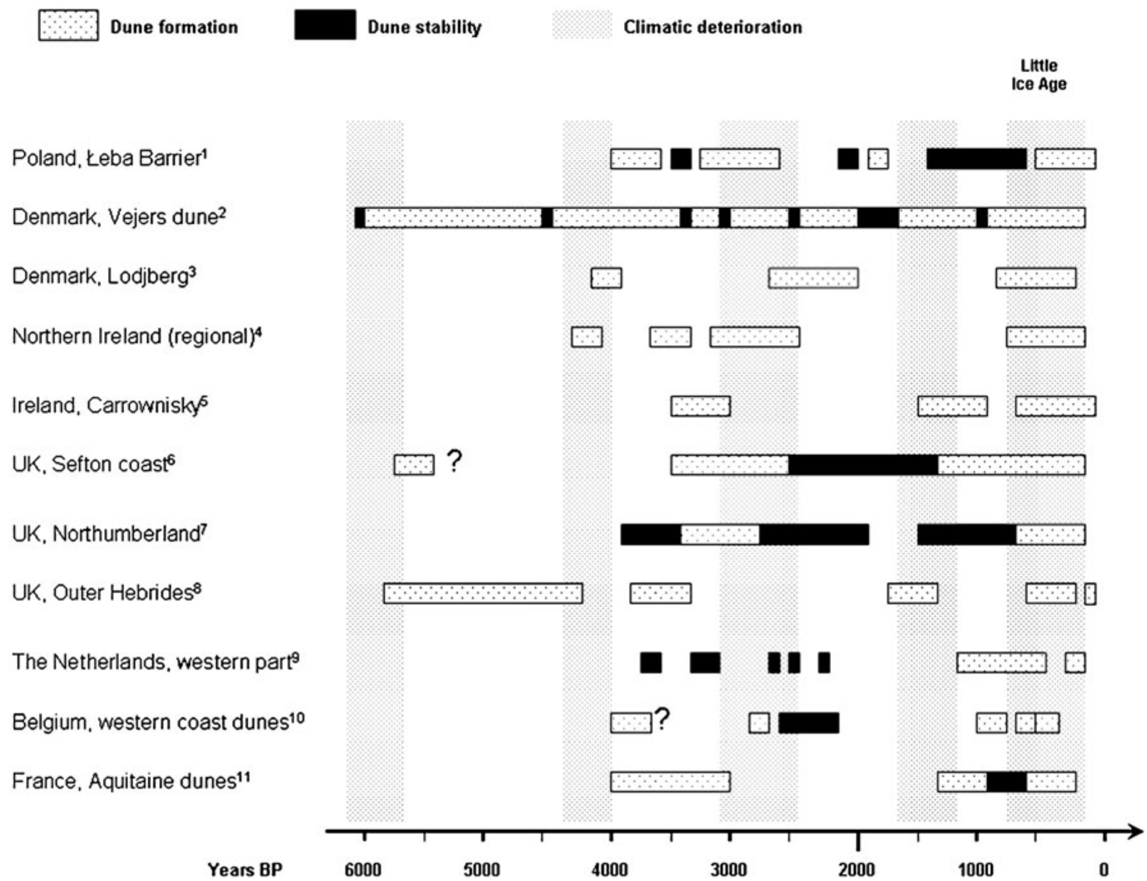

Fig. 1 Chronology of dune formation in a number of Northwest-european dune sites or regions. 1) Borówka 1990, 2) Clemmensen et al. 1996; Clemmensen et al. 2001a, 3) Clemmensen et al. 2001b, 4) Wilson et al. 2004, 5) Delaney and Devoy 1995, 6) Pye and Neal 1993, 7) Wilson et al. 2001, 8) Gilbertson et al. 1999, 9) Jelgersma et al. 1970; Klijn 1990a, 10) De Ceunynck 1992, 1985 and 11) Clarke et al. 2002. Periods of marked climatic deterioration in the northeast Atlantic region according to Wilson et al. (2004)

Changes in relative sea level (RSL), both rise and fall, are another regional trigger for dune formation. On rising RSL, frontal erosion of the dune face creates ideal conditions for recycling of sediment into blow-outs and other dune forms. Klijn (1990a) argues that such a secondary dune building mechanism was responsible for the development of the Young Dunes in The Netherlands. In this case, the high frequency and intensity of storm floods is seen as the specific cause for sand mobilisation. De Ceunynck (1985) postulates a similar hypothesis for dune development in the western Belgian coastal plain, relating dune formation to marine transgressions. In contrast, Christiansen et al. (1990) associate the main dune formation periods in Denmark with a fall in RSL. Falling RSL releases sediment and exposes emerging beach plain areas to aeolian activity (Hansom 1988). Low sea levels would also increase the availability of sediment and would moreover. Wilson et al. (2001) consider the same mechanism to be responsible for the historical dune formation in Northumberland, northeast England.

Acting on a regional scale (order of magnitude of about 100 km), climate and RSL dynamics therefore seem to be responsible for the timing and a variety of mechanisms of dune formation throughout northwest Europe. In addition local factors are significant. First, the physical environment of a specific site; geomorphology, marine or estuarine hydro- and sediment dynamics, orientation of the coastline etc… can outweigh all other elements. A striking example is the aeolian activity at the Dune du Pilat in southwestern France (Gascogne), caused by a large sand supply on the beach (Tastet and Pontee 1998). Secondly, dune building can be influenced by human interference in the physical or biological environment. Striking examples of rapid dune formation due to human interference in sediment transport are North Bull Island in Dublin Bay (Jeffrey 1977) and the Baie d'Audierne in Brittany (Guilcher et al. 1992). But also destruction or planting of dune fixing vegetation can drastically change geomorphological processes. Several authors relate land use such as grazing or cutting of marram to phases of increased aeolian dynamics (e.g. Van Dieren

1934; Borówka 1990; Christiansen et al. 1990; Wilson 1990; Gilbertson et al. 1999, Sommerville et al. 2007).

In general, dune building chronologies are geographically limited and knowledge about local circumstances is crucial for the understanding of the exact mechanisms involved. Gilbertson et al. (1999) made a detailed description of machair sand stratification on the Outer Hebrides in Scotland and found that very local episodes of sand drift occurred. Also Delaney and Devoy (1995) mention large local differences in former aeolian activity on dune systems on the western coast of Ireland.

Vegetation reconstruction of historical dunes

Geomorphological dynamics, with alternating phases of dune stability and aeolian dynamics, are an essential characteristic of coastal dunes. This lack of stability complicates palaeo-ecological reconstructions of former dunes as fossil evidence of historical vegetation mostly refers to stable landscapes. The composition of former open and mobile dune vegetation is very hard to determine because of the absence of organic soils containing fossil remains.

Phases of dune stability were characterised by the development of dune woodland in various parts of Europe, historical records and fossil remains revealing the frequent occurrence of natural dune woodland, at least up to the middle ages (Fig. 2). We briefly discuss these sources from north to south.

On several sites around the Baltic Sea and in the Kattegat, dune forests were found. In Poland, Borówka (1990) observed palaeopodzols dated to about 2,000 years BP, formed under *Quercus* forest. Fukarek (1961) describes the postglacial arrival of tree species in the coastal area of Northern Germany (Darßer Ort), firstly *Betula* and *Pinus*, then *Corylus*, *Quercus* and *Alnus* and finally *Fagus*, around 500 BC. In this area, patches of the original dune woodland persisted until present (Fukarek 1961). At Hiddensee, the Dünenheide area was a *Quercus-Betula* forest until the middle ages (Schubert 1996). In Denmark, the isle of Anholt was largely covered with forest dominated by *Pinus sylvestris*, probably accompanied by *Quercus*, *Betula* and *Corylus* (Christensen and Johnsen 2001). Similar woodlands in the dunes of southern Sweden are described by Olsson (1974).

