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BOREAL ENVIRONMENT RESEARCH 18 (suppl. A): 4–12
ISSN 1239-6095 (print) ISSN 1797-2469 (online) © 2013 Helsinki 18 December 2013

Long-term consequences for vegetation of ungulate introductions to North Atlantic Islands

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Received 12 Nov. 2012, final version received 12 Apr. 2013, accepted 7 June 2013

Hannon, G. & Bradshaw, R. H. W. 2013: Long-term consequences for vegetation of ungulate introductions to North Atlantic Islands. *Boreal Env. Res.* 18 (suppl. A): 4–12.

The Faroe Islands are relatively treeless today, but were more heavily wooded in the past. Woody vegetation disappeared following the arrival of people and their grazing livestock in the mid-700s AD, but there is some recent plantation in fenced areas. While soil conditions and exposure to wind and salt spray undoubtedly restricted the area of suitable habitat for woody vegetation in the past, climatic conditions were probably favourable for the growth of several woody species. There are no large natural herbivores so the relatively late introduction of pastoral and agricultural farming had a profound effect on the natural vegetation, transforming the flora on these relatively small islands, contributing to a widespread change in vegetation and removal of the limited, native woody cover.

Introduction

Island floras are often more impoverished than their nearest mainland, which to a large extent can be attributed to dispersal processes, local micro-climatic conditions, timing of human settlement and history of land-use. The study of long-term ecosystem change on islands, where clear 'settlement horizons' and the associated introduction of large herbivores can be reliably identified, yields insight into the effects of grazing and browsing animals on forest cover and vegetation development.

Human settlement of the Faroe Islands occurred relatively late in European terms (Jóhansen 1985, Hannon and Bradshaw 2000, Hannon *et al*. 2001, Edwards *et al*. 2005). The arrival of people on these relatively small islands had an immediate and profound effect on the landscape, because of tree and scrub clearance, the introduction of their animals and cultivated crops. Human settlement not only transformed the flora, but of the 90 vascular plant species present only since settlement, 30 have become naturalised and the other 60 commonly occur as weeds on cultivated land or in urban areas (Hansen and Jóhansen 1982). People and their grazing animals contributed to the widespread change in vegetation, causing a severe reduction of already restricted native woody cover (Hannon and Bradshaw 2000).

The Faroe Islands had probably become climatically suitable for *Pinus*, *Alnus*, *Corylus*, *Sorbus*, *Betula*, *Ulmus*, *Populus* and *Juniperus* during the early Holocene although conditions on Iceland were unlikely to have ever suited *Corylus* and *Ulmus* (Sykes *et al*. 1996). The Holocene pollen record on the Faroe Islands includes all

Editor in charge of this article: Eero Nikinmaa

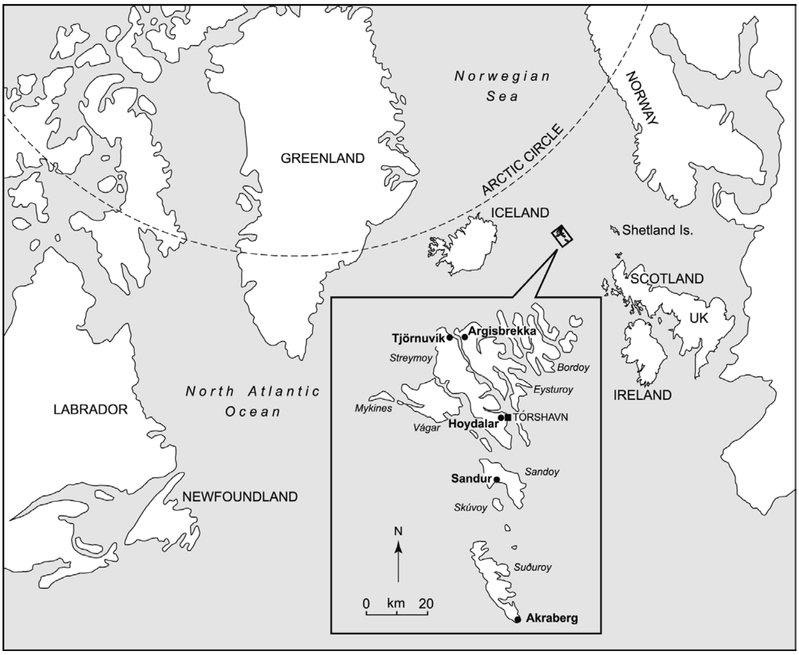

Fig. 1. The North Atlantic and The Faroe Islands with the localities mentioned in the text.

