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Floristic change in the province of Scania in southernmost Sweden 1800-2020: using fragmented data to study landscape-level shifts

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Floristic change in the province of Scania in southernmost Sweden 1800-2020: using fragmented data to study landscape-level shifts

Thesis project by Cassandra Karlsson for Master of Science in Biology with a focus on Conservation

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Abstract

Vascular plant observances were compiled for 10 well-documented parishes throughout southernmost Sweden from published floras, herbarium specimens, modern inventories, and a large citizen-science database to provide presence/absence of species from 1800-2020 at the decade level. A regionally-specific database of species-specific plant traits and ecological indicator values was used to examine floristic and ecological changes across an extended timeline which indicates that several of the most apparent conservation issues including climate warming, woody encroachment, and soil chemistry alterations have acted for long over a century. The flora has shifted in favor of species with an affinity to higher N and P levels, a warmer climate, and which are generally more competitive. Additionally, species with lower requirements for grazing/mowing, sunlight, and moisture have also increased. In general, the landscape has become more homogenous over time. While these findings show that the impacts of human activity on wild plant species have not suddenly materialized, the acceleration of these changes over the past 50 years is evident. Investigations into the utility and limitation of fragmented data that spans centuries reveal biodiversity loss in a more holistic way by incorporating species already locally extinct more than 100 years ago. When combined with trait-based analyses, it is clear that quantifiable and long-ranging anthropogenic effects have shifted which species dominate the landscape in Scania across time and space.

Swedish summary: Jag har sammanställt kärlväxtobservationer från 1800 till 2020 för 10 väldokumenterade skånska socknar från publicerade florer, herbariematerial, moderna inventeringar och fynd från ArtPortalen. En karaktärslista med ekologiska indikatorvärden har sedan använts för att undersöka vilka miljöförändringar som påverkat floran och vilka egenskaper hos växterna som premierats. Analysen visar att flera av de faktorer vi vet påverkar floran idag, såsom klimatförändringar, igenväxning av landskapet och förändringar i markemin, har påverkat i över ett sekel. För att kvantifiera dessa antropogena effekter är det viktigt att även ta hänsyn till de arter som har förlorats längre tillbaka i tiden. Floran har sedan 1800 förändrats mot dominans av arter som gynnas av högre N- och P-nivåer, varmare klimat och som är konkurrenskraftiga, medan arter som har högre bete-, solljus- och fuktkrav har missgynnats. I allmänhet har landskapet blivit mer homogent med tiden. Även om dessa resultat visar att effekterna av mänsklig aktivitet på den vilda floran pågått länge är det uppenbart att takten i förändringarna har ökat under de senaste 50 åren. Genom att undersöka användbarheten av och begränsningar i fragmenterade vegetationsdata lägger jag grunden för en metodik som förhoppningsvis kan utnyttjas för att utforska vad som driver långsiktiga floraförändringar i andra delar av världen där det också finns omfattande botaniska traditioner.

Introduction

Alarming declines exceeding background level extinction rates have recently been reported across groups, including for vascular plants (Humphreys et al. 2019), insects (Hallmann et al. 2017, van Klink et al. 2020), and birds (Rosenberg et al. 2019). In Sweden, survey-based studies have quantified the complex interplay of decreasing and increasing frequencies for vascular plant species over the past several decades, indicating climate warming, land-use changes, and N-deposition as key drivers of regional floristic change (Hedwall & Brunet 2016, Tyler et al. 2018). However, these recent and dramatic findings are time-limited and focus largely on changes over the past few decades. To better understand the scale and extent of vascular plant species decline and associated drivers of change, floristic data analyses across a longer time-series are needed.

Well-established drivers of floristic change and potential biodiversity loss in southern Sweden include a warming and less stable climate (Swedish Meteorological and Hydrological Institute 2019), the abandonment of traditional agricultural practices which favored floristic diversity (Cousins et al. 2015), the deposition of nitrogen and associated soil acidification (Falkengren-Grerup 1987), the intensification and increase of industrial forestry (particularly of coniferous species) (Fredh et al. 2012), the draining of lakes and wetlands (Hasselquist et al. 2018), and the recent introduction of non-native invasive species (Tyler 2015). These factors are complex and interrelated, and the intensity of their effects is interwoven in time, fluctuating regionally and locally in large part in response to technological, political and economic changes. Metric data for these climate and land use factors were not always recorded at the local level, but the presence of vascular plant species was, for this region, documented.

The spatial and temporal distributions of wild plants rely upon multiple factors that are often considered so complex and intertwined that they cannot be disentangled: land use history, geology, precipitation, temperature, nutrient availabilities, dispersal events, disturbance regimes, and so on. However, each species has a unique association to the biotic and abiotic factors for a given region, and when assembled as a local flora (all recorded naturalized species), their associated values reveal change over time. Many iterations of such character trait values have been postulated since those first proposed by Ellenberg in 1974. Ecological indicator values have been used for a variety of applications (Diekmann 2003), and have been informative for both conservation purposes (Möckel et al. 2016) and for describing vegetation change (Hedwall & Brunet 2016).

A regionally adapted and extensive list of traits for vascular plants in Scania has been available since 2013 (Tyler & Olsson). This methodology has been applied by Tyler et al. (2018) to highly comparable inventory data based on 6.25 square kilometer grids across Scania over an approximately 50 year span, which indicated climate warming and land use as significant drivers of floristic change. In this study, I evaluate the practicalities and limitations of using observance data from multiple sources to evaluate landscape level changes to the flora of Scania over the last 220 years (1800-2020) and to what degree the drivers of these changes can be inferred. The goal of this research is to observe if the major trends in floristic change in the region are following a relative trajectory or if the same drivers appear to have been playing a major role for the past two hundred years.

To push the lower bound of comparison back to the year 1800, I investigated the relevance of the earliest available data in the context of modern statistical analyses and question to what extent this data type can be compared to recent inventory-based studies. As presence-only data is often incomplete for both historical and modern observations (Rich & Smith 1996), it is difficult to incorporate these valuable, yet fragmented and stochastic, sources in a way that provides a relatively complete picture of the regional flora through time. To accomplish this, I chose 10 study regions in southern Sweden which correspond to parishes, the most historically relevant geographic division for botanists, the flora of which have been thoroughly documented for 200 years.

A high level of documentation and careful selection of the study region made this study possible. Criteria for prioritization of parish selection included the existence of published local floras from the 1800s or early 1900s. Additionally, priority was given to the parishes near to institutions from which botanists have generally continuously documented proximal floristic sites. The remaining selected parishes have interested botanists historically in some way, leading to extensive examination and documentation. The activity and dedication of early botanists thereby drove the parish selection process, and their work has provided ample baseline data for early comparison.

