The History (1620–2003) of Land Use, People and Livestock, and the Relationship to Present Plant Species Diversity in a Rural Landscape in Sweden

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ABSTRACT

The traditional agriculture in Europe favoured numerous plant and animal species that are presently declining. Integrated studies based on various sources are needed in order to unravel the complex relationships between changing landscapes and biological diversity. The objectives of this study were to describe changes in land use during c. 350 years in a Swedish agricultural landscape in relation to changes in human population and livestock, and to analyse relationships between historical land use and present-day plant species diversity. There were only minor long-term changes in land use, population and livestock between 1640 and 1854 in the two studied hamlets, but detailed data 1620–41 showed a large short-term fluctuation in livestock numbers. After 1854 larger changes took place. Grasslands were cultivated and livestock composition changed. After 1932, livestock number decreased and most of the former grazed outland (areas located outside the fenced infields) turned into forest by natural succession. 7 per cent of the study area is still grazed semi-natural grassland. The highest plant species richness is today found on semi-natural grassland with a long continuity of grazing. The distribution of five target species suggests that previous land use still has an important effect today. The majority of their occurrences are remnant populations located in previous outland pastures which are today forests.

KEY WORDS

Land use history, human population, livestock, plant species diversity

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INTRODUCTION

The landscapes of most parts of Europe have been shaped by human activities extending far back in history.[1] Modernisation of agricultural practices, globalisation of economies, urbanisation and a general increase in human populations (but a population decrease in rural areas during the last decades) have caused a drastic transformation of these landscapes, particularly during the last 60 years. These landscape changes have severe implications for values associated with the 'traditional' agricultural landscape (loosely defined as the landscape existing before mechanisation and extensive use of artificial fertilisers). Numerous plant and animal species were favoured by traditional agriculture[2], and in 'modern' society, many people highly appreciate the traditional landscape for beauty, cultural history, identity and recreation. Thus, ongoing landscape changes are often considered negative and extensive programmes for maintaining or restoring traditional landscapes (or elements of such landscapes) have been launched across Europe. Despite the concern about landscape change, we lack basic knowledge on details in the transformation processes and how they translate into long-term changes in biological diversity and other values associated with traditional landscapes. Still relatively few studies have tried to combine knowledge from separate disciplines, such as ecology, agricultural history and geography, to produce syntheses of how land use has changed during recent centuries, and how these changes are manifested in the present-day landscape.[3]

Since this study concerns landscape change in Sweden, a brief account of the development of the Swedish agricultural landscape is necessary. In Sweden, the introduction of agriculture took place 6000 BP (Before Present) as a slash-burn culture in combination with a mobile hunter-gatherer culture.[4] Around 2500 BP agriculture developed from being mobile to the use of permanent fields. This change was manifested by the development of infields and outland. The farms and hamlets were surrounded by infields comprised of small arable fields and more extensive areas used for haymaking.[5] Hay-meadows were often wooded, and the trees were used for pollarding.[6] Extensive outland areas used for grazing surrounded the infields, and this outland was probably mostly semi-open forest. Generally, the management systems with semi-natural grasslands used for haymaking (infields) and outland grazing existed up to the late nineteenth century, when modernisation of agriculture took place – in particular the transformation from mowing hay in semi-natural grasslands to growing ley for fodder on arable fields.[7] Between the late nineteenth century and the 1940s, there were still vast areas of semi-natural grassland used for grazing, but ongoing modernisation reduced these areas also. At present, there is approximately 350,000 hectares managed semi-natural grassland left in Sweden compared to 2 million hectares 100 years ago.[8]

In this study, we have focused on two farms (previously hamlets) located on the island of Selaön in Lake Mälaren, Sweden, and compiled data on changes

in land use, human population and livestock from the early seventeenth century and onwards. This information has been combined with recent survey data on plant species diversity. The overall objective of our study was to describe land use history on Selaön, with a focus on these hamlets, using different kinds of information: written sources, old cadastral and land use maps, and evidence from present-day species diversity. More specifically, our aims were to answer the following questions: (1) What are the relationships between changes in human population and land use? (2) Is there evidence of changes in livestock number and in the exploitation of land used for grazing, before the modernisation of agriculture in the late nineteenth century? (3) What are the relationships between infields and outland, before modernisation? (4) What are the relationships between land use and (i) present-day plant species diversity in different grasslands, and (ii) the presence of grassland species in present-day forests with a history of previous grazing management? We conclude with a discussion of the potential of in-depth historical analyses of land use change, people and livestock for conservation programmes and for the assessment of values in traditional agricultural landscapes.

METHODS

Study area

The study area is located in Överselö parish, on Selaön (59° 24' N, 17° 10' E), an island in Lake Mälaren 50 km west of Stockholm, in the county of Söder-

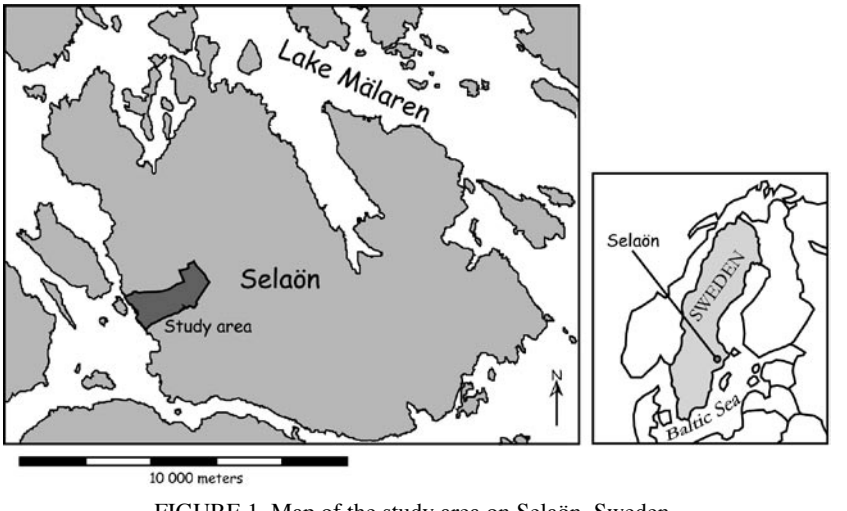

FIGURE 1. Map of the study area on Selaön, Sweden.