these taxa although potential long-distance pollen dispersal complicates the interpretation of local tree presence (Jóhansen 1985, Hannon *et al*. 2003, Hannon *et al*. 2010). Only *Betula pubescens*, *Sorbus aucuparia*, *Juniperus communis* and possibly *Populus tremula* are indigenous woody trees and shrubs on Iceland. Large herbivores are only associated with human introductions on all these islands with skeletal remains identified for sheep, goats and cattle (Hannon *et al*. 2001, Arge *et al*. 2005). In this paper we review the impact of ungulate introduction to the Faroe Islands on woody vegetation and compare the results with records from Iceland. We test the hypothesis that ungulate introduction irreversibly altered regional vegetation pattern.

Setting

The Faroe Islands are a series of small islands situated in the North Atlantic between Iceland, Norway, and Scotland (Fig. 1). Steep mountainous plateaux, narrow terraces and cirque valleys divided by narrow fjords and sounds are more common in the northern reaches, while some lower relief areas can be found to the south, particularly on the island of Sandoy. The present climate is strongly maritime with mild winters (mean January 3.2 °C) close to sea level and cool summers (mean June, July, August up to 11 °C), while at higher altitudes conditions are arctic in character (Humlum 2010). Rainfall varies both with altitude and regionally with the highest rainfall on the northern islands of over 3000 mm pa and lowest on the western islands of less than 900 mm pa. The lowlands in centre of the islands receive ca. 1500 mm pa (Fosaa 2010). The dominant winds which come from W, SW and S have an average speed of 7.2 m s^{-1} (1961–1995), recorded at Akraberg (Fig. 1), on the southernmost tip of the southern island, Suðuroy (Humlum 2010).

The islands are characterized by windswept, low growing vegetation, heavily influenced by sheep grazing and to a lesser extent by geese, hares and domestic cattle (Fosaa 2010). Although 70% of the land area is over 200 m a.s.l., the mean temperature of the warmest months on a certain proportion of the islands is above the isotherm used to define tree growth (Körner 1998). Nevertheless, soil conditions, wind and exposure to salt spray may severely restrict suitable habitat. Griffiths (2006) showed that salt spray restricted tree growth in the coastal zone of heathland areas for up to 200 m in moderately wind-stressed environments in northeastern USA, and Burley *et al*. (2010) found that salt spray limited the distribution of *Betula* and other trees in coastal Nova Scotia. Salt spray is likely to have even greater effects on vegetation composition of the highly wind-stressed, steep-sided Faroe Islands, where primarily coastal species such as *Armeria maritima* and *Plantago maritima* are widely distributed. A variety of woody plants occur on the Faroe Islands today, but the 'native' status of some has always been unclear. Moist dwarf shrub vegetation characterises the lowlands up 200 m a.s.l. today, with some variation between north-facing and south-facing slopes (Fosaa 2010). At higher altitudes, moist grasslands dominate up to 400 m a.s.l., and alpine vegetation is above 400 m a.s.l. (Fosaa 2010). Forestry plantations were first established at Hoydalar in 1885 (Fig. 1), but it was only in the mid-1900s that other types of tree planting became mildly successful in sheltered localities or close to urban areas, particularly the capital, Tórshavn (Leivsson 1989). Sheep are the most common domestic animal and have unrestricted access to uncultivated areas throughout the year and on the infields during the winter months with the result that only 'untouched' vegetation remains in clefts, ravines or on the most inaccessible slopes (Jóhansen 1996).

Evidence from the past

The last 2000 years covers the time before and after a reliably dated 'human settlement horizon' can be established on the Faroe Islands (Jóhansen 1985, Hannon and Bradshaw 2000). There are different estimates for colonisation and settlement derived from three available sources: (1) historical documents, (2) archaeological evidence, and (3) palaeoecological data. The contested literary source for first colonisation by Irish monks and their sheep (Tierney 1967) is prior to the arrival of the Norse (Thorsteinsson 2005). The palaeoecological data support the former where pollen and macrofossil data point to cereal cultivation and the use of fire from at least the mid-700s AD (Jóhansen 1985, Hannon and Bradshaw 2000, Hannon *et al*. 2001) while the Viking farmsteads and artefacts date from the 9th century (Arge *et al*. 2005).