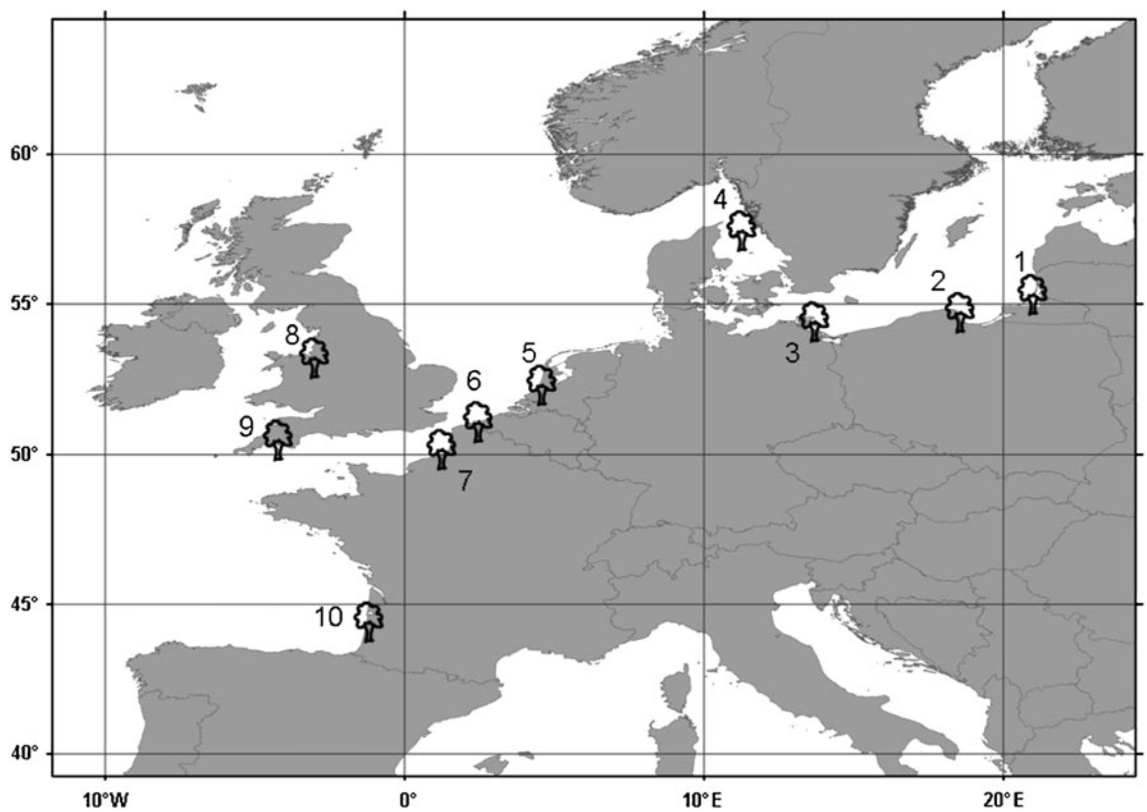

Fig. 2 Palaeo-ecological evidence of the occurrence of woodland in some northwest European coastal dunes. 1) Curonian Spit, Lithuania (Paul 1944, cit. in Savukynienė et al. 2003), 2) Łeba Barrier, Poland (Borówka 1990), 3) Darss, Germany (Fukarek 1961; Schubert 1996), 4) Anholt, Denmark (Christensen and Johnsen 2001), 5) Mainland dunes, The Netherlands (Zagwijn 1971; Boerboom and Zagwijn 1966; Kuijper 1993), 6) De Panne, Belgium (De Ceunynck 1985), 7) Northern France (Petit-Berghem 1996), 8) Sefton coast, UK (Huddart et al. 1999b; Pye and Neal 1993), 9) Cornwall, UK (Spencer 1975) and 10) Biscarosse, France (Clarke et al. 2002; Tastet and Pontee 1998)

The old dunes near Zandvoort in the Netherlands were largely forested, probably up to the 10th century, the forest being mentioned in historical records as "Haarlemmerhout" and extending westward up to the present coastline. Preserved trunks and pollen records from the remaining podsolic soil indicate that the woodland was rich in *Fagus*, with an optimum between 800 and 1000 AD (Zagwijn 1971). Kuijper (1993) found a variety of tree pollen (*Quercus*, *Alnus*, *Salix*, *Betula* and *Populus*) in peat layers from buried old dune slacks (0–1000 AD) in the same area. Boerboom and Zagwijn (1966) describe several periods of forest development in the dunes near The Hague. These authors found a peak of woodland around 300 AD, composed of a wide range of tree taxa (*Quercus*, *Fraxinus*, *Betula*, *Alnus*, *Ulmus*, *Tilia*, *Carpinus*, *Fagus* and *Pinus*). De Jong (1984) found indications for woodland development on the old dunes (about 800 AD) on the Dutch Wadden island Vlieland.

De Ceunynck (1985) analysed pollen in buried organic soil layers in the dunes near De Panne in Belgium. He found a climax of scrub and woodland development around 300 AD, similar to the dunes near The Hague. The most abundant tree pollen came from *Quercus robur* and *Alnus* but *Betula*, *Fagus*, *Pinus* and *Corylus* were also present. The same samples also contained scrub (*Juniperus* and *Hippophae*) and herbaceous pollen.

In northern France, traces found in peat layers indicate that the coastal forests were mainly present in swampy environments. In the Baie de la Canche, pollen records reveal the presence of dune scrub with a peak in the *Hippophae* presence in about the 9th Century AD. *Salix*, *Betula* and *Pinus* pollen was also present (Petit-Berghem 1996).

On the Sefton coast, UK, Pye and Neal (1993) found evidence of mature woodland (*Quercus* stumps) on dune sediments aged about 2500 BP. Also Spencer (1975) concludes that several dune sites in the UK were forested based on analysis of fossil mollusc communities in buried dune soils in Cornwall and the Orkneys.

Finally, Tastet and Pontee (1998) mention a historical document dated 1277 describing the forest which covered the dunes near Biscarosse, south of Arcachon Bay in southwest France.

This selection of palaeo-ecological studies demonstrates the historical presence of woodlands in coastal dunes in various parts of northwest Europe. However, the descriptions are often based on point samples and do not necessarily represent the entire landscape. Questions about the extent of the forests, both seaward and landward, and the structure or openness of these woodlands largely remain unanswered.

Human activity as an ecosystem component

The coastal dunes of northwest Europe have a long history of human activity. Traces of Neolithic or even Mesolithic occupation have been found in a large number of dune sites including Vendée, France (Joly 2004), Belgium (De Ceunynck 1992; Baeteman et al. 1984), The Netherlands (Jelgersma et al. 1970), County Donegal, Ireland (Knight and Burningham 2007), Newborough (Ranwell 1959) and Merthyr Mawr (Locock 1996) in Wales, UK, the Sefton Coast, UK (Huddart et al. 1999a), Northumberland, UK (Boomer et al. 2007), Luce Sands, Scotland (McInnes 1964) and Orkney, Scotland (Leinert et al. 2000; Sommerville et al. 2007).

In the Netherlands and Belgium, the Bronze and Iron Ages were characterised by a phase of dune stability (Fig. 1) that enabled human occupation of the largely forested dunes (Louwe Kooijmans 1993). At an Iron Age site in De Panne, Belgium, salt making pottery was found (De Ceunynck and Thoen 1981). This activity required substantial quantities of fuel and probably had a large impact on the environment. Gilbertson et al. (1999) describe a similar phase of dune stability on the Outer Hebrides of Scotland and found the impact of significant human activity through micromorphological soil analysis. Around Liverpool Bay (UK), archaeological evidence suggests major activity around the coastal dunes in the same period. Metal finds, but lack of associated pottery, suggests that the settlements may have been inland, and that the dunes were visited only for grazing, hunting and fishing (Huddart et al. 1999b). At Merthyr Mawr in South Wales, archaeological finds span millennia from early Mesolithic shell mounds to the Neolithic, early Bronze Age (finds of cist graves and tumuli) and Iron Age (with evidence of metalworking), through to Roman, medieval and up to the 14th Century and onwards (Locock 1996).

These examples illustrate our scattered knowledge about the impact of these former communities on the coastal dune landscape. During the course of time, the impact of man's activities generally increased until it became a substantial part of the ecosystem's functioning. The history of the isle of Anholt in Denmark (Christensen and Johnsen 2001) is a striking example of this evolution. The establishment of a lighthouse in 1560, which required a lot of wood, was the starting point for large scale forest clearing. By the early 17th century, the forest on Anholt had already disappeared. Since the deforestation, the landscape was heavily over-exploited by the inhabitants, who had to combine farming with fishing and seal hunting in order to survive. Vegetation development was prevented by grazing and scrub cutting. Virtually all sources of organic matter, including cattle dung, peat and scrub roots were used for fuel. Marram was used for thatching and winter fodder until at least the end of the 19th century. At this time, the dune landscape at Anholt was completely devastated. It is no coincidence that the area is called 'Ørkenen', Danish for 'desert'.