manland, Sweden, and has a focus on two farms, former hamlets, Ettersta and Viggeby (Fig. 1). Throughout this paper we will refer to Ettersta and Viggeby as two hamlets. Selaön is the largest inland island in Sweden (91 km^2). Historically, the island had a strategic position on the route to the old cities of Sigtuna and Birka.[9] The topography on Selaön is slightly undulating with broad valleys filled with clay. Moraine and almost bare bedrock dominate the hills, and the bedrock is composed of gneiss and granite. Mean temperature for January is –3° C and for July 18° C. Annual precipitation is 600 mm. Both hamlets are situated on the west coast of Selaön and have in historic times consisted of two farms in each of equal size, sometimes managed by one owner and sometimes by two.

Map analysis, aerial photos and statistics

To estimate and visualise spatial land use change we have used a combination of cadastral maps (from the seventeenth, eighteenth and nineteenth centuries), agricultural statistics (twentieth century) and aerial photographs from 1954 and 1996 (Fig. 2).

Sweden has a unique collection of old, large-scale cadastral maps, from cartographic work that was initiated in the 1630s.[10] The rationale behind making these maps was a demand for land redistribution schemes and land reforms, but also for providing a basis for taxation. The maps are generally of high technical quality and the scale is usually 1:4,000.[11] The maps depict detailed information on the enclosed land (i.e., infields) around a village or hamlet, such as land use, ownership, yield and physical properties (for example, if meadows are very wet or if there are boulders or outcrops of bedrock in fields). The land outside the enclosures, i.e., outland used for grazing, was usually not included in the early maps. However, in the maps used in this study the outland was included (except for the map from 1635). Old cadastral maps have been used in order to obtain spatial historical data in several ecological studies on the influence of past land use on present-day vegetation patterns.[12] The main use of agricultural fields, meadows, enclosed pastures and outland can often be understood through comments on productivity (seed/yield ratio, harvested hay loads and the number of livestock that could be kept in an area) in the cadastral maps. However deviations such as temporary fields in meadows and occurrence of slash-and-burn agriculture in the outland are usually absent in the descriptions. Moreover, there was a slight change in terminology during the nineteenth century which altered the earlier infield-outland classification. The late cadastral maps also included an element of planning, so that land suitable for future cultivation could be called agricultural fields even if cultivation had not yet occurred. We also know that some terms, such as forest, have changed meaning with time.[13]

We had to use several cadastral maps in order to obtain spatial land use change, over Viggeby from 1635 and 1722 and over Ettersta from 1746 and 1830. In the maps from the eighteenth century, the outland grazing area is recorded for