Since the time of Linnaeus, Sweden has had an extensive history of distinguished botanists. Their associated documentations are widely available in herbarium collections and published floras, as well as in unpublished handwritten sources. However, there were no cars, no quadrats, and no standardized survey methods 200 years ago. The botanists of this time had an intimate knowledge of the region they were documenting and were roaming by foot, horse, or, later, by bike, but without any grid-based precision. To recreate an unmodern inventory, the

parishes were surveyed by foot and bike in 2019. In between 1800 and 2019, numerous collections and surveys provided by citizen scientists and professional botanists alike have amassed. By incorporating these multiple data sources to create a continuous presence of species by decade, I resurrect Scania's oldest, reliable botanical data for analytical use.

Materials and methods

Study area:

Scania is the southernmost province of Sweden. It has a mild climate with mean temperatures of -2 to 0 °C in January and 15 to 17 °C in July (Open data from the Swedish Meteorological and Hydrological Institute 2019). Compared to other provinces of Sweden, Scania more closely resembles mainland Europe in having a higher population density, a larger area of land used for agriculture and grazing (Atlas Över Skåne 1999), and in belonging mostly to the Nemoral vegetation zone (Swedish Forest Agency). Scania is therefore a relevant and reasonably comparable region for climate and floristic change within the continent.

I selected 10 parishes for study (**Fig. 1**) based on a combination of availability of older records and their representativeness of the province as a whole. Parishes with a relatively high degree of botanical documentation were selected in order to include data from as many observations as possible. Parishes with an abundance of herbarium specimens or published records, particularly pre-1900, were prioritized to capture the largest number of older records possible.

Parishes containing large cities were excluded because the focus of this study is on general landscape-level changes of the region, and not on the effects of urbanization. Likewise, parishes containing large national parks were not chosen because their protected status prevents them from representing typical changes of the regions. Overall size (**Table 1**) was taken into consideration and adjoining small parishes were combined to create a more comparable area. Parish lines were already drawn by the early 1700s in Scania and have been used consistently as a survey unit since the first botanical inventories were made. In this way, observations which lack precise locality information, as old herbarium specimens often do, can be used within the parish-level dataset even though they do not meet modern standards of GPS accuracy.

Each parish was selected carefully as to include as many early observance records as possible. The work of Nils Lilja in Billinge (1846), Teodor Brown in Vittskövle (1870), and J. G. Gunnarsson in Vellinge (1932) provide complete local inventories. Hardeberga/Södra Sandby parishes near Lund University and Lomma parish near the Swedish University of Agricultural Sciences (SLU) and its predecessors at Alnarp have been heavily visited and documented by botanists due to the proximity of these institutions. Öved parish was home to Elias Fries who reported many rare species in the surrounding area, attracting subsequent botanists to revisit. Östra Broby was home to many prominent botanists, including C. O. Hamnström, O. J. Hasslow, and Elsa Nyholm, who were in turn visited by botanists and researchers. Lastly, some regions have inherently attracted botanists for various reasons, resulting in historical and consistent documentation. This includes a wool factory where foreign seeds were spread in Kävlinge/Lackalänga combined parishes (Lange et al. 1954), Ringsjö Lake and the relative easy access of Stehag by train, and lastly, a plant-breeding and forestry research center founded in 1886 in Svalöv.



Figure 1 The studied parishes are dispersed mainly throughout central Scania but also encompass Östra Broby to the northeast and Vellinge to the southwest.

Scania can be divided into three distinct agricultural production areas which correspond to geological and floristic boundaries and which describe land use over an extended period of time (Swedish Board of Agriculture, Jordbruksverket 2011). The three distinct agricultural production areas are 1) landscapes where agriculture predominates (including Hardeberga/Södra Sandby, Kävlinge/Lackalånga, Lomma, Svalöv, and Vellinge parishes), 2) where animal husbandry predominates (Hardeberga/Södra Sandby, Stehag, Vittskövle, and Öved parishes), and 3) where forestry predominates (Billinge, Stehag, and Östra Broby parishes), with some parishes in multiple areas. In this way, analyses of combined parishes can be considered representative of the province.

Present-day regional land use differences (**Fig. 2**) between and amongst parishes range from domination of coniferous forest plantations (mostly Norway Spruce, *Picea abies*) of Östra Broby in the north to intensive agriculture of Vellinge in the southwestern coast of the province. Overlying geological and climatic differences, all parishes were strongly influenced in modern times from a range of anthropogenic alterations due to forestry, agriculture, and development, which is representative of the province as a whole.

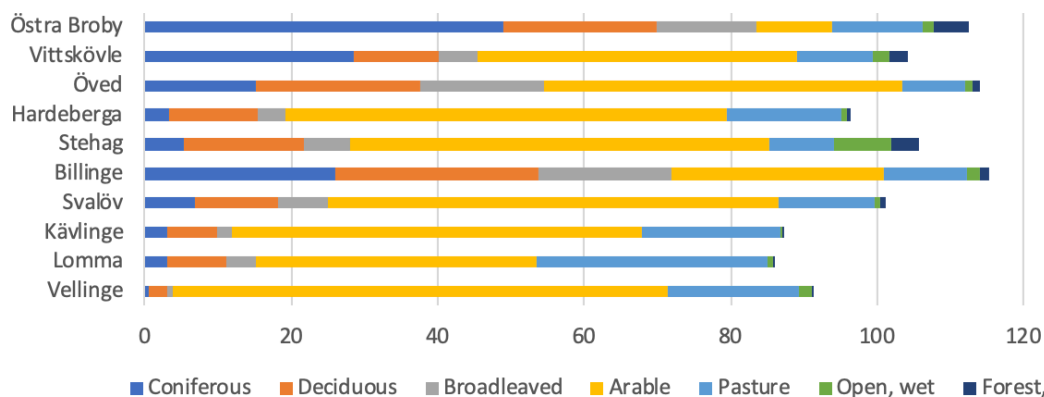


Figure 2 Modern land cover data (% of total land area) from The Swedish Environmental Protection Agency (Nationella Marktäckedata, 2019). All parishes are exploited for agriculture and have pasture coverage. Forest cover varies, with abundant deciduous and coniferous cover in Östra Broby to a small percentage of deciduous and virtually no coniferous cover in Vellinge parish. Due to overlap in some land use categories, sums can exceed 100%.