The Viking grave site at Tjörnuvík is on the northern end of the island of Streymoy (Fig. 1), at the end of a large valley meadow close to the sea. Pollen analysis from this meadow (Hannon and Bradshaw 2000) revealed evidence for arable and pastoral agriculture from ca. the mid-700s AD along with a micro charcoal record, a clear indicator of human activity, as in the wet cool climate of these islands, natural fires are extremely unlikely. The pollen flora (Fig. 2) included cereal pollen grains. The main woody pre-settlement shrub pollen was *Juniperus*, but tree (*Betula*) pollen was also recorded. The decline in *Juniperus*, which was probably used for fuel and for charcoal, was accompanied by an expansion of arable weeds and a change in the flora from the original damp fen, to a drier, more diverse community with several grassland and ruderal species including *Rumex* cf. *longifolius*, *Filipendula* and Asteraceae. Apart from the arable crops, these species almost certainly grew elsewhere on the islands before settlement. Graminoids showed substantial increases when people arrived, not only because of the disturbance from cultivation, but also presumably, from their grazing domestic animals. Plant macrofossils (visible remains of plants such as leaves, buds and seeds) (Fig. 3) provided even more convincing evidence for the major shift in vegetation composition. The records of abundant *Montia fontana*, *Stellaria media*, *Lychnis flos-cuculi*, *Sagina procumbens*, *Chenopodium album*, *Rumex* cf. *longifolius*, *Plantago* sp., *Rumex acetosa*, *Cardamine flexuosa*, *Galaeopsis speciosa*, *Linum catharticum*, *Ranunculus repens*, *Stellaria alsine* and *Sedum villsoum* followed settlement, supporting the pollen interpretation of a major change in species diversity in the meadow.

While pollen is the sub-fossil most usually used to reconstruct past vegetation, some can be transported over long distances and in an exposed island setting can be difficult to interpret. Very low percentages of arboreal pollen recorded over the last 9000 years on the Faroes include *Betula*, *Fraxinus*, *Tilia*, *Corylus*, *Sorbus aucuparia*, *Alnus*, *Ulmus*, *Quercus*, *Populus* and *Pinus* (Jóhansen 1985, Hannon *et al*. 2005, 2010, Lawson *et al*. 2008). While local occurrence of *Corylus*, *Sorbus aucuparia* and *Populus* has been debated, other arboreal pollen have in