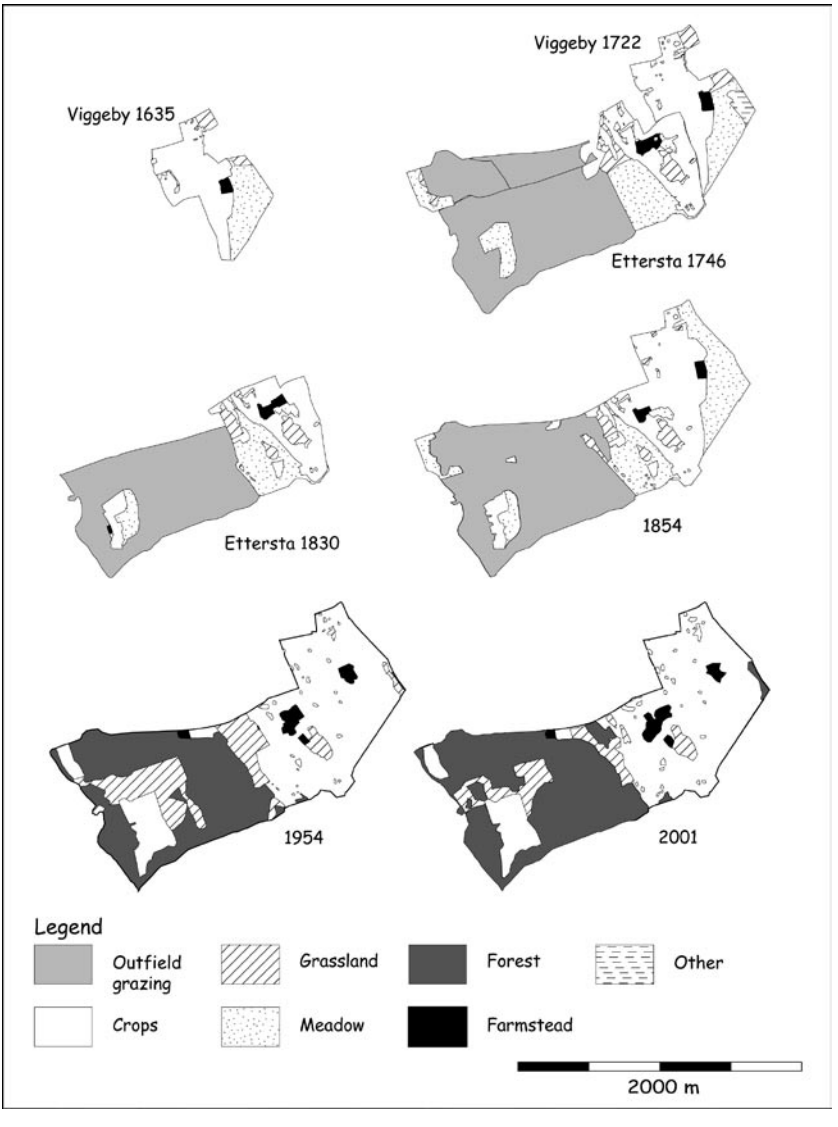

FIGURE 2. Land use maps over the study area on Selaön, Sweden, from 1635 until 2001. The maps from 1635 to 1830 are based on old cadastral maps depicting each hamlet separately. There is a map over the area from 1854 that comprises both hamlets. The later maps derive from aerial photographs.

each hamlet. From 1854 we used a map covering the whole Överselö parish but used only the part covering Ettersta and Viggeby. This map was made as a compilation of hamlet maps from the eighteenth and nineteenth centuries. The parish map covers all of the outland. We also used a map from 1900 covering the whole 'hundred' of Selebo (a 'hundred' is an old administrative unit incorporating several parishes) that was produced in the same way as the parish map. However it is much less precise as it contains fewer land use categories. Before the maps could be analysed some geometrical irregularities needed to be overridden.[14] A geocoded ortophoto was used as baseline for the rectification. All maps were digitised, interpreted and rectified, and then analysed in a GIS, geographical information system.[15]

The old cadastral maps include slightly different land use classes. The parish map from 1854 contained eight categories: farmstead, meadow, moist meadow, moist meadow with trees, outland, moist outland, arable fields and dry grassland. In the map over Ettersta from 1746 there were details on the outland such as slash and burn areas and conifer forest. In order to compare and analyse the land use change, the different categories were generalised into four land use classes: crops, grazed outland, mowed grassland and farmstead or croft. There was a class 'other' in Viggeby hamlet both in 1722 and 1854, which is a fen, probably mowed or grazed (Fig. 2).

Aerial photographs were used to analyse land use in 1954 (black and white) and 1996 (colour-infrared). The interpretation was carried out in zoom-stereoscope that makes it easier to differentiate small topographical differences, and thus correctly classify the vegetation. The interpretation of the 1996 photographs was thoroughly field-checked and used as a base for the present-day (2001) land use and land-cover map. Land use was divided into five classes: forest, crops, grazed land, farmstead, and other (Fig. 2). 'Other' denotes midfield islets, i.e., small impediments in arable fields that cannot be tilled. In the past the midfield islets were mowed and grazed.[16]

Agricultural statistics have been produced since the early nineteenth century. However, the classification of land use types and the ways of collecting statistical information have been changed several times.[17] From Selaön there are data for single farms, e.g. from 1915, 1932 and 1957. In 1915 the land was divided into garden, fields and other types of cultivated land, natural hay meadow, forest and pasture and finally other types of land. From the 1930s there was a separation between natural hay meadow and cultivated meadow. The former outland was defined as either forest or pasture. This reflects a change in the view of land use on the outland, i.e., from being essentially pasture that could also deliver wood products to the households, to becoming forest primarily used for production of timber or paper-pulp.

People and livestock

The estimated number of people living in the two hamlets, and in the whole of Överselö parish, was based on population tax registers. People under the age of 21 or over 65, poor people or people having difficulties in earning a living for other reasons, did not need to pay tax. The early records only registered taxpayers, but from the eighteenth century the registers usually covered all people living in the parish. The tax registers were not consistent in the way croft holders and cottagers were registered. In the eighteenth-century records, from this area, it is often difficult knowing to which hamlet a specific croft or cottage belonged. This is of interest since they and their livestock to some extent lived off the hamlet resources. There were no registered crofts in Ettersta until around 1812. In 1862 there were at least one croft and three cottages in the hamlet. In 1762 Viggeby had one soldier's croft (at this time hamlets and farms had to provide a piece of land for soldiers in the Swedish army, that they could cultivate as long as they were in the army). No other croft seems to have been added in Viggeby during the period.

The livestock tax registers from 1620 to 1641 were used as the earliest source to estimate the number of livestock in the area. The number of horses, cattle, sheep, goats and pigs owned by each farmer was registered nearly every year during this time-period. Several historians have used the livestock tax registers and concluded that the figures are reliable, even though tax registers are usually suspected of underestimating.[18] The tax did not include livestock less than one year of age. Thus, the number of juveniles was approximated using detailed accounts from Tynnelsö estate, Överselö parish, from the early seventeenth century, where the number of calves, lambs and foals born per adult was registered. The same relationship between young and adults was assumed to hold for other farms and was thus used for the approximation of young livestock. After 1641 there were no sources on livestock numbers until 1750 when a law proclaimed that probate inventories should be made after all deaths. Probate inventories differ from tax registers in several ways. They were not a basis for tax but for inheritance, thus the risk for underestimates is less compared to tax registers.[19] The inventories included all animals belonging to the deceased. Since people's deaths may occur at different times, the inventories from different farms in a hamlet are not contemporary. Moreover, it has to be considered whether the person died at an active age or if it was an old person whose belongings, including most of the livestock, had been passed on to younger people. Taking this into account it is possible to estimate the approximate livestock numbers for some years during 1750 to 1850, but not an exact number for each year. The agricultural statistics from the nineteenth century also included information on the number of all categories of livestock, young and adult. Livestock calculations were performed less frequently than other agricultural surveys, and data from some years are no longer available at the single village, hamlet or farm level. On the other hand the data from the nineteenth century are considered very reliable.[20]