Data collection

Data was retrieved from all available sources including **1**) herbaria, **2**) published local floras, **3**) miscellaneous early literature incorporated in the Lund Botanical Society card index, **4**) the parish-based inventory conducted by H. Weimarck and associated botanists (1938-1971), **5**) two repeated grid-based inventories (Skånes Flora 1987-2007 and Millora (Miljö- och floraövervakning i Skåne, 2008-2015), **6**) observation data extracted from the Species Observation Portal (1980-2019), and **7**) own parish-level inventories conducted spring and mid-season 2019. The data was incorporated largely by hand due to variability amongst sources. The presence of a species on a decadal basis from 1800 to 2019 resulted in a combined 76,183 entries across 22 time steps and 10 parishes. Species for which ecological trait values have been assigned include those which are considered resident or commonly encountered in Sweden. Rare alien species were thus ignored in this study.

(1) Herbarium specimen occurrence data was retrieved from Sweden's Virtual Herbarium (Virtuella Herbariet, retrieved January and February 2019), which compiles digitized records from the nation's six largest institutions and which included digital records for more than 5 million vascular plant specimens at the time of data extraction. Because the Lund Botanical Museum is the primary source of specimens for the region, and the Swedish collections at the facility were approximately 90 % digitized at the time of retrieval, this is an accurate estimation of the available physical vascular plant specimen records, although the complete digitization of records from all herbaria would contribute additional specimens from these parishes. The preliminary parish selection process

included estimations of available herbarium data, with emphasis on earlier records (**Table 1**). Note that the low early specimen counts of Billinge and Vittskövle are compensated for with data from early literature.

Table 1: Parish data Descriptive values for each parish including various data sources, as described in the methodology.

	Size (sq. km)	Total no. herbarium specimens	No. pre-1940 specimens	Oldest specimens (year)	2019 inventory (no. spp.)	Max spp. per decade	Decade of max spp.	20% "cut-off"
Billinge	41	905	679	1860	460	556	2000s	111
Hardeberga/S. Sandby	52	4720	3507	1820	471	899	1990s	180
Kävlinge/Lackalånga	19	3078	2028	1830	461	650	1990s	130
Lomma	17	4012	3458	1840	569	791	2000s	158
Stehag	36	1686	1310	1860	385	638	2010s	128
Svalöv	25	2271	1969	1850	282	682	1990s	136
Vellinge	16	1833	1204	1840	382	581	2000s	116
Vittskövle	47	1012	624	1860	492	704	2000s	141
Östra Broby	67	2188	1063	1850	483	826	1990s	165
Öved	35	1910	1581	1850	421	711	1990s	142

(2) Historical floras were incorporated for Billinge (Lilja 1846), Vittskövle (Brown 1870), and Vellinge (Gunnarsson 1932) parishes. These texts are the earliest complete inventories for the selected parishes. Performed by distinguished botanists, they are assumed to be thorough and representative. There are still some missing common species which are presumed to have existed at the time, such as *Prunus* spp. in Billinge parish (Tyler 2008), indicating that there will always be some level of human error involved with species inventory.

Nils Lilja (1808-1870) has contributed the largest proportion of data within these 10 parishes prior to the 1900s. He published two editions of Skånes Flora (1838, 1870), a flora of Billinge and Röstånga parishes (1846), and travelled extensively in the region to contribute additional early observations for several parishes in this study.

(3)/(4) An extensive survey of all of Scania was initiated and overseen by Henning Weimarck for the publication *Atlas Över Skånes Flora* and data was collected from the years 1938-1971 by the Lund Botanical Society. It was conducted systematically by numerous botanists from across the region and spans several decades. As different botanists were assigned different parishes, these surveys are likely biased by the specific tendencies of the surveyor. Notably, 283 species were regarded as so ubiquitous in the landscape of that time that surveyors were instructed not to record their presence, and this gap in the data was accounted for at the incorporation stage of compilation.

This extensive survey has provided biogeographic data for numerous research projects during the past 50 years but is only accessible in physical copy in card register form. This register also contains historical observations from both published floras and herbarium specimens from various resources which were also compiled around the time of the survey for reference. In this way, additional historical occurrence data and the inventory data from *Atlas Över Skånes Flora* were extracted simultaneously. Though the value for biogeographic studies of the regional flora are tantamount, it is estimated by the Lund Botanical Society that the digitization of the 750,000 records in this card register would require several years of full-time work.

(5) Two large, grid-based surveys upon which most of the original research on floristic change in the region were included. Many of the survey grids were located at least partially within the selected parishes. Data from the project Skånes Flora (performed year 1989-2007) was downloaded through the Species Observation Portal. Data from the MILLORA project (performed years 2008-2015) was extracted from a database which is now publicly

accessible through the Species Observation Portal. These surveys were performed uniformly and systematically by volunteers, though surveyor bias is likely present at some level.

(6) Publicly accessible records were downloaded through the Species Observation Portal (years 1980-2019). The limitations of these observations are not unlike many of the spatial biases encountered with herbarium specimen data in general, in which more observations correspond to more densely populated areas and the available infrastructure. In particular, citizen science can be prone to biases from the individual collector, and there may be interesting species or localities which are overrepresented (Isaac & Pocock 2015) and do not reflect random sampling. In the Species Observation Portal, this often corresponds to the overrepresentation of rare or endangered species reports. Additionally, though all records will ideally be confirmed by an expert, there are presumed errors in identification or location.

(7) To replicate survey methods used by the earliest botanists, inventories of each region were performed by bike and foot during the summer of 2019. Attention was given to the known areas of botanical interest in order to capture the diversity of habitats and species in each parish. For example, extra care was taken to visit mapped or otherwise known species-rich areas of botanical interest such as wet meadows and grazed pastures. The species contained within each parish were recorded during one full day until all locations were visited and additional, unrecorded species were rarely encountered. In this way, each parish received an approximately equal sampling effort, with some adaptation of hours sampled for larger and smaller parishes (**Table 1**). The inventories served an additional purpose in familiarization of local landscapes in observing prevalent land uses, management or mismanagement of sensitive habits, approximate frequency of invasive species establishment, and so on. This inventory data is publicly accessible and has been uploaded to the Species Observation Portal.

Data incorporation

A list of synonymy was used for the adaption of various species lists to correspond to modern taxonomy (Karlsson & Agestam 2019). Separate data files for each parish were maintained through the various rounds of incorporation. An individual species was marked as present for each decade if it was found at any year within the given interval. If the species was found once in 1850 and once in 1960, it was considered to be “present” at all decades between those two time stamps. However, in almost every case there were multiple observances both within each decade and within longer timestamps, creating a continual and semi-complete representation of all species within every time interval from 1800-2020. Importantly, the common species left out in Weimarck’s inventory in the mid-20th century were re-incorporated into the data at the year that the survey was performed for the individual parish, only if there was at least one occurrence of the species before or after this time.