Historical deforestations in the Baltic, The Netherlands and France (Petit-Berghem 1996) suggest a similar evolution in many European dune systems. “Haarlemmerhout” on the old dunes near Zandvoort in the Netherlands was cut in the 11th–12th century. Many toponyms in that area remind of the forest clearing; e.g. ‘Boekenrode’, referring to the felling of *Fagus* (Zagwijn 1971). The deforestation of Kuršių Nerija (Curonian Spit) in Lithuania is probably the most recent phenomenon. Based on historical maps, Paul (1944, cit. in Savukyniené et al. 2003) shows a major decline of the old mixed dune woodland in the 18th Century. Dune woodlands in the Darss region in Germany were largely unaffected until the 13th century, from which time, human influence can be derived from the pollen record. Also at Hiddensee, east of Darss, the Dünenheide area was an Oak-birch forest until the middle ages. It was largely burned during the 30-year war (Schubert 1996).

In non-wooded dunes, the collection of plant material for human use of species such as *Ammophila arenaria*, *Hippophae rhamnoides*, *Calluna vulgaris* or *Salix repens* is documented in several countries such as the Netherlands (Van Dieren 1934), United Kingdom (Angus 2001; Jones et al. 1993) and France (Petit-Berghem 1996). The use of marram (*Ammophila*) is particularly interesting because of its relation with dune stability. Exploitation of marram has been subject to extensive regulation through history (e.g. Ranwell 1959). Examples from the Sefton Coast are given in Jones et al. (1993). In 1637, three local people were fined for gathering of marram grass and records from 1710 show that it was a duty under some land leases to plant marram on the dunes. Until the end of the 19th century in the islands and northern parts of Scotland marram was routinely used for a variety of domestic and agricultural purposes (Angus 2001). Wholesale removal of marram destabilises sand dunes, allowing wind erosion and sand drift across adjacent land. One of the best known examples is the estate of Culbin in N.E. Scotland, which was buried by storm-driven sand in AD 1694, causing the permanent abandonment of the village and loss of large areas of prime agricultural land (Steers 1937; Ross 1992). In acknowledgement of the impact of humans on the dune resource, the Scottish Parliament passed an Act in 1695 forbidding the removal of bent (marram), juniper and broom from sand dunes (Ross 1992).

The long history of grazing by domestic stock on many sand dune systems in Europe had a significant impact on landscape and vegetation. (e.g. Westhoff and van Oosten 1989; Isermann and Cordes 1992; van der Maarel et al. 1985a; Ehrenburg et al. 1988; van der Vegte et al. 1985; Termote 1992; Owen et al. 2000; Lemauviel et al. 2003). Grazing was mostly practised in commons (e.g. Westhoff and van Oosten 1989; McKenna et al. 2007), consequently the entire dune system was affected. In 1818, Dutch civil servants made an inventory of grazing animals in what are currently the Belgian coastal dunes (De Smet 1961). This report is one of the few sources providing quantitative data on historical grazing. The main grazers were cattle but also sheep, donkeys and to a lesser extent horses are mentioned. The intensity of grazing was high in respect to the type of ecosystem; about one livestock-unit (cattle, horse or donkey) per 2–7 ha. In a number of sites, grazing pressure was higher, with one sheep per 3–6 ha in addition to cattle, horses and donkeys.

A particular herbivore with large impact on the vegetation development of coastal dunes is the rabbit. The species was introduced to northern Europe in the middle ages, probably the 11th–12th century (Thompson 1994; Wallage-Drees 1988). Abbeys played an important role in its introduction and distribution. Certainly in dunes, rabbits were mainly bred in warrens, as we know from the UK (Jones et al. 1993; Thomas 1960), Belgium (Termote 1992), The Netherlands (Wallage-Drees 1988) and France (Petit-Berghem 1996). There is much evidence that rabbits in Britain were not in a feral state before 1850 (Thomas 1960).

In the vicinity of the villages, land use was more diverse and more intensive. Around the villages, moist dune slacks were often turned into fields where crops such as barley or potatoes could be cultivated (Termote 1992; Owen et al. 2000). Manure for these fields but also waste from fishery activities and intensive trampling resulted in particular soil properties of the dunes surrounding these villages. In the Netherlands, distinct vegetation associations are recognised which are associated with these ‘sea villages’: the Silene-Tortuletum ruraliformis Doing 1993 and the Anthyllido-Silenetum De Leeuw in Braun-Blanquet et Moor 1938 (Slings 1994; Mourik et al. 1995; van Til 1996; Doing 1993). Also the exposed, calcareous dunes of the west coast of Ireland and Scotland (Machair) are a good example of the intertwining of human use, geomorphology and vegetation development, resulting in a highly distinctive and ecologically rich habitat type (Hansom and Angus 2006).

Recent changes, 1900 onwards

Calcareous dunes of the Netherlands, Belgium and France

Characteristic for this region is the abundance of scrub, notably *Hippophae rhamnoides*. Changes over this period show a general pattern of stabilisation, although rates of change and vegetation types differ by region. The dunes near Oostvoorne in the Netherlands have been thoroughly investigated using a series of aerial photographs starting from 1934 (van der Maarel et al. 1985a; van Dorp et al. 1985). These authors used the term ‘revolutionary succession' for the changes they observed. Succession in the Oostvoorne dunes seems to follow multiple pathways but the overall tendency is mainly an expansion of scrub and woodland. *Hippophae rhamnoides* played a major role in pioneer primary scrub development in dry to moist environments. This young *Hippophae* scrub, accompanied by *Ligustrum vulgare*, *Rosa rubiginosa* and *Sambucus nigra*, was already well developed in 1934. Its extent remained constant at about one third of the area until the 1970s since when it declined, mainly at the expense of secondary scrub with *Crataegus monogyna* and *Rhamnus catharticus* and low woodland, dominated by *Betula pendula* and *Quercus robur*. In dune slacks *Salix repens* and *Salix cinerea* are the most important species in respectively low and tall scrub.

Marram dominated areas showed a steep decline during the studied period, mainly turning into scrub or tall grassland, and are now only found in the foredunes. Tall grassland with *Calamagrostis epigejos* and *Carex arenaria* increased until about 1960 and has since been replaced by scrub. Low dune grassland is mainly found in the older dunes and is linked to the grazing system. Consistent grazing maintained this vegetation, without which it developed into tall *Crataegus* scrub. A substantial area of young dune slacks was formed in the early 20th century but without active management they evolved towards scrub and low woodland. Since the 1970s local vegetation retrogression is observed through dying of scrub and woodland (e.g. *Populus tremula*).

Detailed investigation of the population structure of woody species (trees and tall shrubs) revealed that there was an exponential population build-up from the early 20th century until the beginning of the 1960s. From then onwards until about 1975, there was a severe decrease of rejuvenation for most species with the exception of *Sambucus nigra*. At least for some species, the vegetation succession itself resulted in an environment which is less suitable for rejuvenation (van der Maarel et al. 1985b).

Similar changes have been observed for the dunes along the western part of the Belgian coast (about 3,600 ha) based on the analysis of two series of aerial photographs; 1948 and 1989 (Provoost and Van Landuyt 2001). Increasing urbanisation is the most striking difference from Oostvoorne, about half of the Belgian coastal dune area now being developed. Urbanisation showed an exponential increase from the mid 19th until the end of the 20th century. Within the remaining dunes, the increase in scrub and woodland at the expense of open dune habitats is most apparent. The scrub encroached into wet dune slacks as well as onto dry dune ridges and increased from about 180–400 ha in 40 years. At the beginning of the 20th century, the dune landscape was almost devoid of woody vegetation, as can be derived from aerial photographs taken during World War I and contemporary landscape descriptions and photographs (e.g. Massart 1912). De Bruyne (1905) for example, mentions that *Sambucus nigra* and *Ligustrum vulgare* are rare in the Belgian dunes in this period. Pioneer scrub is mostly dominated by *Hippophae rhamnoides* but older grasslands can also be colonised by *Ligustrum vulgare*. As scrub matures, the assemblage of woody species becomes more diverse, similar to the developments in Oostvoorne. Increase in woodland in the Belgian dunes (170–290 ha) is mostly due to plantation. The contribution of spontaneous succession to woodland is limited. Mobile dune, including bare sand and *Ammophila* vegetation, shows a spectacular decrease of 60%, indicating large-scale stabilisation (Fig. 3). Corresponding trends are observed within the floristic assemblage. More than 100 scrub and woodland species, currently present in the dunes, were not found before 1940 (Provoost and Van Landuyt 2001).