All data on livestock numbers were transformed to 'livestock equivalents', in order to facilitate comparisons. One livestock equivalent equals 1 cattle, 0.7 horse and 4 sheep, based on the approximate relationship in energy demand between cattle, horses and sheep. The calculations of livestock equivalents do not take into account the increase in size and productivity of livestock, due to breeding. Before 1850 the impact of breeding in Sweden was insignificant because of fodder limitations.[21]

Plant species diversity

Two field surveys were conducted in 2002 and 2003, aimed at examining plant species diversity at the two hamlets. The fieldwork contained two parts. Firstly, the field work was directed towards finding and recording patches of five selected target species, considered characteristic for traditionally managed grasslands: the forbs *Ajuga pyramidalis*, *Antennaria dioica*, *Lotus corniculatus*, *Polygala vulgaris* and *Primula veris*.[22] The present-day vegetation map over the study area was used, and a grid-mesh with cells measuring 100m x100m was draped over the map and used as a base for the survey. In all, 213 cells covered Ettersta and Viggeby (cells located over the borders were excluded). All plant patches of the target species were positioned in the field by GPS (Global Positioning System), and assigned to a 100m x 100m cell. Each cell was assigned to a present-day vegetation type and the land use in 1854, based on the majority of land-cover or land use within each cell.

Secondly, the fieldwork included a survey of plant species richness in five land-cover categories: open grassland (0–10 per cent trees and shrubs), semi-open grassland (10–50 per cent trees and shrubs), semi-closed grassland (>50 per cent trees and shrubs), cultivated grassland and deciduous forest. The investigated categories represent the present-day succession stages of grassland. For each category of grassland the number of plant species was recorded in plots of one m^2. Previous studies have confirmed that small-scale species density is a valid estimate for 'quality' of the grasslands (from a conservation viewpoint) and also for estimating total species richness at spatial scales up to 1–5 hectares.[23]

The land use documented for 1854, and species density (species/m^2) and presence/absence of the selected target species, were used for descriptive examination. The cells, which are arbitrary units in the landscape, cannot be used as true replicates, and the data are thus not useful for statistical analysis. The relationships between land use history and present-day plant species diversity should therefore be viewed as tentative.

RESULTS AND DISCUSSION

Land use change

For Selaön in general, there were only small changes in land use and land cover from 1640 to 1854, but during the second half of the nineteenth century the fields almost doubled in extent through cultivation, primarily of former hay meadows, but also of pasture (Fig. 3). It is noticeable that the arable field area slightly exceeded the meadow area throughout the 200-year period between 1640 and 1854. The meadow area normally exceeded the area of the cultivated fields, and a common relationship of infield grasslands (meadows):crop-fields in Sweden was 3:1 to 6:1.[24] Another study from the same province show that the meadow:crop-field ratio changed from between 1.5:1 and 3:1 to between 0.25:1 and 1.25:1, between 1800 and 1860.[25] Deviating ratios between land use types can be explained by differences in productivity in different areas, and a varying proportion of the winter fodder that consisted of, for example, leaves and straw. Hay-meadows nearly disappeared on Selaön after 1854, and grazed and mowed grassland decreased, from covering more than half of the total area in 1854 to 15 per cent in the 1950s.

There was hardly any change in the infield area (arable field and meadow) in Viggeby between 1640 and 1854 but a dramatic cultivation of primarily

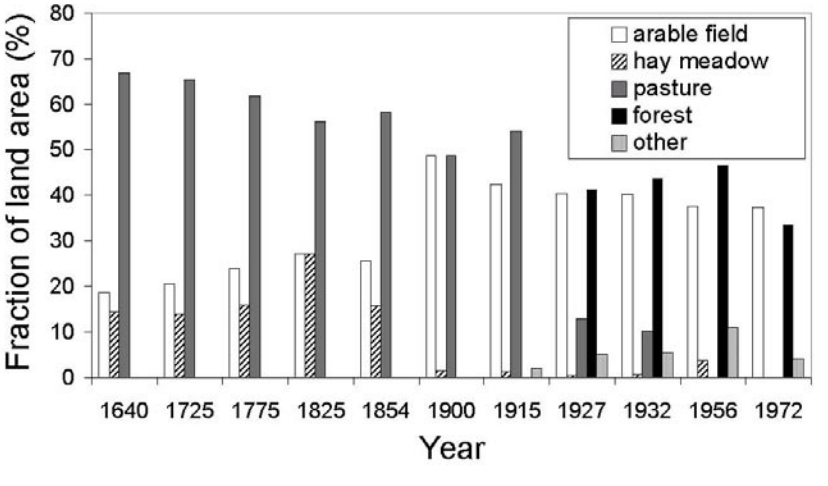

FIGURE 3. The percentage of different land-cover on Selaön, Sweden, from 1640 to 1972. Based on cadastral maps (15th to 19th Century) and agricultural statistics (20th Century).

meadow, but also some outland pasture, between 1854 and 1900 (Table 1). In Ettersta, some of the outland was cultivated between 1746 and 1835, and after 1854 nearly all meadows were turned into arable fields. Today only 9 per cent of the area is grazed, which also includes grazed former arable field. The actual grassland area with a long continuity of grazing (i.e. more than 200 years) left in the two villages, is 7 per cent, which is in the same order of magnitude as in the rest of Sweden. However, the grassland with a long continuity is restricted to Ettersta only and more than half is in the former outfield. There is no mowed grassland left today.