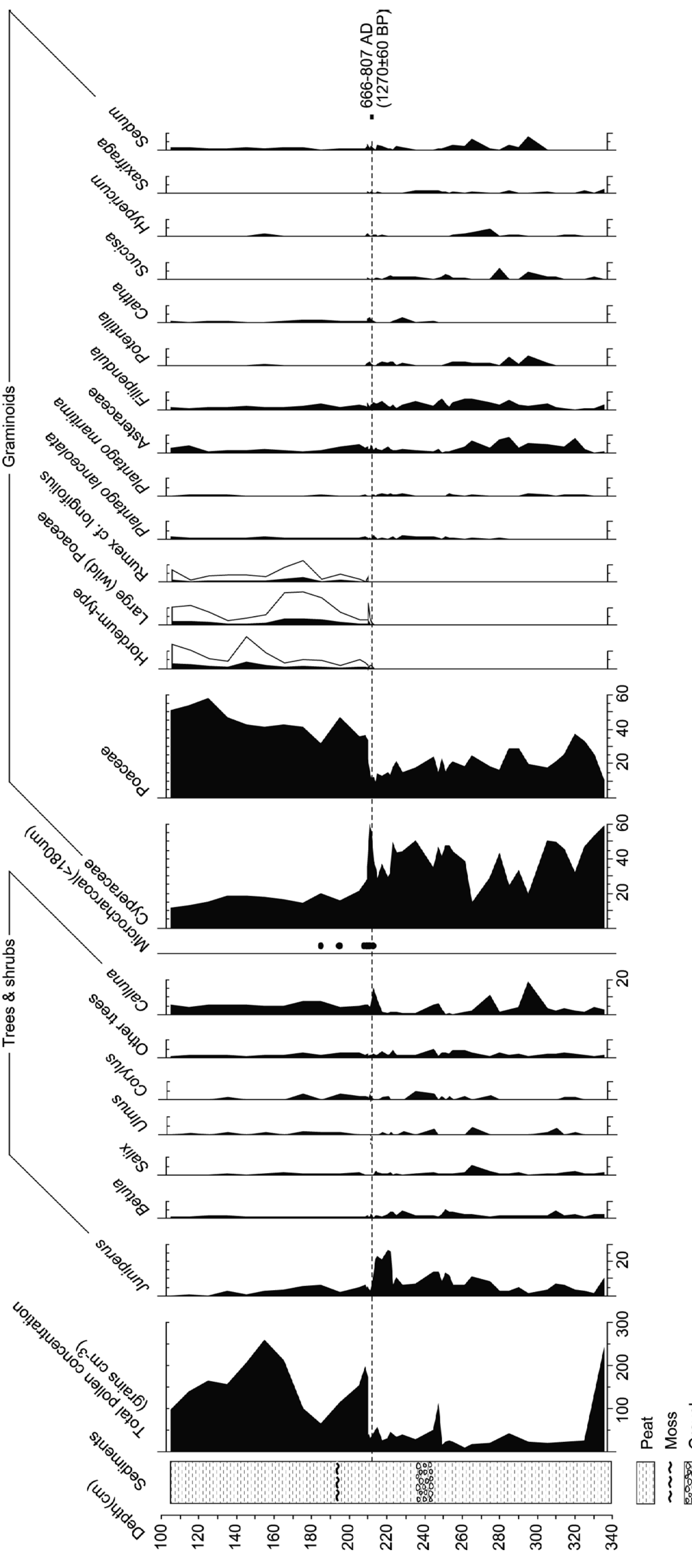

Fig. 2. Total pollen concentration and selected pollen percentages from Tjörnuvík (after Hannon and Bradshaw 2000). The dashed line marks where the first pollen of cultivated crops was recorded and the scale of selected taxa is exaggerated by five.