In the Dutch mainland dunes, vegetation changes of the Haasvelderduinen have been investigated using a series of aerial photographs dating from 1938 to 1985 (Ehrenburg et al. 1988). The main change occurred between 1958 and 1968 and was characterised by the extension of low scrub with *Hippophae rhamnoides, Ligustrum vulgare* and *Salix repens* (from about 35% to 55%). Between 1968 and 1985 there was mainly an expansion of tall scrub. The scrub in the Haasvelderduinen mainly has an open structure, which is probably related to groundwater extraction. In the slacks some woodland with *Betula* spp. and *Crataegus monogyna* developed. Locally a tendency towards more open vegetation is noticed, probably due to a combination of increased rabbit population, recreation pressure and drought. Moving sand was historically counteracted by planting of thickets; in 1938 there was less than 5% bare sand in the Haasvelderduinen.

In an overview of scrub invasion in the Netherlands and Belgium (van Til et al. 2002) recorded parallel trends of increase in scrub and woodland at all investigated sites, with most rapid changes clearly occuring in calcareous dunes.

Little information is found on changes in the vegetation of French dunes. In northern France the situation is largely similar to the Belgian and Dutch dunes. Anderson and Romeril (1992) noted an increase in *Ulex europaeus* with approximately 46% between 1957 and 1979 on Les Quennevais, Jersey, UK. This trend is probably typical for the Normandy dunes.

In south western France, most information on changes in dune vegetation relates to afforestation or artificial dune fixation (Favennec 2002). In a study on fixed dune vegetation in the dunes of Pointe d'Arçay (Vendée), Jun et al. (2004) describe bryophyte and lichen communities along a gradient of fixation date. Even in dunes which are

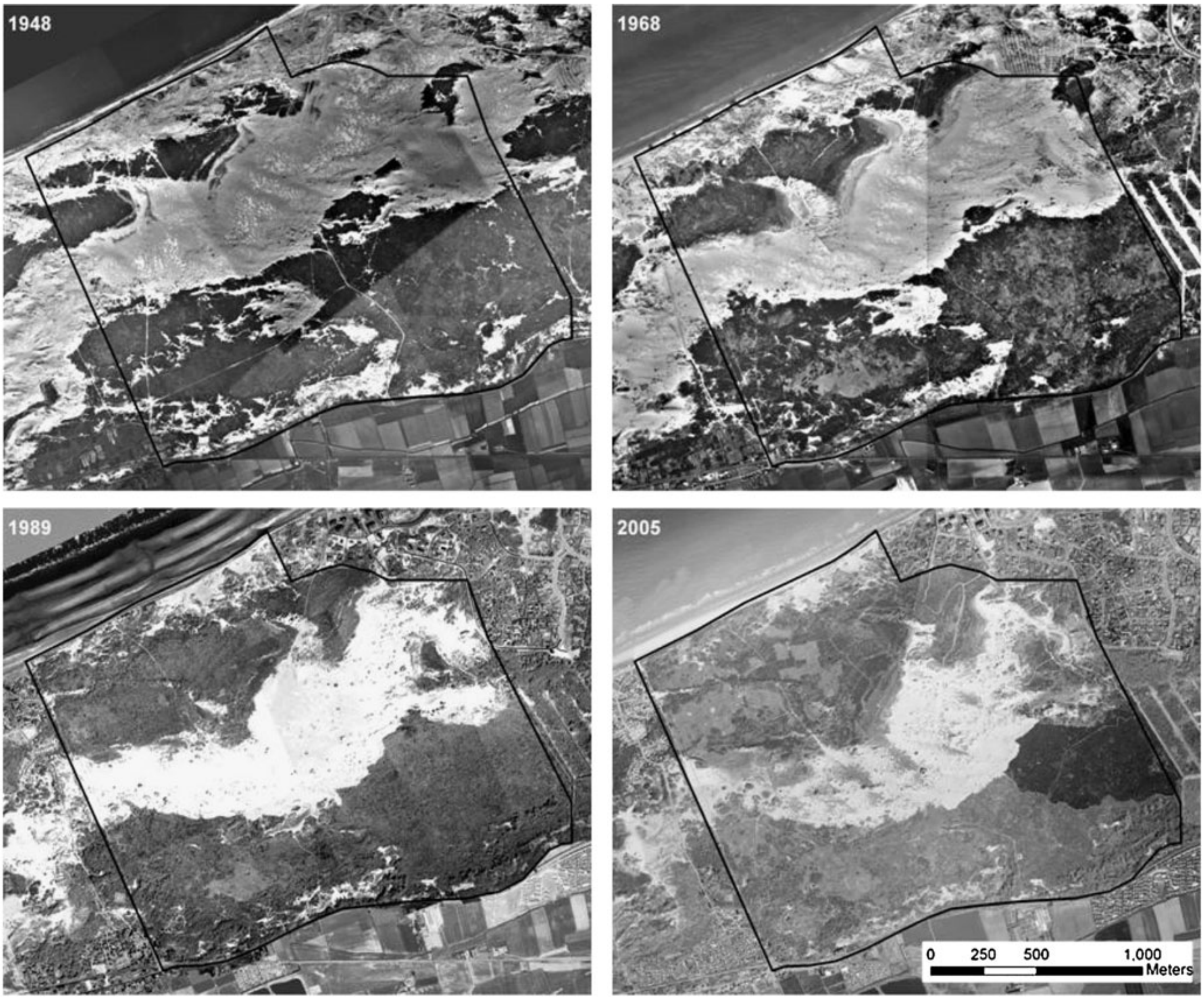

Fig. 3 Changes in 'De Westhoek' nature reserve in De Panne, Belgium illustrated by a series of aerial photographs. The decline in aeolian activity is especially apparent

fixed for over a hundred years, cryptophyte dominated vegetation occurs and soil organic matter content only attains 1.65 (±0.05)%. This indicates that vegetation dynamics is completely different to that of northwest Europe.

Decalcified dunes of the Wadden Islands, Denmark and the Baltic

Ketner-Oostra (1993) investigated changes in plant communities on the Dutch Wadden Island Terschelling. A sample of 100 permanent plots, recorded in 1966 and 1990, showed that dune vegetation structure changed drastically. Bare sand decreased from about 25% on the northern and 60% on the southern slopes to less than 1%. The cover of typical elements of *Violo-Corynephoretum* vegetation, including *Corynephorus canescens* itself, decreased dramatically. In contrast there was a large increase in graminoids, mainly *Ammophila arenaria, Carex arenaria, Festuca rubra* and *Calamagrostis epigejos*, and also the mosses *Dicranum scoparium* and *Campylopus introflexus*. A similar increase in *Empetrum nigrum* indicated a progressing succession. The increase in cover, vitality and biomass of marram is apparent and characteristic for decalcified dunes. In calcareous systems, *Ammophila* shows a decline in vitality during the course of vegetation succession due to soil pathogens (de Rooij-van der Goes et al. 1997; van der Putten et al. 1993). Also on Terschelling, Ketner-Oostra and Sýkora (2004) surveyed lichen dominated vegetation in two periods; 1966–72 and 1990–96. A strong decline in lichen diversity was observed, a trend to which the invasion of the alien *Campylopus introflexus* had a large contribution.

Based on two successive vegetation maps (1959 and 1989–90), Isermann and Cordes (1992) describe a general tendency of vegetation succession and soil development on the German Wadden Island of Spiekeroog. Patches of bare sand developed into fixed grey dune. Mobile *Ammophila* dunes developed into *Phleo-Tortuletum* or *Hippophae* scrub in the more calcareous parts and into *Violo-Corynephoretum* in the decalcified areas. The *Hippophae* scrub itself seemed to be fairly stable on the southern slopes although the overall area of *Phleo-Tortuletum* decreased. The total area of *Violo-Corynephoretum* only slightly decreases, partly because new patches developed at the expense of mobile dune communities. Well developed *Corynephoretum* vegetation gradually became restricted to southern slopes, where it was still fairly abundant in 1990. Locally, acrocarpous mosses such as *Dicranum scoparium, Polytrichum piliferum* or *Campylopus introflexus* tend to dominate. Grassland (*Agrostio-Poetum humilis* Tx. ex Menke 1969), showed a strong decrease in surface area and an internal degradation (domination of *Carex arenaria* or *Deschampsia flexuosa*). Grasslands in slacks or on flat dunes seem especially vulnerable to grass encroachment. *Empetrum nigrum* strongly increased, mainly on the northern slopes. Whereas it only occurred in small patches in 1959, it is characterised by a continuous cover in 1990. Locally and mainly in slacks, succession continues towards scrub and woodland with *Betula* spp. and *Sorbus aucuparia*.

In the Baltic area, most dune systems are also highly decalcified and the observed vegetation changes are very similar to the ones described from the Wadden Islands. Schubert (1996) for instance, reports severe grass encroachment with *Deschampsia flexuosa* in the dry heathlands, *Molinia caerulea* in moist slacks and *Phragmites australis* in the wet parts of Dünenheide (Hiddensee, Germany). Invasion of lichen rich dunes by *Campylopus introflexus* is also observed.