Before the 1930s most of the outland was grazed on Selaön, and some outland areas are still grazed. After the restriction of outland grazing, the expansion of forest was dramatic (Fig. 3). Thus, 41 per cent of the study area is forest today. From 1932 a large part of the former outland pasture was recorded as forest, in both hamlets. Arable fields increased from 19 per cent in 1640 to 49 per cent in 1900, and today arable fields have an extent of 47 per cent. Today, Viggeby is a completely open agricultural area without any other grassland habitats left apart from midfield islets.

TABLE 1. Land use given in hectares (ha) in the hamlets Ettersta from 1746, and Viggeby from 1640 until today. Based on cadastral maps, parish map, hundred map, agricultural statistics and vegetation map.

Year	Arable field (ha)	Meadow (ha)	Cultivated pasture (ha)	Natural pasture (ha)	Forest and other (ha)	Total area (ha)	Source
Ettersta							
1746	19.3	20.0	0	85.9	0	125.2	cadastral map
1835	25.7	20.8	0	78.0	0	125.2	cadastral map
1854	26.2	20.8	0	78.3	0	125.2	parish map
1900	53.0	0.3	0	71.0	0	125.2	hundred map
1915	53.0	0	0	72.5	0	125.2	agr. statistics
1957	47.3	0	5	23.0	51.4	126.7	agr. statistics
2001	52.9			17.2	57.2	127.3	vegetation map
Viggeby							
1640	19.3	14.6	0	35.7	0	69.6	Cadastral map
1722	20.7	12.7	0	36.2	0	69.6	Cadastral map
1854	21.8	15.6	0	32.2	0	69.6	parish map
1900	41.2	0	0	29.4	0	71.6*	hundred map
1932	45.0	0	0	6.0	21.0	75.5*	agr. statistics
1957	40.5	0	0	0	18.2	58.7*	agr. statistics
2001	43.8			1.3	26.4	71.5*	vegetation map

* The total area differs from earlier records because of changes in registered units.

Land use in relation to population changes

The number of people at Ettersta and Viggeby did not increase from 1767 to 1862 (Table 2), although Ettersta allowed a croft holder from the 1830s and some three cottagers later on. In Viggeby the only registered croft is, as mentioned, a soldier croft that was there already in 1762. The average number of people was 14 in each of Ettersta and Viggeby during this period. A small peak can be seen after 1870 but from 1900 the population decreased again. For the whole parish of Överselö, in contrast, the total number of people increased during the same period (Fig. 4). Considering tax payers only, the increase between 1717 and 1762

TABLE 2. The human population in the hamlets Ettersta and Viggeby on Selaön, from 1767 to 1939. x indicates that no data are available from that year in Ettersta. Based on population registers.

	Ettersta	Viggeby
1767	18	14
1770	14	13
1775	20	15
1780	17	16
1785	11	17
1791	20	14
1795	16	14
1799	10	13
1804	12	14
1810	11	12
1814	14	12
1820	15	11
1825	8	16
1829	10	14
1836	9	13
1840	15	15
1846	15	13
1850	16	16
1862	x	17
1871	21	21
1880	18	23
1901	20	9
1909	12	14
1920	18	16
1930	15	4
1939	12	3

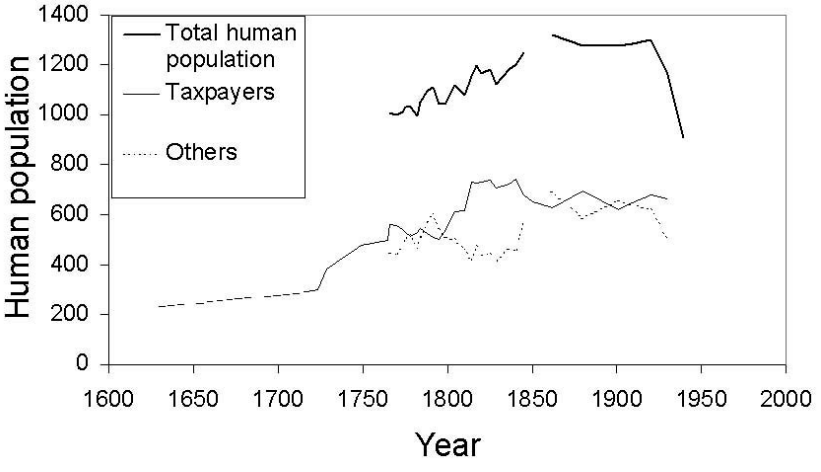

FIGURE 4. The change in human population since 1630 to 1950 on Selaön, Sweden. *Others* refers to people freed from tax. Based on population registers.

was considerable, from 300 to 500. From 1800 to 1850 the number of tax payers increased from 500 to 700. The population in Överselö parish was at its peak between 1860 and 1920 (Fig. 4). After 1920 the human populations decreased considerably, coinciding with the overall urbanisation of rural Sweden. The general population increase in Sweden during the nineteenth century consisted of an increase in the number of labourers working on larger farms and not in the number of farmers. The labourers' work with digging ditches, building stone walls and preparing new fields was important for the large increase in arable fields.[26] Even though people in Sweden were generally not starving during the nineteenth century, as food production increased, there was an imbalance in the input-output system. Fewer animals produced less manure, thus, the increasing crop-fields were depleted of nutrients. When the population was at its maximum in the study area, a new agricultural system was introduced, including growing leys as a rotational crop, enabling an expansion of arable fields. Similar changes occurred in the rest of Sweden. The nutrient depletion of arable fields continued until the introduction of artificial fertilisers in the late nineteenth century.