Although these combined data sources are variable and prone to bias, the sheer volume of observations should compensate for lesser errors and the impact of individual collectors. However, as there are inherently fewer records farther back in time (**Appendix A**), the influence of individual collectors may be more apparent for earlier decades. This is taken into consideration when interpreting results, particularly in regard to larger confidence intervals observed in earlier decades. This is compensated for in part by establishing a cutoff range for useable data, detailed within the description of statistical analyses.

The Trait List

This attribute table, hereafter referred to as the Trait List, was developed by leading experts to supply an open resource of highly detailed ecological and biogeographical information which can be used for a multitude of applications (Tyler, Herbertsson, Olofsson & Olsson, in prep.). Akin to the more commonly used Ellenberg values (Ellenberg et al. 1992), the Trait List is largely adapted for regional Swedish species and it is much expanded upon in terms of the number of attributes considered. The Trait List includes scalar values for traits such as temperature optimum and tolerance of or affinity towards nitrogen and phosphorus. Categorical information is provided for

traits such as mycorrhizal associations and pollinator dependence. The Trait List contains 29 traits with assigned values for most of the 2,427 resident vascular plant species of Scania. A selection of 20 relevant traits was used for analysis (**Table 2**).

Table 2 Selected traits for analysis, as adapted from the Trait List (Tyler, Herbertsson, Olofsson & Olsson (in prep.))		
Potential Driver	Indicator and scale	Description
Climate change	Heat requirement 1-14	Species distribution reaches high-alpine (1), mid-alpine (2), low-alpine (3), timberline (4), subalpine (5) zones, followed by cultivation zones 8-1 descending (6-13), and species not present or reproducing due to climatic constraints (14)
	Cold requirement 1-20	Annual minimum temperatures rarely below 10° C (1) to rarely below -15° C (6) in 5° increments, then Swedish cultivation zones 1-9 (7-16), then approaching timberline (17-20)
	Phenology 1-15	Onset of flowering, starting early February (1) to late September (15) in 15-day increments
	Temperature optimum 1-18	A representation of climate at the center of the geographic range of a species, ranging from subtropical (1) to high-alpine/arctic species (18)
	Extreme phenology 1-8	Onset of flowering at mid-June (1) and then in 15-day increments in either direction towards outlying values, early February and late September (8)
Disturbance, woody encroachment	Continentality 1-9	Seasonal distribution of temperature and precipitation: hyper- (1), strongly- (2), moderately (3), and weakly (4) oceanic, indifferent (5), weakly (6), moderately (7), strongly (8), and hyper- (9) continental
	Grazing / mowing 1-8	Endures no (1), sporadic (2), or regular (3) grazing/mowing, thrives in grazed/mowed or unmanaged habitat (4), favors some (5), strongly favors (6), strongly favors at frequent intervals (7), or requires continuous (8) grazing/mowing
	Light 1-7	Optimal conditions from deep shade (1), moderate-deep shade (2), half- to moderate-shade (3), half shade (4), sun to half-shade (5), sun, enduring some shade (6), full sun (7)
Draining/diking	Soil disturbance 1-9	Colonizes established vegetation and is competitive (1) or is outcompeted (2) without disturbance, reproduces in undisturbed established vegetation but not competitive (3) or no stable population size (4), requires disturbance for reproduction but subsists without it (5), disappears with vegetation closure within decades (6) or years (7), not competitive in closed vegetation and requires disturbance every second year (8) or every year (9)
	Moisture 1-12	Mean realized water niche from very dry (1), dry (2), fry-mesic (3), mesic (4), mesic-moist (5), moist (6), moist-wet (7), wet (8), wet to temporarily inundated (9), temporarily inundated (10), shallow permanent water (11), deep permanent water (12)
	Nitrogen (N) 1-9	Very (1), moderately-very (2), and moderately (3) N-poor, moderately N-poor to moderately N-rich (4), moderately (5), moderately to very (6), and very (7) N-rich, confined to naturally most N-rich (8), and artificially N-enriched (9) soils
Soil chemistry	Phosphorus (P) 1-5	Avoids high P (1), disfavored by high P (2), thrives with average P (3), favored by high P (4), and confined to high P (5) availability soils.
	Soil reaction (pH) 1-8	Mean realized pH niche from strongly acidic pH<4.5 (1), moderately-strongly base-poor (2), moderately acidic pH=4.5-5.5 (3), moderately acidic – subneutral (4), subneutral (6), circumneutral (7), to alkaline pH>7.5 (8)
	Longevity 1-4	Strictly annual (1), biennial (2), short-lived perennial (3), or long-lived perennial (4) life form
Biological strategy	Biodiversity relevance 1-8	Number of associated or dependent species is <6 (1), 6-12 (2), 13-24 (3), 25-50 (4), 51-100 (5), 101-200 (6), 201-400 (7), >400 (8)
	Seed bank 1-4	Seeds are viable outdoors in buried soil up to one or rarely two years (1), for one to five years (2), 5-25 years (3), or more than 25 years (4)
	Seed dormancy 1-4	Non-dormant; germinates within 10 days (1), no or non-deep dormancy; germinates within 10-30 days (2), intermediate dormancy; slow germination independent of season (3), strong dormancy; only germinates after > 35 days cold stratification (4)
	Nectar production 1-7	Incremental increases (1-7) from no nectar production(0 kg/ha/year) to very large nectar production (>1333)
	Non-native and invasive species	Time of immigration 1-8

Invasive concern 0-38	No (<10), low (14-17), moderate (14-17), considerable (17-22), to severe (>22) risk/impact
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Statistical analyses:

Using the Trait List and the presence of individual plant species over time, an average for each decade and for each indicator value was calculated for the combined ten parishes. Within the computation program R (version 3.6.1, 2019), a mixed model using the function lmer from the package lmer4 was used to model means of the decadal presence data for each trait, i.e. with decade as a fixed factor and parish as a random factor (random intercept). Estimated marginal means and 95% confidence intervals from these models were calculated with the effects package and plotted in decadal increments from 1831-1840 (shown as 1840) to 2011-2019 (shown as 2019). Data starting at 1840 is presented because observances for the decades prior often had large confidence intervals, explained by the relative scarcity of early observances and described further below.

Mean value changes for selected traits on the individual parish level were calculated and are plotted with standard deviations (**Appendix B**). As less data is available in the earliest decades and each parish has been treated differently by early botanists and surveys, a unique cut-off year was assigned. To achieve this, the highest recorded species count within a single decade was used as a baseline value. Any decade with fewer than 20% of the baseline count was considered too low and was removed from analysis (**Table 1**).