Christensen and Johnsen (2001) observed an increase of *Calluna vulgaris* and *Juniperus communis* since the early 20th century on the island of Anholt (Denmark). The latter had nearly disappeared at the end of the 19th century but is currently a common species. Similar vegetation developments are found on Laesø, another island in the Danish Kattegat.

United Kingdom

In the UK, a change from very mobile to more stable dune systems in the second half of the twentieth century is widely documented, especially for England and Wales. Ranwell's records of Newborough Warren in Wales in the 1950s (Ranwell 1960a) show a landscape dominated by bare sand, dotted with patches of low, hummocky *Salix repens* dunes. Photographs of the Sefton Coast in the 1920s show similar expanses of dune sand, with significant patches of bare sand still visible in photographs of the early 1960s (Smith 1999). Periods of active sandblowing at Newborough Warren and Sefton are known to have occurred since the extensive phase of sand encroachment of the Middle Ages (Pye and Neal 1993). Historical documents cited in Ranwell (1959) describe parts of Newborough in the late 19th Century being an open expanse of blowing sand (Rhind et al. 2001). Rhind et al. (2008) provide a detailed record of change at Newborough over 50 years, based on Ranwell's detailed surveys in the 1950s and Ashall et al.'s 1991 National Vegetation Classification (NVC) (Rodwell 2000) survey. Ashall et al. (1992), reports 'the system has changed almost beyond recognition' (p. 348)—see Jones et al. (unpublished) for aerial photographs documenting the drastic change in the dune system from 1951–2000. Ranwell recorded 376 ha of the dune area as a mosaic of mobile dunes with embryonic dune slacks. In 1991, none of this mosaic was recorded, with only 24 ha of mobile dune Ammophiletum remaining, all confined to the coastal fringe. Overall, a decline of mobile dune occurred from 75% to 6%.

Hodgkin (1984) reports the scrub invasion in Newborough Warren. In 1954, there was no scrub or woodland, except for some *Crataegus monogyna* stands which were heavily rabbit chewed. After Myxomatosis, spread of scrub with *Crataegus monogyna*, *Betula* spp. and 17 other shrub or tree species was observed.

The 1988 NVC Survey of the Sefton Coast reports a large, relatively recent increase in dune scrub, traceable by post-war aerial photographs, and large areas of senescent fixed dune (Edmondson et al. 1999). Extensive scrub was recorded mainly in four categories; *Populus/Salix* spp. dominated, *Betula* spp./*Crataegus monogyna* dominated, *Pinus* spp./mixed scrub and *Hippophae rhamonides*. (Holder 1953) had reported a spread of *Hippophae* and a rapid growth of *Rubus fruticosus* agg. on both dunes and slacks, but did not report other scrub types, which developed rapidly largely since that time. Species-rich fixed dune grassland was rare and not found to succeed semi-fixed dunes in the low grazing pressure provided by the fluctuating populations of rabbits recovered after the 1950s crash. Instead, a dense, grassy vegetation was found, although still with frequent *Ammophila arenaria* and thus in NVC classified as semi-fixed dune. It was characterised by tall, sometimes dominant *Festuca rubra*, often associated with grass species typical of more mesotrophic conditions such as *Dactylis glomerata, Arrhenatherum elatius* and *Holcus lanatus* and with frequent *Rubus caesius*. *Arrhenatherum elatius* coarse grassland was commonly associated with dune scrub, drying out slacks and senescent dunes.

The Sefton Coast NVC survey was repeated in 2003–4 (Gateley and Michell 2004). The proportion of species-rich fixed dune grassland reported in 1988 was very low; only 0.4% of the area. This was associated with continued large areas of vegetation with *Arrhenatherum elatius*. The most notable increase recorded in 2003 was the expansion of SD10 *Carex arenaria* dune community. This gain is mirrored by a loss of the open SD19 *Phleum arenarium-Arenaria serpillifolia* dune annual community. It is also associated with expansion of SD7 semi-fixed dune, much of which in Sefton is a relatively stable community, rather species-poor, often dominated by *Rubus caesius*, and not conforming well to the reference SD7 descriptions in Rodwell (2000). This distinction was identified in the 1988 survey described above, when much of the dense grassy vegetation had to be assigned to SD7. These observations are a further indication of a continued trend towards increased stability and biomass. Gateley and Mitchell record significant scrub clearance that has reduced scrub in Sefton on some sites, but scrub development has continued on both dunes and dune slacks where these actions have not occurred.

In spite of the large coastal dune resource in Scotland (over 50,000 ha), there is little information on changes in vegetation during the past decades. Dargie (2000) mentions the abundance of short dune grassland, clearly associated to stock grazing.

Causes of recent change

Changes in land use

Over the last century there have been many changes in land use affecting the vegetation of dune systems. Dominant among these changes is a reduction in 'traditional' dune activities such as harvest of marram (see "Human activity as an ecosystem component"), and a decline in the use of dunes for marginal agriculture such as livestock grazing, coupled with increasing perception of dunes as providing coastal defence. Most studies discussed in "Recent changes, 1900 onwards" strengthen this point of view. The dunes of Oostvoorne for example were heavily grazed with cattle and horses until the beginning of the 20th century. Around 1910, livestock was removed and marram was planted in order to ensure the coastal protection. The quite sudden withdrawal of livestock seemed to be the start of the 'revolutionary succession' described by van der Maarel et al. (1985a) (see "Recent changes, 1900 onwards"). On other sites, such as Haasvelderduinen (Ehrenburg et al. 1988), Schiermonnikoog (Grootjans et al. 1988) and Terschelling (Ketner-Oostra and Sýkora 2004), the Netherlands; Spiekeroog, Germany (Isermann and Cordes 1992); Anholt, Denmark (Christensen and Johnsen 2001) North-Wales, the differences between the evolution of Newborough Warren and the nearby system of Aberffraw, where a close-cropped sward typifies the fixed dune grassland and large expanses of mobile dune vegetation still occur as much as 1.5 km inland, is largely attributed to grazing by domestic stock (Rhind et al. 2001; Ashall et al. 1995; Bailey and Bristow 2004).

Crashing rabbit population

The eradication of rabbits by Myxomatosis on many (dune) sites in the 1950s is considered by a number of authors to have contributed to an acceleration of succession and a general increase in biomass. Especially in the UK, the Myxomatosis outbreak was grasped as an opportunity to investigate a landscape scale ecological experiment. The disease spread in Wales in 1954. During this year, Ranwell (1960b) noted a reduction of the rabbit population on Newborough Warren of more than 95%. Before the outbreak, about 14,000 rabbits were caught annually; after 1954, this number was reduced to 30–50. Ranwell observed a boost of vegetation growth with a large increase in vegetation height already in the first year after the rabbit reduction. A number of grass, sedge but also moss species showed an increase in abundance (e.g. *Carex arenaria*, *Festuca rubra, Pseudoscleropodium purum* and *Rhitidiadelphus squarosus*. In contrast, several low forbs, graminoids, mosses and lichens decreased (e.g. *Festuca tenuis, Luzula campestris, Prunella vulgaris, Climacium dendroides* and *Syntrichia ruraliformis*).

Similar observations were made on Blakeney Point, Norfolk where the Myxomatosis outbreak occurred in February 1954 (White 1961). Before this date, the dunes were heavily over-grazed by rabbits. Using four permanent line transects set out in 1955, White found that following the eradication of rabbits in 1954, significant grass encroachment occurred, particularly with *Festuca rubra* which increased from 14–43% to 80–89%. The area of open sand decreased, mosses such as *Brachythecium albicans, Ceratodon purpureus* and *Syntrichia ruraliformis* declined. Rabbits were not recorded again until 1959.

Edmondson et al. (1993) attribute the development of scrub and extensive areas of fixed dune vegetation with significant amounts of *Salix repens*, tall grasses and *Rubus caesius* along the Sefton Coast to the outbreak of myxomatosis in the mid-1950s, although the general abandonment of agricultural activities might also play a part. Ehrenburg et al. (1988) also see a relationship between scrub expansion and the first outbreak of myxomatosis in 1954 in the Haasvelderduinen, the Netherlands. Scrub seedlings only seemed to establish after the decline of rabbits. Several other studies support the evidence for a relationship between scrub encroachment and rabbit numbers (Van der Maarel et al. 1985b; Drees and Olff 2001; Binggeli et al. 1992; Hodgkin 1984; Anderson and Romeril 1992).