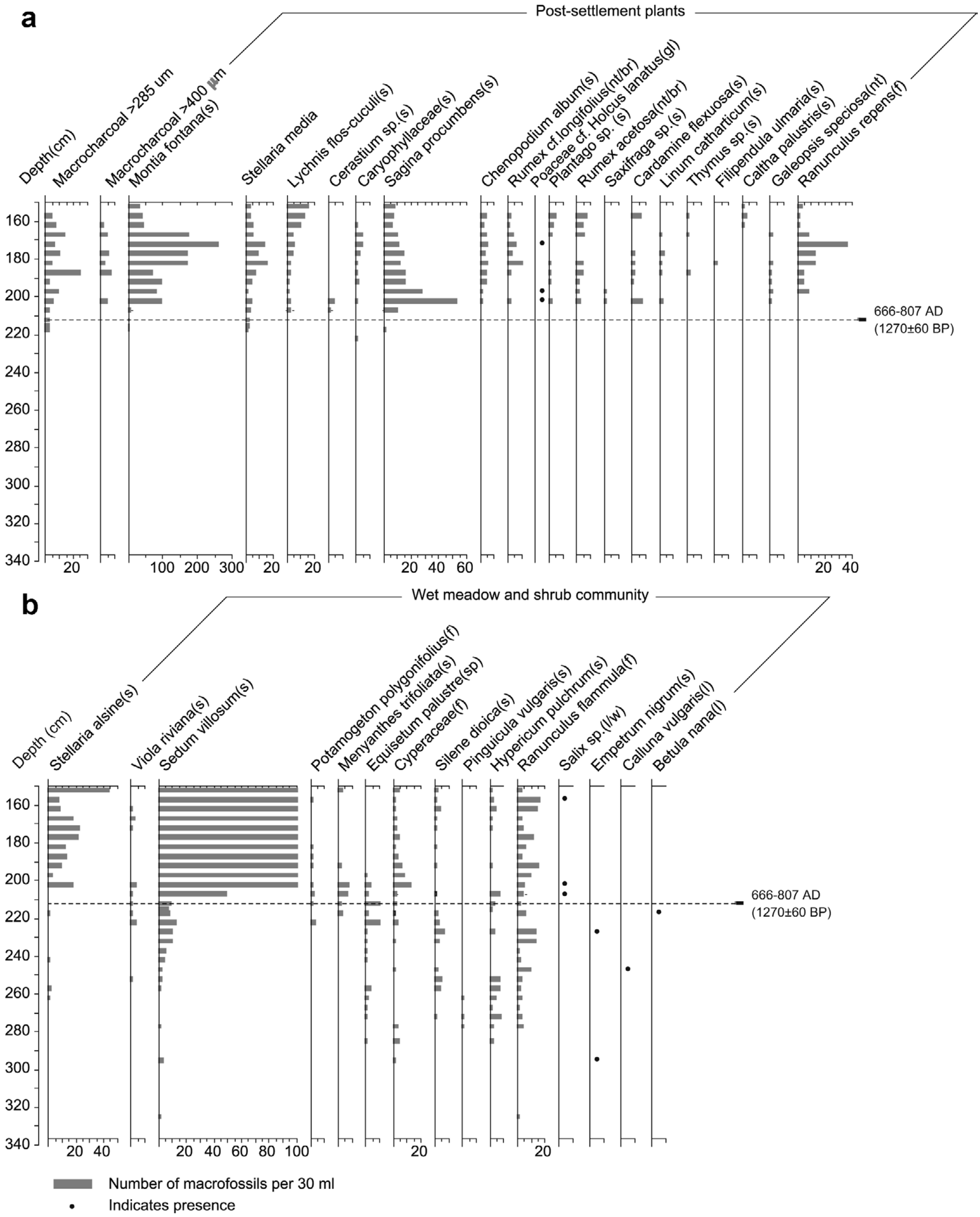

Fig. 3. Selected plant macrofossil concentration diagram from Tjörnuvík (after Hannon and Bradshaw 2000). (**a**) Post-settlement plants, and (**b**) wet meadow herbs and shrubs. Abbreviations: br = bract, f = fruit or fruitstone, l = leaf, nt = nut or nutlet, s = seed, sp = sporangial cone, w = wood. The dashed line marks where the first pollen of cultivated crops was recorded.

the past thought to be of long distance origin. *Sorbus aucuparia* can be difficult to identify, while *Populus* pollen does not preserve well, especially not in the minerogenic peat or lake sediments from the Faroes, and is probably much underestimated in most pollen records.

Hannon *et al*. (2005) reviewed the evidence for former woody cover and collected wood megafossils of *Betula*, *Salix* and *Juniperus communis* buried in peat from 5 of the islands (Fig. 4). The megafossils dated were from each millennium between ca. 8000 years ago up until 730 AD, and revealed that the islands had supported woody cover up until the arrival of people (Hannon *et al*. 2005). Megafossils provide best evidence for local presence when they are preserved in the same position as when they lived, and the only locality to fulfil these criteria on the islands is at the Norse archaeological site of Argisbrekka (Fig. 1) on the northern island of Eysturoy at an altitude of 130 m a.s.l. (Mahler 1991). A thick layer of wood peat containing *in situ Betula pubescens* roots was recorded 60 cm below the surface sediments together with *Juniperus communis* and *Calluna vulgaris* dating from ca. 4250 years ago until the Norse settlement horizon (Jóhansen 1989, Mahler 1991). A series of trenches showed just how extensive the woodland had been in this valley (Mahler 2007). An 8 cm thick branch of *Corylus* dating from 890 AD was also uncovered with basal axe marks indicating felling. This was originally considered to be a human import as it was not in situ (Malmros 1994), but in the light of pollen influx data from several long pollen records, this species, together with *Betula*, *Salix* and *Juniperus*, was probably an indigenous tree from the earliest Holocene (Bradshaw *et al*. 2010). *Sorbus aucuparia* and *Populus* are also thought highly likely to be natives based on their pollen accumulation rate values and *Ulmus* is a possible native candidate, although the pollen evidence is less secure (Bradshaw *et al*. 2010). The decline of *Juniperus communis* populations on the islands has been reviewed by Edwards (2008) who concluded that "even though natural causes may be involved, such as climate or soil change, anthropogenic factors — of which goat husbandry might have been one — were probably contributory but are not the only answer" (Edwards 2008). The earliest goat/sheep bones date to within the range 560–900 AD (1320 ± 80 BP) (Hannon *et al*. 2001).