Canonical Correspondence Analyses (CCAs) were performed within the PAST (version 4.01) program, both for individual parishes and for the combined parishes. 21 selected relevant traits were included from the Trait List to avoid redundancies. Additionally, the time periods surpassing the 20% cut-off and all species presence values were included (**Appendix C**).

Extinctions and introductions

Any species not found since 1980 but recorded at any time prior to that year was recorded as a local extinction for that parish. The extinctions for each parish were compiled and investigated for total extinctions, unique species, and number of extinctions per species. Mean trait values were calculated for the species which were locally extinct in at least 2 parishes in order to remove outlying or atypical species. For the species with the highest percentage of extinctions from the parishes, a description of the known habitat and ecology is presented as summarized from the Flora of Scania (Tyler et al. 2007). This process was then repeated for local introductions, as defined as any species which occurred only after 1989. Average mean trait values for all parishes across all decades were calculated to provide a baseline comparison for the trait values of locally extinct and introduced species. The frequency with which a species went extinct or was introduced within the ten parishes was also calculated and compiled to indicate the most frequently extinct and introduced species overall.

Land cover analyses

General map comparisons were made using regional reconnaissance maps (Skånska rekognosceringskartan, Riksarkivet open data 2019) from 1812-1820 which correspond to some of the earliest observations and published regional floras. These maps provide estimates of total households present at the time, coverage of open lands used for farming and pasture, and coverage of both deciduous and coniferous forest. This was compared to modern satellite imagery and to the national landcover data maps (Nationella Marktäckedata from The Swedish Environmental Protection Agency, open data 2019) which give estimates for roughly the same categories. QGIS was used to draw polygons for easier comparison and for manipulation of the landcover layers (QGIS Development Team 2019). Though no statistical analyses have been performed, it is valuable in describing the major land use shifts of each parish and for the parishes as a whole (**Appendix D**).

Results

Traits

The following figures correspond to mean values for the combined flora of the ten parishes. The decadal trait mean values and 95% confidence intervals presented reflect subtle changes which are presented and discussed in the following groupings: climate change, land use changes, soil chemistry, biological strategy, and immigrant and invasive species. For mean trait values of individual parishes over time, see **Appendix B**.

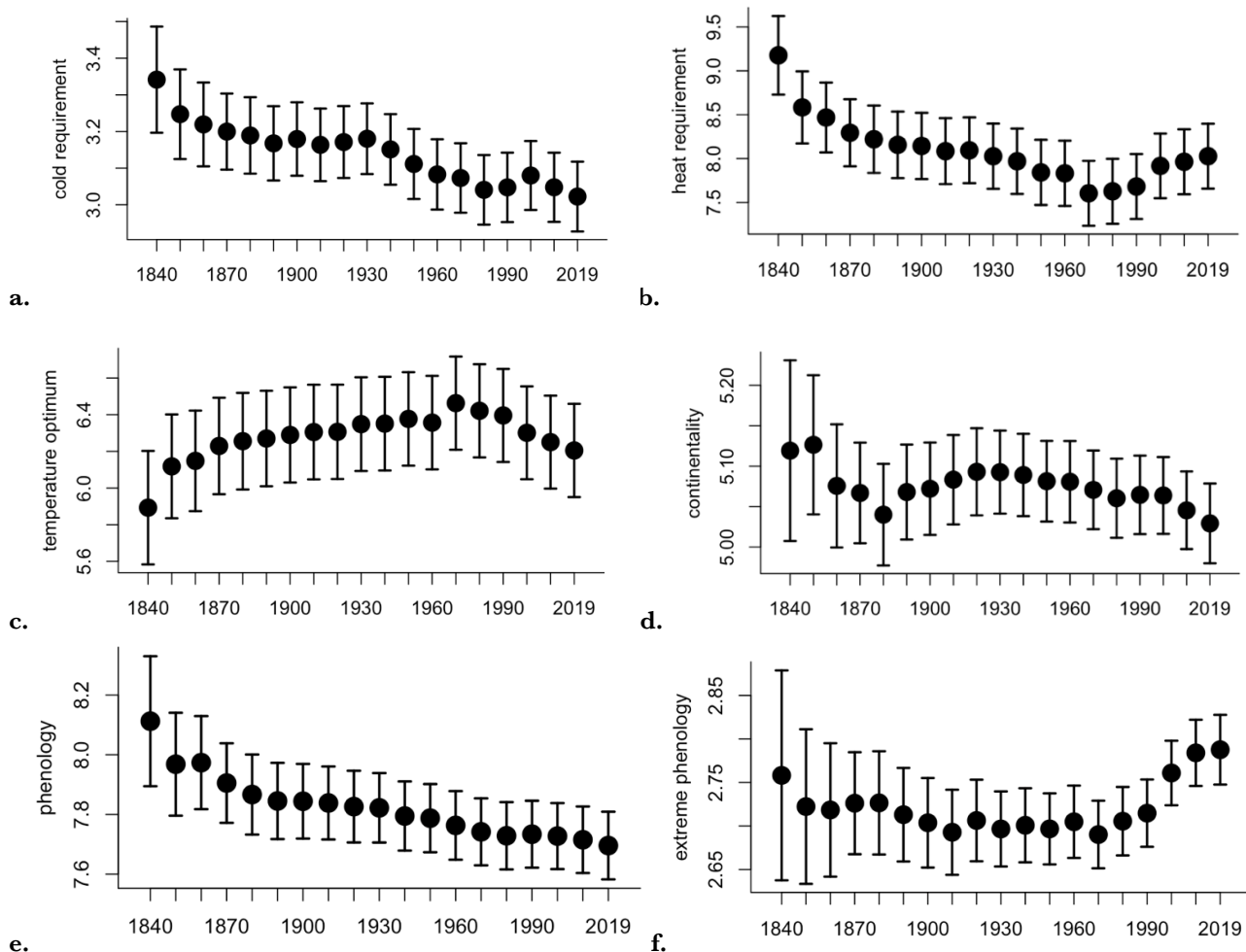


Figure 4 (panels a-f) Cold and heat requirements, temperature optimum, continentality, phenology, and extreme phenology traits are associated with climate change. Species mean trait values for cold requirement (**Fig. 4a**; $\chi^2_{18}=178.37$, $P<0.0005$) has steadily decreased, indicating a floristic shift towards plants who are adapted to shorter and warmer winters. Heat requirement mean values (**fig.4b**; $\chi^2_{18}=461.37$, $P<0.0005$) steadily decreased until around 1970, indicating a shift towards plants with a cooler climatic distribution. After 1970, trait means rise for 50 years, indicating a trend reversal favoring plants which are more adapted to warmer climates. As the temperature optimum (**Fig. 4c**; $\chi^2_{18}=125.66$, $P<0.0005$) trait scale ranges from tropical to arctic biogeographical center for an individual species, there is an early trend towards colder species. However, an obvious trend reversal beginning at 1970 favors species with a warmer temperature optimum. After a slight early trend favoring trait