Especially the detailed observations of Ranwell (1960b) and White (1961) demonstrate the large and direct impact of rabbits on dune grasslands. There is certainly a general parallel with the impact of livestock grazing, although diet preferences and impact of trampling differ (Wallage-Drees 1988). Therefore, the history of livestock grazing and fluctuation in rabbit population will at least theoretically enable the clarification of site specific vegetation patterns and processes. In general however, lack of detailed information will complicate the unravelling of these two types of herbivore impact. Furthermore, other factors play a role. Jones (unpublished) in a detailed study of the aerial photographic record at Newborough Warren showed that the onset of stabilisation preceded myxomatosis by at least 5 years. While the catastrophic decline in the rabbit population may have accelerated the rate of stabilisation, evidence suggests that other factors such as climate were operating at the same time to alter rates of vegetation establishment and rates of soil development (Jones et al. 2008).

Natural and enhanced dune stability

The decline in aeolian dynamics seems to be a common feature on many dune sites (see "Recent changes, 1900 onwards"). This does not only mean loss of mobile dune habitat but also prevents the development of new dune slacks. In general, stability initiates ageing of dunes implying a gradual loss of young, often calcareous habitat, which is one of the most characteristic features of coastal dunes.

Natural dune mobility is influenced by three groups of factors: climate (wind, precipitation, moisture, …), sediment (availability, grain size, …) and vegetation (Klijn 1990b). Although many of the small scale sand drift processes are well understood, the upscaling to the level of dune formation seems to be extremely difficult or is even confronted with fundamental uncertainties (Bauer et al. 1996). The heterogeneity in dune chronologies presented in Fig. 1 will at least partly be an expression of this complexity. Pye (2001) presents a comprehensive overview of potential geomorphological changes in the long term. In general, the picture is very complex because several parameters can influence dune mobility in a different way according to their magnitude. An increase in temperature, for instance, will generally lead to drought and a higher susceptibility of dunes to sand drift. On the other hand, a limited increase in temperature will stimulate vegetation growth, which has a stabilising effect. Similar ambiguous effects can be expected from sea level changes and coastal erosion (see discussion in "Landscape and dune formation"). Talbot (1984) and Lancaster (1988) amongst others discuss the relative importance of climatic factors on dune mobility which is generally recognised to be a function of windspeed (most important) and the balance between precipitation and actual evapotranspiration which broadly governs the rate and extent of vegetation growth.

Furthermore, human activities can drastically influence geomorphological processes, both in terms of erosion and stabilisation. Recently, people have had considerable influence in stabilising dune systems. Dunes are recognised as an important element of coastal defence, especially after the great storm-surge flooding around the North Sea in 1953. Even before this time, the leading dune ridge was often stabilised and raised in elevation to protect areas lying behind (e.g. van der Meulen and van der Maarel 1989; Adriani and Terwindt 1974). There is for instance a long tradition of marram planting throughout Europe (e.g. Isermann and Cordes 1992; Edmondson et al. 1993). Particularly in the Netherlands, considerable dune stabilisation occurred, reducing sand supply and altering aeolian dynamics in the lee of these dunes which resulted in rapid stabilisation and vegetation succession (see e.g. van der Maarel et al. 1985a for the dunes near Voorne). Arens et al. (2007) largely attribute the decline in aeolian dynamics of coastal dunes in the Netherlands, to artificial stabilisation efforts, a view shared by Pye (2001) for the UK dunes. Clemmensen and Murray (2006) see a similar cause for the decline of aeolian sand transport in Denmark but argue that an overall decline of storminess also contributed. Also Clarke and Rendell (2009) found a relationship between historical storminess and sand drift based on a review of 16 studies. Large-scale processes appear to be discernible above those of local scale effects. Aerial photographs from Welsh dune systems show that the rapid decline in sand mobility from the mid 1940s to present day is observed at many sites from North to South Wales (Jones MLM, pers. obs.), with similar soil development curves at two well-studied sites: Newborough Warren in North Wales and Merthyr Mawr in South Wales (Jones et al. 2007).

Once vegetation is established and dune systems stabilise, it becomes hard to de-stabilise them. This hysteresis, or the difference in stabilisation and destabilisation trajectory (Fig. 4), is caused by the function of vegetation as a dune stabiliser. The destabilisation of a dune requires much more energy, in terms of wind stress of vegetation destruction, than the fixation (Tsoar 2005). This partly explains the difficulties encountered with re-mobilisation projects (Arens et al. 2007).

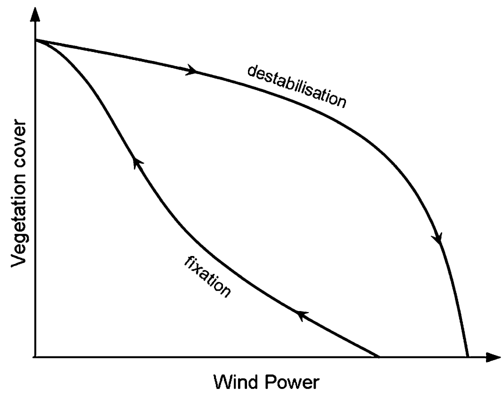

Fig. 4 Hysteresis curve relating changes in vegetation cover to wind energy (Tsoar 2005)

Soil conditions and eutrophication

Soil type exerts an important control on vegetation development. In dune systems, the initial carbonate content of the sand and meteorological conditions (precipitation) control the decalcification rate. The resulting soil pH subsequently affects decomposition processes and nutrient dynamics. Decomposition generally slows down in acidic soils (pH<4, 5 to 5), resulting in an increased soil development (Wilson 1960; Aggenbach and Jalink 1999). Key elements in nutrient dynamics of dry dunes are nitrogen (N) and phosphorous (P) (Kooijman et al. 1998). In pre-industrial times, soil N was mainly supplied by decomposition of plant residues and animal waste; more recently the dominant input to most semi-natural habitats in Northwest Europe, including dunes, comes from atmospheric N deposition (Bobbink et al. 1998). P availability is pH dependent and shows an optimum at pH 5, 2 in calcareous dunes in the Netherlands (Kooijman and Besse 2002). At higher pH, P is largely fixed in calcium phosphate, in acid soils it is immobilised in Al and Fe compounds. Kooijman et al. (1998) and Kooijman and Besse (2002) have shown that through this mechanism, P availability in Dutch dunes governs plant productivity. For this reason, some nutrient addition experiments in dunes have shown no changes in plant community composition (ten Harkel and van der Meulen 1996). Phosphorus limitation is more common where there has been a long history of N deposition, or of nutrient removal by mowing or grazing. Phosphorus limitation prevents many of the adverse plant community responses to N deposition, although it does not prevent N accumulation in the soil and plant system (Plassmann et al. 2009). N deposition may also deplete seedbanks by stimulating germination of dormant high-longevity seeds (Plassmann et al. 2008).

However, P limitation is not universal in coastal dunes. Co-limitation of N and P can occur (e.g. Willis 1963). Kooijman and Besse (2002) showed for the largely decalcified dunes of the Dutch Wadden Islands that, although the total P pool is low, P availability is relatively high and consequently deposition of atmospheric N alters competitive relations between species, with a range of consequences for dune plant assemblages.

Pre-industrial levels of N deposition were probably between 2–6 kg N ha^{-1} yr^{-1} (Fowler et al. 2004), while current levels in Europe are at least twice as high and in some parts of Europe can be ten times higher. According to Achermann and Bobbink (2003), the critical load (i.e. damage threshold) for N in dune habitats is 10–20 kg N ha^{-1} yr^{-1} for dry dunes and dune heaths, and 10–25 kg N ha^{-1} yr^{-1} for dune slacks. Remke et al. (2009) however, argue that the critical loads for acidic dry coastal dune vegetation might be lower, in the range of 4–6 kg N ha^{-1} yr^{-1} wet deposition.

As a result, many dune systems in Europe exceed at least the lower end of the critical load range while some also exceed the upper range of the critical load and we might expect to see adverse impacts of N deposition around Europe, particularly where N deposition is highest.

Anecdotal and empirical evidence for detrimental effects of N deposition on dunes comes predominantly from the Netherlands, Denmark and the UK. In the Netherlands and Denmark where N deposition can be particularly high, observations of tall grass encroachment at a number of sites, and prolonged vigour of *Ammophila arenaria* where it should be in its senescent phase are attributed to N deposition (Dopheide and Verstraten 1995; van der Laan 1985; Ovesen 2001). In the UK, a survey was conducted specifically to test for signals of N deposition (Jones et al. 2004). This showed increases in biomass and decreases in species diversity in dry dune grasslands with increasing N deposition. Even in the mobile and semi-fixed dunes, plant biomass and cover of *Ammophila arenaria* increased with N deposition.