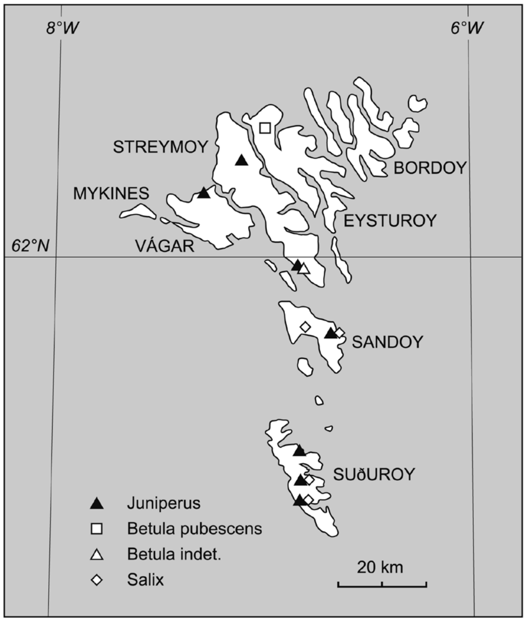

Fig. 4. The locations where the wood megafossils were found on the islands of Streymoy, Eysturoy, Vágar, Sandoy and Suðuroy

Discussion

Herbivores are considered by some authors to exert a major control on the composition and structure of much European semi-natural vegetation (Humphrey *et al*. 1998). Sheep and goats, in particular, tend to feed selectively, suppressing the herb flora and allowing the spread of grasses (Grant *et al*. 1985, Lagerås 1996). The limited floristic diversity and absence of large natural herbivores meant that the introduction of domestic animals caused an upheaval to the already restricted native woody cover of the Faroe Islands. The effect on the ecosystem of these relatively small islands was profound and contributed to a widespread change in vegetation, the loss of restricted native woody cover and possible local species extinctions. The modern population of sheep at an average of 44 ewes km^{-2} (Thorsteinsson 2001) outnumbers that of people, which in January 2010 totalled 48 574 (34.5 per km^2) (http://www.visitfaroeislands.com). The uncontrolled numbers of sheep which graze grassland and the dwarf-shrub heathlands now dominated by *Calluna*, *Vaccinium* spp. and *Empetrum*, prevent any establishment of trees and shrubs in unfenced areas at the present time. The numbers of sheep on the Faroe islands have varied in the past following their introduction at