mean values for continentality (**fig.4d**; $\chi^2_{18}=19.86$, $P=0.341$), a decline from 1920 and onwards indicates a shift towards oceanic species. Phenology trait mean values (**Fig. 4e**; $\chi^2_{18}=74.21$, $P<0.0005$) lie on a scale from early flowering species to late flowering species (1-15) and have steadily decreased over time. This indicates an increase in earlier flowering species. Trait mean values for extreme phenology (**Fig. 4f**; $\chi^2_{18}=46.09$, $P=0.000288$) increase as species with outlying values (early February and late September = 8, the highest value on this scale) increase in the overall flora. Here, values are relatively stable until about 1980, after which there is a sharp increase in phenologically outlying plant species.

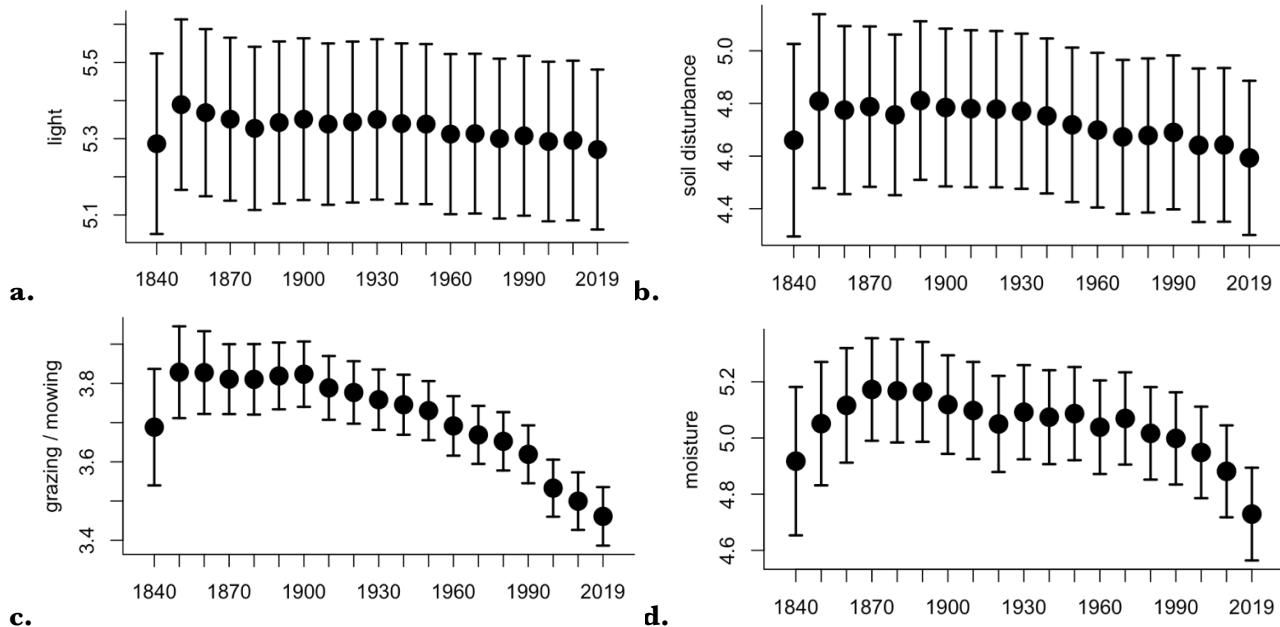


Figure 5 (panels a-d) Traits for light, soil disturbance, grazing/mowing, and moisture are associated with disturbance regime and land use changes. A slow but steady shift towards a flora with lower sunlight (**Fig. 5a**; $\chi^2_{18}=29.75$, $P=0.0399$) and disturbance (**Fig. 5b**; $\chi^2_{18}=43.30$, $P=0.0007$) requirements are reflected by the respective trait mean values. Grazing and mowing mean trait values (**Fig. 5c**; $\chi^2_{18}=437.33$, $P<0.0005$) show a more pronounced requirement decrease from 1900 onwards, with a particularly steep decline after 1990. This indicates that plants with little grazing or mowing requirements have been favored, while those which require more frequent grazing or mowing have been disfavored. Moisture requirement mean trait values (**Fig. 5d**; $\chi^2_{18}=154.74$, $P<0.0005$) shift upwards until 1870, then decrease until 1920, level out until 1970, and then finally begin a fairly pronounced decrease until 2019. This indicates an overall shift towards species occurring at lower soil moisture. The earliest data points for the above traits also have the largest confidence interval of the presented decades and are difficult to interpret as “starting points” without pre-1800s historical context.