In other ecosystems, N-mediated impacts include species shifts and, in extreme cases complete community shifts, as in the Netherlands where excess N deposition has turned heathlands into grasslands (Heil and Diemont 1983). Mesocosm experiments with dune vegetation have shown that graminoids tend to dominate at the expense of forbs when exposed to high levels of N (Mohd-Said 1999; van den Berg et al. 2005; Willis and Yemm 1961), confirming both the shift to grass-dominance and a loss in overall species diversity.

Changes in dune systems due to N deposition can occur very rapidly. Plassmann et al. (2009) showed increases in moss biomass within 2 years addition of low levels of N (+15 kg N ha^{-1} yr^{-1} on a background of 10 kg N ha^{-1} yr^{-1}). This may be because dunes have thinner soils than most other semi-natural habitats, with relatively small soil N pools. As a consequence, N deposition can alter plant community structure but may also alter soil processes either directly through greater input of organic matter to the soil, thus increasing soil fertility and the capacity to further retain nutrients, or indirectly via impacts on soil N cycling. Soil %N contents in UK dunes are currently greater than values reported in the older literature (Jones et al. 2002) while Jones et al. (2004) showed that available inorganic N decreased with increasing N deposition and soil C:N ratio increased with N deposition, in contrast to relationships observed in other habitats where available N increases and C:N ratio decreases. These findings suggest that N deposition can alter soil processes, although not always in the way expected. A proportion of the extra deposited N may be stored by dune vegetation, particularly mosses (Plassmann et al. 2009). Since additional N can be stored in both the vegetation and the soil, N deposition may well be speeding up the rate of succession itself. Evidence from a recent chronosequence study suggests that rates of soil development in dry dunes are considerably faster than those reported in older studies of comparable dune systems. Although the effects of temperature and N deposition can not be separated, both show strong correlations with rates of soil development (Jones et al. 2008).

Land management also plays a part in moderating vegetation development in response to eutrophication. Heavy grazing or mowing serves to reduce the dominance of vigorous species (Hewett 1985) and may counter the spread of nitrophiles, thus preventing competitive exclusion by faster growing species and retaining species of conservation interest. Grazing can therefore mitigate some adverse effects of N deposition (Boorman and Fuller 1982; Kooijman and Smit 2001; ten Harkel and van der Meulen 1996). By contrast, other management activities such as use of dunes for water filtration, have resulted in severe eutrophication and rapid spread of nitrophiles (van der Meulen 1982; van Dijk 1989).

Biological N fixation is both a natural process in dunes and a major factor governing the rate and speed of succession. N input in early successional habitats through N-fixation by legumes and by cyanobacteria facilitates colonisation by other species. However, non-native N fixers such as *Lupinus* spp. or locally *Hippophae rhamnoides* which has been widely planted outside its natural range to stabilise dune vegetation, can greatly increase local rates of N fixation, with resulting spread of nitrophiles such as *Urtica dioica*, *Rubus fruticosus* or *Chamaerion angustifolium*.

Climate change

The contribution of climate change to the recent changes in dune vegetation is difficult to asses. The impact of climate on ecosystems is complex because it affects many processes on different levels. On a European or even a global scale, sea level is largely determined by climate and this factor, as discussed in "Landscape and dune formation", is of major importance in the formation or erosion of dunes. Historical phases of aeolian activity have been linked to climatic conditions (Clarke and Rendell 2009; Clemmensen and Murray 2006), although there is still debate about the contribution of climatic factors to the recent stabilisation of dunes (see "Natural and enhanced dune stability").

On the vegetation level, climate exerts a direct influence on species through their specific climatic requirements or tolerances. Substantial evidence has been collected for shifts in phenological timing and geographical ranges of species in response to global warming (Root et al. 2003; Berry et al. 2002). However, little is known about the actual influence of these shifts on the functioning of ecosystems such as the temperate coastal dunes of Europe. Potential climate change related mechanisms contributing to the observed increase in phytomass and accelerated succession are the prolongation of the growing season due to the warming and the growth stimulation of plants caused by an increased ambient CO_2 concentration (Ziska and Bunce 2006; Nowak et al. 2004). Finally Jones et al. (2008) showed that changes in climatic conditions over the last 60 years at Newborough Warren were correlated with rates of soil development in dry dunes, with fastest soil development correlated with periods of higher temperatures, and with periods of low summer rainfall.

Anthropogenisation of the landscape

Most of the above mentioned causes of change in plant communities are linked to human activities but they have a geographically widespread effect. In this paragraph, we add a number of anthropogenic influences which are locally or regionally specific. A first element is human infrastructure development on sand dune coasts, which is widespread in northwest Europe. A major consequence, apart from habitat loss, is landscape fragmentation, which is particularly disrupting large scale geomorphological processes. Moreover, the presence of urban areas, agricultural land and other economically valuable assets within or inland of the dunes is an extra motivation for coastal protection and fixation measures, which further decreases the potential for aeolian dynamics. Apart from housing and infrastructure, development includes the layout of golf courses, which have a large impact on dunes, especially in the UK and Eire.

Major landscape change in European coastal dunes during the past centuries however, has been caused by afforestation, either for stabilisation or economic return (Favennec 2002; Petit-Berghem 1996; Provoost and Van Landuyt 2001; van der Maarel et al. 1985a; Ehrenburg et al. 1988; Rhind et al. 2001; Christensen and Johnsen 2001; Jensen 1994; Olsson

1974; Ovington 1950). Apart from the loss of herbaceous vegetation, the presence of woodland weakens the wind stress in the landscape and can cause a lowering of the groundwater table because of enhanced evapotranpiration from the woodland vegetation (e.g. Bakker 1990; Rhind et al. 2001). Furthermore, most of the plantations consist of non-native species, mainly conifers.

An important consequence of urbanisation is the large numbers of non-native vascular plant species introduced to gardens and landscaped areas, that potentially could escape and become invasive on the dunes. Along the highly urbanised Belgian coast, the proportion of non-native species increased from 5% to 20% over the last 50 years. Many of the invasive species are characteristic for scrub and woodland (Provoost and Van Landuyt 2001). On the Sefton Coast 35% of the vascular plant species are non-native. Along over 9 km of housing/dune boundary, a non-native introduction occurs every 12 m (Edmondson 2009). Williamson's 10:10 rule (that gives an adequate fit for British plant data) suggests that 10% of all introduced species become established and that 10% of established species become invasive (Williamson 1993). In terms of ecosystem functioning therefore, only a limited number of species are likely to become invasive and threaten natural dune vegetation, but continuous inoculation by garden escapes will increase the probability. The relatively recent explosion of *Prunus serotina* that is causing huge problems in the Amsterdam Water Supply Dunes, (Baeyens and Martínez 2008), is an illustration of the invasion potential. Urbanised areas often have more woody species than would be typical of open dune landscapes. In addition to *Prunus serotina, Mahonia aquifolia* and *Rosa rugosa* are problem species, the latter often being introduced as a dune stabiliser and causing large scale problems for example in northern Germany (Isermann 2008a, b).

Groundwater extraction is also linked to the presence of urban areas on or adjacent to the coastal zone. Especially in the Netherlands and Belgium, a relatively large portion of the dunes is hydrologically influenced by groundwater pumping, with drastic changes in dune slack communities (van der Hagen et al. 2008; Provoost and Van Landuyt 2001; van Dijk 1989). However, the importance of dunes as water abstraction zones also gave the dunes protection from development, and was initially the reason for their continuing existence as protected areas before nature conservation was deemed worth preserving.

Implications for management

Understanding change

During the past century, three major groups of driving forces caused changes in landscape and vegetation of coastal dunes on pan European scale: 1) changes in land use, 2) nitrogen enrichment and 3) climate change. Certainly within the climate of northwest Europe, most of these processes reinforce each other and generally lead to landscape stabilisation and increased vegetation succession. These synergistic effects complicate the understanding of causes. For example, analysis of the soil organic matter content in Newborough Warren in relation to fixation date (Jones et al. 2008) suggests an acceleration of soil development during the past decades. However, it is very difficult to separate the effects of N-deposition and elevated temperature in this process.

Moreover, some processes are characterised by internal positive feedback. This is shown for grass encroachment by Veer (1997). Litter accumulation in tall grass vegetation increases nitrogen mineralisation which on its turn stimulates grass growth. Another example is scrub encroachment. The expansion of scrub leads to an increasing availability of berries. This attracts migrating birds which on their turn disperse the seeds and stimulate scrub colonisation (van Dorp et al. 1985; Izhaki et al. 1991).