Land use in relation to livestock changes

The composition of livestock in the Överselö parish was relatively stable from the 1620s to 1854 (Fig. 5): c. 10 per cent horses, 30–40 per cent cattle, 35–40 per cent sheep and 15–25 per cent pigs. Goats comprised less than one per cent of the livestock numbers. Livestock composition reveals something about the agricultural production in an area. From a Swedish perspective, the agricultural

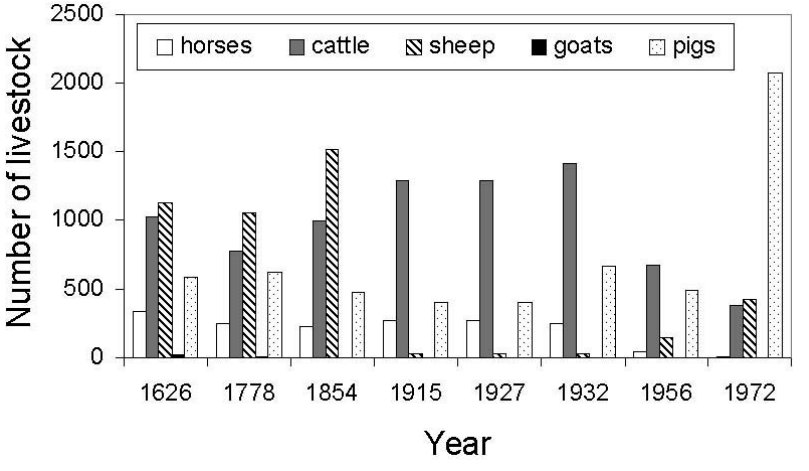

FIGURE 5. The change in numbers of livestock and livestock composition from 1626 to 1972 on Selaön, Sweden. Based on livestock registers (17th century), probate inventories (18th and 19th centuries) and agricultural statistics (20th century).

production on the island of Selaön had a focus on crops. This is underlined by the early livestock composition, with a large proportion of pigs, horses and oxen; the two latter were needed for ploughing and transportation, i.e. they were working animals. Forested areas, where crop production was less important, had a larger proportion of cattle, sheep and goats and few working animals.[27] Associated with land use, larger changes in livestock composition occurred after 1854. The number of sheep decreased drastically during the following years but the number of cattle increased. The introduction of crop rotation including ley, enabled an increase in livestock number as well as an increase in cattle size, as a result of improved fodder quality.[28] After 1932 the number of cattle and horses also declined. Instead, pig breeding expanded. The changes in livestock were similar at the national level.[29]

In Ettersta hamlet livestock numbers decreased from 49 livestock equivalents in 1620 to 33 in 1932 (Table 3). In Viggeby the number of livestock increased between 1620 and the nineteenth century from 27 livestock equivalents to 40 but decreased again to 25 in 1932.

The detailed records 1620–1641 also revealed a large short-term fluctuation (Fig. 6). Livestock numbers in Ettersta fluctuated between 35 and 65 (average=49.3, s.d.=10.3) and in Viggeby between 17 and 37 (average=26.7, s.d.=5.5). After 1641 there is only a limited number of records on livestock numbers with a large time span between them. But, it is likely that the changes over the longer time interval, from the seventeenth to the twentieth centuries, at least in the early

TABLE 3. Livestock equivalents in the hamlets Ettersta and Viggeby on Selaön, during more than 300 years. x indicates that no data is available for that year. Based on livestock registers (1620–1639), probate inventories (18th and 19th centuries) and agricultural statistics (20th century).

Year	Ettersta	Viggeby
Average 1620–1639 (1639)	49.3 (43.7)	26.7 (23.2)
1778	34.2	x
1787	33.7	x
1812	29.1	39.6
1837	x	32.7
1854	40.2	33.1
1862	19.6	x
1915	37.2	28.7
1932	33.2	24.5

* 1 livestock equivalent equals 0.7 horse, 1 cattle or 4 sheep.

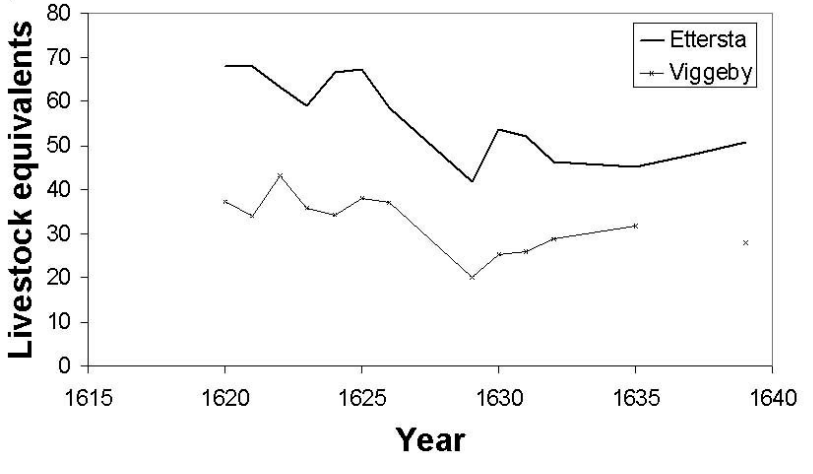

FIGURE 6. Variation in livestock equivalents between 1620 and 1641 in the two hamlets, Ettersta and Viggeby, on Selaön, Sweden. Based on livestock registers.

periods were combined with a short-term variation in the livestock population. This variation is interesting from a conservation perspective, since is shows that the grazing pressure on semi-natural grasslands may well have been variable. Thus, in present-day semi-natural grasslands also, a variation in grazing between years may be an option for conservation management.