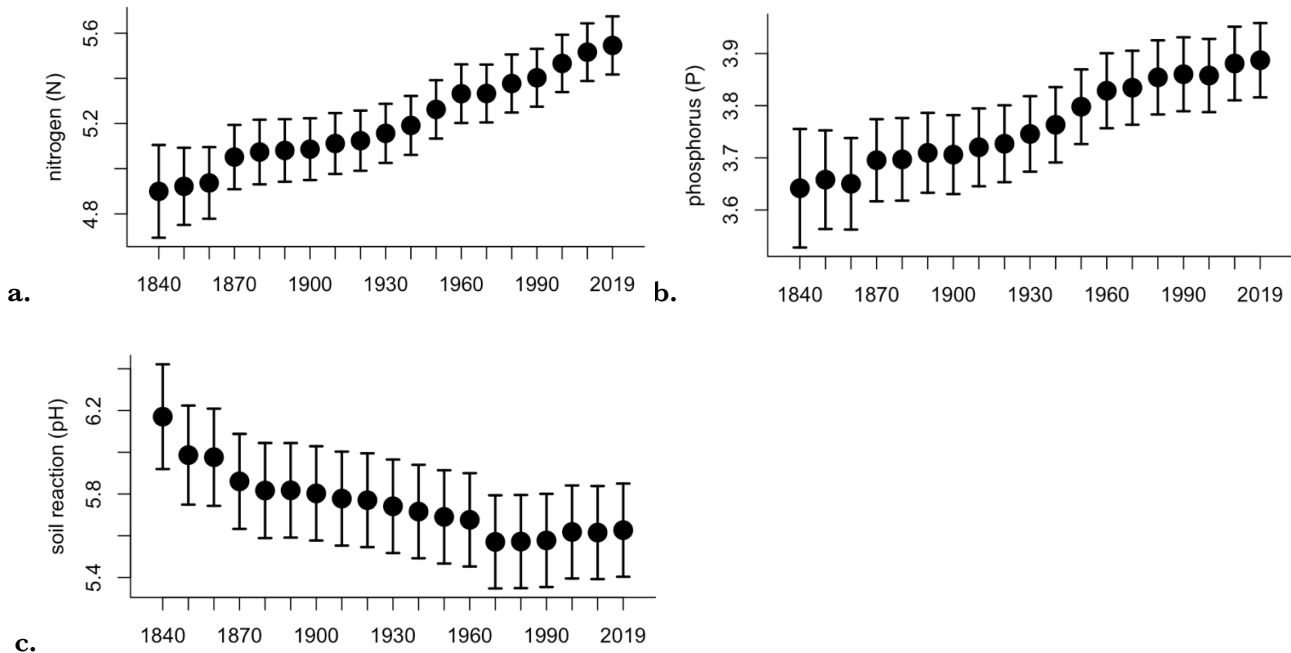


Figure 6 (panels a-c) P, N, and soil reaction (pH) mean trait values are associated with changes in soil chemistry and anthropogenic manipulation. Mean trait values for N (**Fig. 6a**; $\chi^2_{18}=600.88$, $P<0.0005$) and P (**Fig. 6b**; $\chi^2_{18}=331.94$, $P<0.0005$) tolerance have increased steadily over two centuries, with no obvious acceleration in recent decades. This indicates a shift towards species with a tolerance or preference for higher P- and N-content in the soil. Soil pH mean trait values (**Fig. 6c**; $\chi^2_{18}=466.45$, $P<0.0005$) trend towards acidification from the mid-19th century onwards, emphasized by a significant pH drop in 1960. From 1970 onward, pH mean trait values appear to stabilize and slowly increase toward more neutral conditions. This indicates a shift toward plants which have a more acidic realized pH niche up until 1970, at which point pH niche stabilizes and possibly begins to shift towards species with a more neutral pH niche.

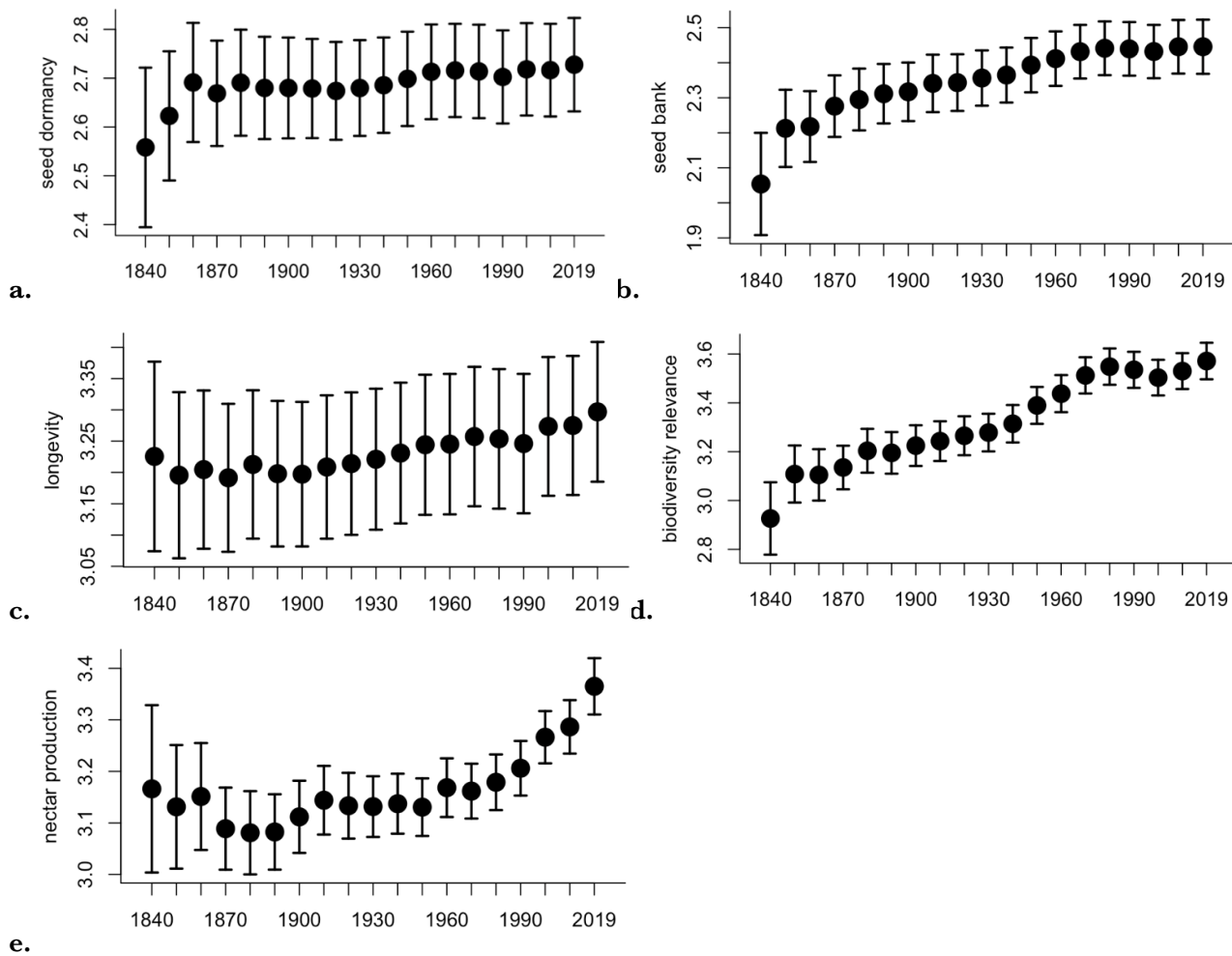


Figure 7 (panels a-e): Traits for seed dormancy, seedbank, longevity, biodiversity relevance, and nectar production are associated with the biological strategy of a plant species. Overall increases over time for seed dormancy (**Fig. 7a**; $\chi^2_{18}=16.64$, $P=0.548$) and seedbank (**Fig. 7b**; $\chi^2_{18}=183.54$, $P<0.0005$) trait mean values indicate a shift towards species with a longer dormancy period and a longer-lived seedbank. Longevity trait mean values (**Fig. 7c**; $\chi^2_{18}=43.58$, $P=0.00066$) describe species life form on an increasing scale from annual to perennial habit, here shifting towards perennial habit. Trait mean values for biodiversity relevance (**Fig. 7d**; $\chi^2_{18}=708.27$, $P<0.0005$) shift over time towards species which have a higher number of associated species. Nectar production mean trait values (**Fig. 7e**; $\chi^2_{18}=135.14$, $P<0.0005$) fluctuate early on, likely as the result of fewer data points as is indicated by larger confidence intervals. By the mid-20th century, mean trait values increase slowly, then increase fairly rapidly in the past 50 years, indicating a shift towards species which produce higher amounts of nectar.