A combination of a large variety of driving forces, local or regional specificity, interactions between processes and feedback mechanisms might suggest an insurmountable complexity. Indeed, every single dune site has its own story to tell and management policy should incorporate this specificity. However, the overall vegetation change shows a remarkable similarity within northwest Europe and certainly a number of common management strategies can be formulated.

Reference landscapes

We suggest that the reconstruction of a former landscape as a ready-made reference for future conservation and management is largely a myth. The information will never be sufficiently detailed to answer all questions and the landscapes and ecosystems we value have mostly been changed irreversibly from their original state. However, historical information can provide useful guidelines. Peterken's (1981) analysis of the concept of naturalness with respect to woodlands suggests a diversity of 'natural' states (original, present, past and future) relating to multifactoral changes in climate and human influence. Change in temperate region vegetation types since the last glaciation has been slow but continual based on species colonisation, changing climate and the ever-increasing influence of people since around 6000 BP. Many dune sites are relatively young and have been influenced by people since their very genesis. What then do we take as a reference condition? Some historical-ecological considerations might be useful in the attempt to answer this question.

A first consideration is the fact that the concept of reference landscapes is a static approach which is very difficult to adopt to a dynamic landscape type such as coastal dunes. A reference therefore needs to include the geomorphological processes characteristic for dunes. On the other hand, processes have no inherent dimensions and are hard to quantify and compare. Therefore it is useful to include patterns in the reference image such as (distribution of) species or habitats.

There is significant evidence of historical development of woodland on stabilised dunes, indicating this is the potential natural vegetation on at least little exposed parts of the dune system. However, most dune sites are characterised by an—at least historical—alternation of stable and dynamic phases (see "Landscape and dune formation"). Furthermore, clearing of scrub and trees and centuries of agricultural use, pushed most systems into a semi-natural state. (Lawesson and Wind 2002) mention an "artificial lack of natural scrub and forest vegetation in most dune areas of the North Sea", a view first presented by Van Dieren (1934). There is an obvious link between abandonment of this historical land use and the observed recent successional acceleration. Present day coastal dune woodland in Europe is badly developed because of this history of land use, planting of non native tree species and the high portion of alien species in the newly developing scrub and woodland (Provoost and Van Landuyt 2001).

The discontinuity in the presence of dune woodland probably partly explains the absence of coastal-specific woodland species in the list of European coastal vascular plants (van der Maarel and Van der Maarel-Versluys 1996). Based on a limited number of taxa, there are indications that the same pattern occurs within fauna and fungi (e.g. Provoost and Bonte (2004) for a biodiversity overview of the Belgian coast). However, a substantial number of species restricted to coastal dunes does exist, which indicates a historical continuity of the habitat in general. These characteristic dune species are linked to open vegetation; beach, mobile dune or '(semi)-fixed herbaceous dune, characteristic of young landscapes (Van der Maarel and Van der Maarel-Versluys 1996). From a conservation point of view, society certainly has a responsibility to ensure evolutionary continuity to the species characteristic for this landscape type, even if unnatural measures are required to achieve this goal.

Reconciliation of both elements, the increasing development of late successional stages on the one hand and the threatened biodiversity of open coastal habitats on the other, will require a strategy applying a mosaic of habitats. Important in this regard is the spatiotemporal pattern and scale at which the mosaic is interpreted. This can be within individual sites, but should also take into account occurrence of habitats at other scales. The optimum scale depends partly on the habitats of interest, and should take into account species characteristics such as dispersal ability as well as local scale issues such as soil type geomorphology and larger-scale factors such as climate.

Management strategies

In general, the recent vegetation developments with grass and scrub encroachment in particular, are considered to have negative impact on biodiversity (e.g. Kooijman and Besse 2002; Grootjans et al. 2008; Jones et al. 2004). Nature conservation can respond to this on several levels. Sometimes, the source of driving forces can be addressed. Policies aimed at reducing air pollution have substantially reduced emissions of nitrogen dioxide (NEGTAP 2001) and have led to a small decrease in nitrogen deposition throughout Europe, although deposition levels are still way above the natural reference situation. Global climate change or urbanisation however, are less likely to be counteracted within a short period of time.

Internal management (grazing, mowing, sod cutting, …) as a symptom mitigating strategy, currently is the major response of nature managers for the maintaining the biodiversity in our coastal dunes. The re-establishment of grazing is a key management tool for this purpose (e.g. Boorman 1989; Hewett 1985, Kooijman and van der Meulen 1996; Wallis de Vries and Raemakers 2001), in general with satisfactory results. However, vegetation dynamics is not a simple linear event with one direction corresponding to fixation and succession and the other direction with regression and aeolian dynamics. De Raeve (1989) considers at least two mechanisms, acting independently to a certain extent. Stabilisation and subsequent soil development is seen as a first mechanism. Decalcification and general aging of the landscape are the main processes acting along this axis. A second mechanism is related to stress and disturbance factors influencing vegetation structure, such as nature management or natural herbivory. Vegetation dynamics such as grass encroachment or woodland development can occur on several points along the first axis, i.e. within landscapes of different ages. An important lesson derived from this scheme is that management such as grazing does not necessarily rejuvenate the landscape but mainly influences vegetation structure within a gradually aging landscape. Rejuvenation usually requires much more dynamics, as shown by the hysteresis model in Fig. 4 .

Furthermore, several moss or lichen dominated grey dune types are sensitive to trampling (Ketner-Oostra and Sýkora 2004; Jun et al. 2004). These communities depend on undisturbed development in a stabilising environment (bottom trajectory on Fig. 4). Consequently, large scale aeolian dynamics are required before these conditions can be met. Acceleration of succession due to elevated temperatures or N-deposition however, implies a decreased life span for these pioneer stages. In southwestern France, moss and lichen dominated grey dune vegetation can be found which developed under (mainly drought) stress conditions for more than a century (Jun et al. 2004). Although similar developments are unlikely to occur under colder and/or wetter conditions of northwest Europe, we can assume that the maturing trajectory of these habitat types has significantly shortened during the last decades, preventing the development of species rich communities which contain slow colonisers. The disappearance of terrestrial growing epiphytic lichens in Terschelling, the Netherlands (Ketner-Oostra and Sýkora 2004) and also in Belgium (Massart 1912) is probably a symptom of this evolution.

In conclusion, future dune management will require creativity and a wide range of techniques in order to effectively oppose current trends in vegetation development without disregarding the desired revaluation of coastal dune woodland on the one hand and the ecological subtleties of open dune habitats on the other. Large-scale remobilisation of stable and senescent dune systems will be a crucial element in this strategy. Although the concept of remobilisation is not new amongst dune managers, especially in the Netherlands (e.g. Arens et al. 2004; Arens and Geelen 2006) and increasingly elsewhere (e.g. Rhind and Jones 2009), it goes against a very long tradition of dune stabilisation. In the 1960s and 1970s, mobile sand was still viewed as undesirable and management handbooks all described methods for rapidly stabilising blow-outs (e.g. Ranwell and Boar 1986; Brooks 1979). A few lone voices called for natural dynamics to be allowed to persist, but these were largely unheard until the European Dune Symposium in Leiden, 1987, where dune nature managers from across northwest Europe called for a more dynamic approach (van der Meulen et al. 1989).

Still, destabilisation is not an obvious recipe, certainly seen in the light of current and future climate change. This will probably bring about major dune management challenges, as already discussed by van der Meulen in 1990. The actual effect on specific sites however, largely depends on local factors, particularly sediment budget (see e.g. Saye and Pye 2007; Rhind and Jones 2009 for the dune systems in Wales).

Future research

Although a large body of literature exists on changes in landscape and vegetation on coastal dunes, most studies are descriptions of local situations. Furthermore, a lot of this information is difficult to access because it is part of the 'grey literature'. It is a challenge to unlock this information within the framework of a European coastal dune network and make it available for future research. There is still challenging work to be done in several fields. Comparative studies within a broad geographical range are one approach. They can reveal relations between parameters which are only sampled in a narrow range in local studies (see e.g. Jones et al. 2004 and Remke et al. 2009 for influence of nitrogen deposition). The other approach is the focused experiment, aiming at the testing of clearly defined hypothesis (e.g. Plassmann et al. 2009; ten Harkel and van der Meulen 1996). Two main research topics need special attention. A first one is sand drift and its relation with climate and other present and historical factors. A second is nutrient dynamics and its relation with nitrogen deposition and a changing climate.

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