There were only weak trends suggesting changes in livestock and grazing

area prior to the modernisation of agriculture in the nineteenth century. It should be noted, though, that it is likely that increase in body size of cattle implied that, in the nineteenth century, cattle demanded slightly more fodder compared to cattle in the seventeenth century.

Land use and plant species diversity

The overall changes in land use between 1854 and the present day (Fig. 3) were reflected using the 213 cells overlaid on Ettersta and Viggeby. This confirms that the changes recorded in the nineteenth- and twentieth-century agricultural statistics have continued to the present day. Of the 48 cells categorised as infield grassland (hay-meadow) in 1854, 39 (81 per cent) are transformed to cultivated arable field today. Of the 50 cells categorised as cultivated arable field in 1854, 46 (92 per cent) are still arable fields today. Thus, the total area that is influenced by land cultivation has increased. Of the 104 cells categorised as outland pastures in 1854, 82 (79 per cent) have been transformed to forest today.

Table 4 shows the mean species density (per m^2) in present-day vegetation and land use, categorised according to the land use in 1854 and 2001 at each sampling-plot. Categorising the plots after the land use provided six different categories. The mean number of species did not differ much if only present-day vegetation categories were considered. The number of species found in cultivated grasslands, i.e., former arable field or artificially fertilised grasslands, were surprisingly high, more than 20 species/m^2 compared to other studies in the area that have found only slightly more than 10 species per m^2.[30] A reason for the relatively high species density even on the former fields may be that the actual shape of these fields, which were long and narrow with semi-natural grassland or deciduous forest bordering, made it possible for species to disperse into the fields once grazing commenced.[31] As expected, the highest species richness

TABLE 4. The species density (per m^2) in present day vegetation and land uses, categorised according to land use in 1854 on Selaön, Sweden. The data derives from inventories of 1-m^2 plots in each present-day vegetation category.

Land use 1854	Vegetation 2001	Mean species no. (± s.d.)
Outland grazing	Open grassland (grazed)	29.3 (± 6.6) n=10
Outland grazing	Semi-open grassland (grazed)	28.7 (± 5.0) n=10
Infield grazing	Semi-closed grassland	20.8 (± 5.8) n=8
Infield grazing	Deciduous forest	20.3 (± 7.9) n=9
Meadow	Cultivated grassland (grazed)	25.2 (± 11.7) n=5
Crop field	Cultivated grassland (grazed)	22.2 (± 8.6) n=6

was generally found on the semi-natural grasslands with a long continuity of grazing.[32] The estimated species density in present-day grassland sward (i.e., the field layer dominated by graminoids and forbs, and not cultivated) was not very different when comparing cells which in 1854 were used for infield grassland (hay-meadow), cultivated arable field, or outland pasture (Table 4). There is no indication in the present-day grasslands of any major differences in diversity due to variation in land use history within the spatial scale covered by the two hamlets. In other words: irrespective of grassland management in 1854, the grassland sward today contains 20 to 30 species per m^2.

However, a closer inspection of the distribution of the five selected target species (Table 5) suggests that previous management indeed has an important effect. For all five species, the majority (62–91 per cent) of occurrences were located in previous outland pastures. Since all five species are characteristic for

TABLE 5. Occurrences of five selected target species, characteristic of traditionally managed grasslands, in relation to land use in 1854 and present-day vegetation, at two hamlets, Ettersta and Viggeby, located on Selaön, Sweden. Only the dominating relationships are shown in the table. See the text for explanation.

Species	# occurrences	Fraction of occurrences
Ajuga pyramidalis	43	39 (91%) in outland pastures 1854
Antennaria dioica	17	15 (88%) in outland pastures 1854
Lotus corniculatus	49	34 (69%) in outland pastures 1854
Polygala vulgaris	32	20 (62%) in outland pastures 1854
Primula veris	62	45 (72%) in outland pastures 1854

semi-natural grasslands[33], it may be surprising that a majority of occurrences are in former outland which is now mostly classified as forest. Plants commonly respond slowly to changes in land use configuration, and model simulations suggest that land use prior to the mid-nineteenth century may still have a significant effect on present-day distributions.[34] Thus the most likely interpretation of our results is that the species in Table 5 were present in 1854 and at that time were favoured by the grazing regime. Their distribution thus suggests that these grassland species in the present-day landscape may occur mostly as remnant populations.[35] Moreover, it is important to note the difference between focusing on quantity (counting number of species) and quality (which species) in research which may serve as a basis for public management decisions.