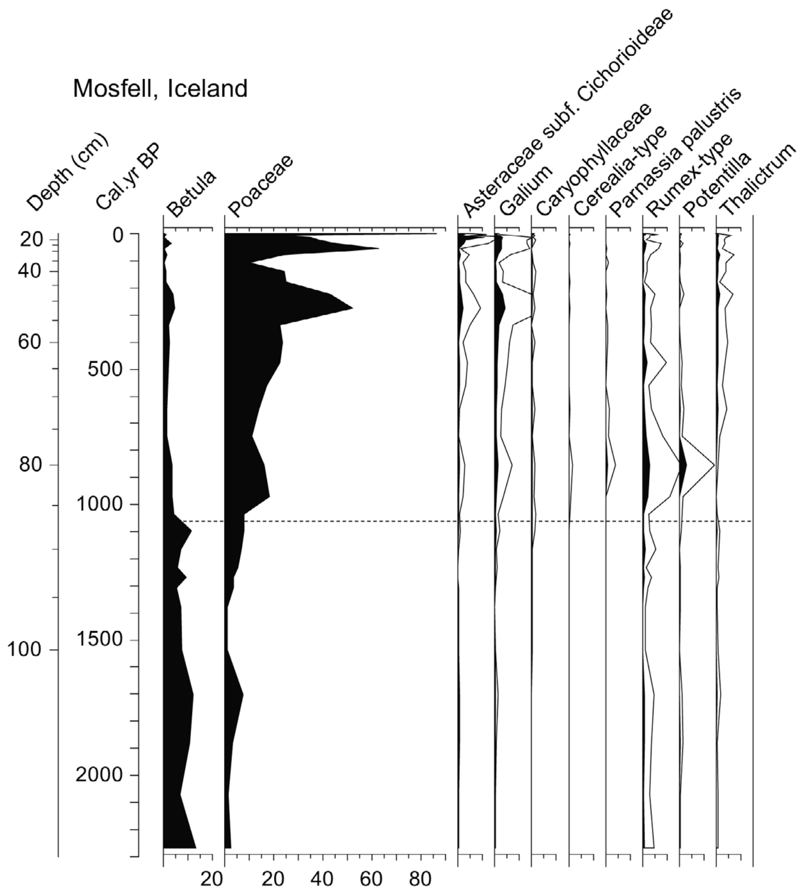

Fig. 5. Selected pollen percentage diagram from Mosfell, Iceland (after Hallsdóttir 1987). The dashed line marks where the first pollen of cultivated crops was recorded and the scale of selected taxa is exaggerated by five.

the time of human settlement, but they appear to have always been considerably higher than at the present time (Table 1) (Austrheim *et al*. 2008). Prior to AD 1600, the number of breeding ewes has been estimated to be three times the present-day population size. Austrheim *et al*. (2008) demonstrated by exclosure experiments the considerable effect sheep have on the current vegetation. Tree regeneration is prevented and tough grasses like *Nardus stricta* are favoured at the expense of other grasses and herbaceous species. It seems highly probable that sheep have contributed both to the loss of woody plants and to the spread of open communities and are the major reason why trees do not regenerate naturally there today (Jóhansen 1996). Arable agriculture may also have contributed to initial tree clearance on the Faroe Islands, but archaeological and paleoecological analyses have shown that field systems were confined to a few coastal sites (Edwards *et al*. 2005).

Table 1. Estimated number of ewes on the Faroe Islands (after Austrheim *et al*. 2008)

Year AD	Estimated number of ewes
Before 1600	200 000
1781	75 000–100 000
1870	100 000
2004	70 000

A similar situation of loss of trees has been proposed for Iceland, where sheep also continue to have a regional influence on vegetation (Einarsson 1963) although there is some debate about when forest cover first began to decline (Òlafsdóttir and Guðmundsson 2002). However, a very rapid decline in *Betula* pollen takes place at almost all pollen sites, often in less than 100 years following first settlement (Fig. 5) (Einarsson 1963, Hallsdóttir 1987, Sveinbjarnardóttir *et al*. 2008, Vickers *et al*. 2011). The loss of trees is coincident with increase in grasses and herbaceous species indicative of grazing animals (Fig. 5). There is also evidence for widespread soil erosion (Thórarinsson 1961). The initial settlements and colonisation of Iceland were based around pastoral farming, particularly dairy cattle and sheep (Sveinbjarnardottir *et al*. 2008), whereas archaeofaunal remains from the Viking settlement at Sandur on the Faroe Islands (Fig. 1) reveal that sheep/goat bones, bird, fish and shellfish were common and cattle were rare (Arge *et al*. 2005). Re-planting programmes are helping begin a restoration process in Iceland and the Faroe Islands, but such programmes have to be carried out in conjunction with soil restoration measures at many sites.

These examples illustrate the greater sensitivity of islands to human impact than the mainland. Their relative isolation contributes to unusual combinations of species and a particular vulnerability to new introductions. Certain sequences of events can be more clearly observed in remote settings. It remains unclear whether the treeless grasslands and heathlands that characterize the Faroe Islands today are solely a cultural product, but herbivores, particularly goats and sheep can be particularly destructive when their populations are unchecked. Islands are useful indicators of the spread of human impact around the world and also provide instructive examples of the consequences of over-exploitation of finite resources, indicating where many heavily exploited mainland systems may be headed. The palaeoecological records from the Faroe Islands and Iceland are strongly indicative of large-scale, regional changes in vegetation brought about by uncontrolled ungulate grazing and browsing. There is evidence from Iceland that re-introduction of trees requires significant ecosystem management measures upholding our original hypothesis.

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