The most important impacts on biodiversity due to historical changes are obviously the deteriorating grassland area. Although the grazed semi-natural grassland area today at Ettersta (Fig. 2) is still quite large (more than 15 hectares) and contains a high species richness, it is still only a fraction of the

former grassland area. In addition to the total habitat loss, the grasslands left have become smaller and more isolated from each other, i.e., typical features of habitat fragmentation.[36] Expected habitat fragmentation effects are that species with poor dispersal abilities have difficulties in dispersing to sites far away, implying that local populations that go extinct are not compensated for by re-colonisation.[37] This is particularly important for many grassland species, which usually are dispersal-limited.[38] Since there is very little of infield pastures left, and Viggeby has no managed grassland habitats left at all, only the small mid-field islets may harbour some of the typical grassland species and may become sources for re-colonisation if grazing is restored.[39]

CONCLUDING REMARKS

There has recently been increasing interest in using the landscape as an operational tool in many ecological studies and conceptual frameworks.[40] Many authors have also pointed out the importance of assessing landscape effects on biodiversity on both spatial and temporal scales,[41] as patterns of plant species distribution and abundance are influenced by landscape history.[42] Even though species-richness is difficult to analyse in a historical perspective as there are few long-term records, old land use maps can be useful tools for studies of the temporal effects of land use, grassland distribution and fragmentation.[43]

Apart from the actual landscape fragmentation, one of the major factors affecting species persistence in a landscape is the change in hay-transport and movement of people and animals within the landscape.[44] For example, midfield islets were grazed after harvest at least every second or third year during fallow, and animals were moved between pastures, fallow fields, grazed outland and farms. These movements gradually disappeared between 1850 and 1930 and probably aided dispersal of plant species. In the 1930s, grazing on outland and in forests was abandoned in Sweden. When grazing became restricted to certain pastures or cultivated grasslands, and the outland became strictly forest, this change probably had a major impact on many species in the landscape. This effect may have been of the same magnitude as the effects of the actual decline in the area of semi-natural meadows and pastures. Once the dynamics of the past landscape with its mosaic of habitats and land use is disrupted, there will be a certain time-lag before fragmentation affects results in changing plant distributions, especially in long-lived perennials forming remnant populations.[45] Thus, an extinction debt[46] (implying that some of the species present today are moving towards extinction) probably exists in the changing Swedish agricultural landscape.

Apart from the specific conclusions relevant for the investigated parish at Selaön specifically, we stress that an integrated approach, using various sources – written documents, maps and biological surveys – is likely to be productive

in aiding understanding of the causes and consequences of land use change. We believe that present-day actions taken to preserve both cultural and biological values associated with the traditional agricultural landscapes in Europe will benefit from a deeper understanding of the actual changes in human population, food production, livestock and utilisation of land. We have here shown how methods from what are usually seen as different research disciplines, history, geography and ecology, can be combined to provide such an integrated picture of landscape changes over the last 350 years.

NOTES

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[1] e.g. Berglund 1991; Chambers 1993; Rackham 1995; Poschlod and WallisDeVries 2002.

[2] e.g. Poschlod and Bonn 1998; Söderström et al. 2001; Eriksson et al. 2002.

[3] e.g. Berglund 1991; de Blois et al. 2002a; Cousins and Eriksson 2002; Motzkin et al. 2002.

[4] Welinder et al. 1998, 56–69.

[5] Welinder et al. 1998, 239–66.

[6] Slotte 2000, 15–26.

[7] Gadd 2000, 307–9.

[8] Bernes 1994, 144.

[9] Clemedson 1965, 28–35.

[10] Kain and Baigent 1992; Tollin 1996.

[11] Sporrong 1990, 136–45.

[12] e.g. Pärtel et al. 1999; Cousins and Eriksson 2001, 2002; Lindborg and Eriksson 2004a.

[13] Lannér 2003.

[14] cf. Cousins 2001.

[15] ArcView GIS 3.2.

[16] Cousins and Eriksson 2002.

[17] Gadd and Jorner 1999.

[18] Friberg 1956.

[19] Gadd 1983, 53–74.

[20] Gadd & Jorner 1999; Gadd 2000, 331–2.

[21] Köll 1983, 163–67; Gadd 1983, 128–30.

[22] Ekstam and Forshed 1992.

[23] Eriksson and Eriksson 1997; Lindborg and Eriksson 2004b.

[24] Cousins 2001.

[25] Köll 1983, 164.

[26] Gadd 1983, 245–6.

[27] Dahlström 2005; Söderberg and Myrdal 2002; Myrdal 1999, 246–52.

[28] Köll 1983, 163–167; Gadd 2000, 131–4; Ulväng 2004, 69–90.

[29] Morell 2001, 242–57.

[30] Cousins and Eriksson 2002.

[31] S.A.O. Cousins and R. Lindborg, unpublished.

[32] Kull and Zobel 1991; Eriksson and Eriksson 1997; Cousins and Eriksson 2002, Eriksson et al. 2002.

[33] Ekstam and Forshed 1992.

[34] Herben at al 2006.

[35] Eriksson 1996.

[36] Harrison and Bruna 1999.

[37] Eriksson and Ehrlén 2001; Hanski and Ovaskainen 2002.

[38] Eriksson and Ehrlén 2001.

[39] S.A.O. Cousins and R. Lindborg, unpublished.

[40] Wiens 1997; McIntyre and Hobbs 1999; Loreau et al. 2001; de Blois et al. 2002a; Murphy and Lovett-Doust 2004.

[41] Eriksson and Ehrlén 2001; Hanski and Ovaskainen 2002; Foster 2002.

[42] Peterken and Game 1984; Foster 2002; de Blois et al. 2002b; Eriksson et al. 2002; Lindborg and Eriksson 2004a.

[43] Pärtel et al. 1999; Cousins 2001; Cousins and Eriksson 2001, 2002; Motzkin et al. 2002; Lindborg and Eriksson 2004a.

[44] Poschlod and Bonn 1998; Kiviniemi and Eriksson 1999.

[45] Eriksson 1996.

[46] Hanski and Ovaskainen 2002.

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