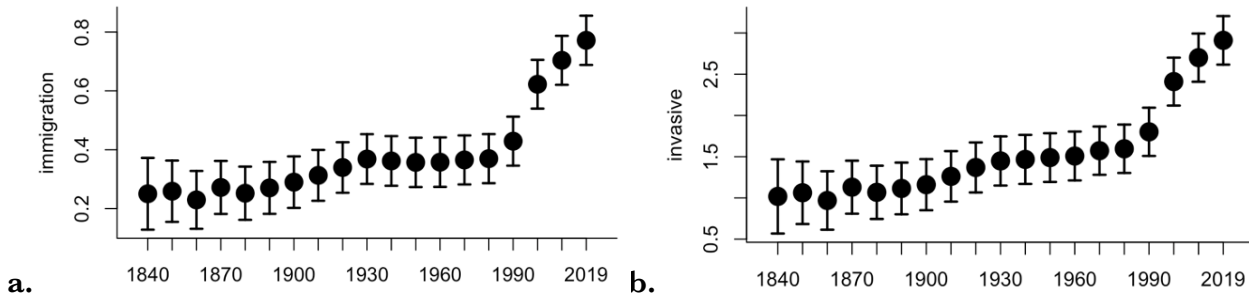


Figure 8 (panels a,b): The time of introduction and the level of concern for invasibility are metrics for newly-introduced species and their associated potential for ecological damage. The proportion of non-native species is represented by the immigration values (**Fig. 8a**; $\chi^2_{18}=1708.6$, $P<0.0005$), while the index of invasive concern values (**Fig. 8b**; $\chi^2_{18}=1472.8$, $P<0.0005$) represent a scale for increasing potential ecological harm. Showing nearly identical mean trait value trends, a slow increase until around 1990 is followed by a jump and continued increase in recent decades. These values indicate a recent and rapid increase of introduced species, as well as species which pose a greater biological risk to the existing flora.

Canonical Correspondence Analysis

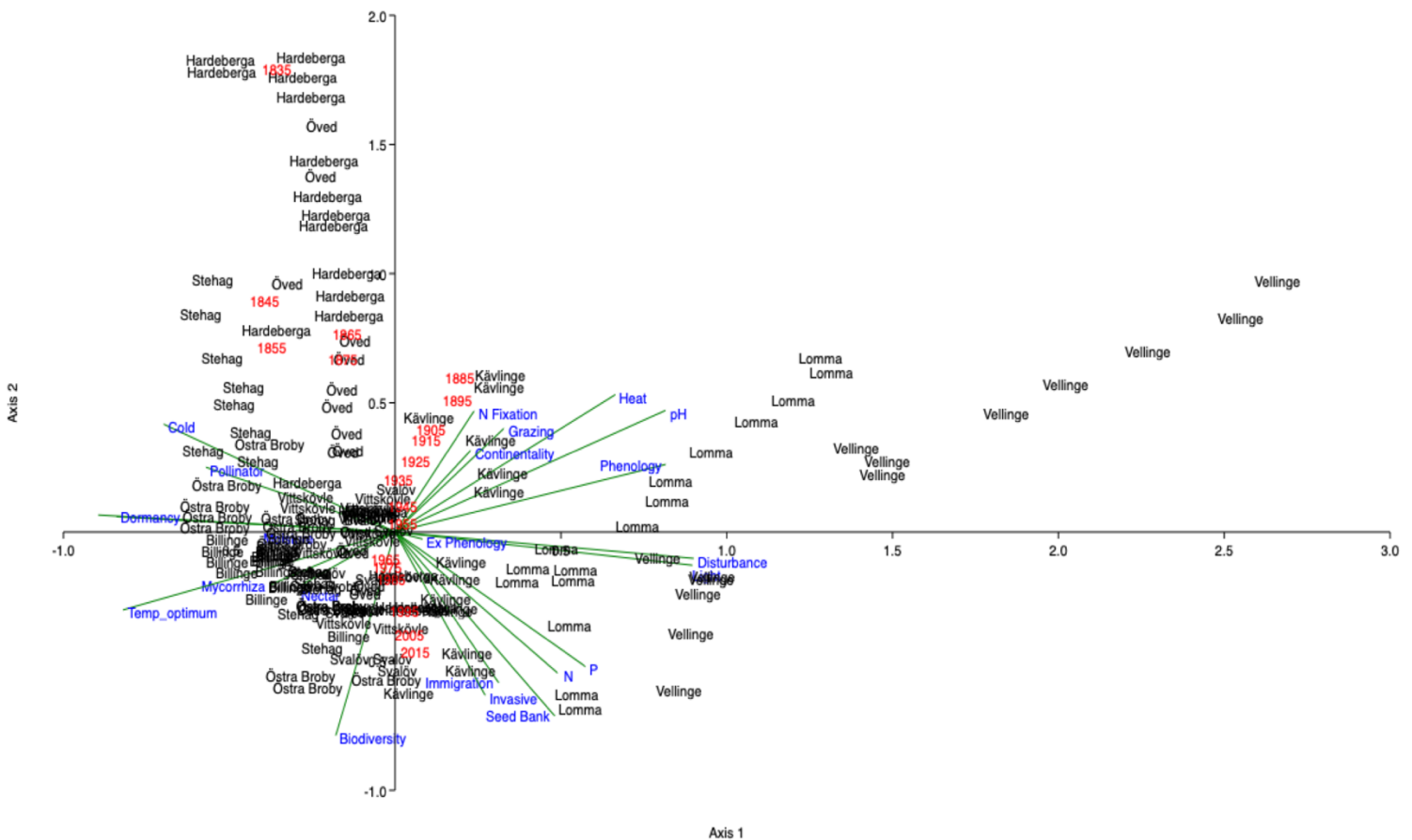


Figure 9: Canonical Correspondence Analyses (CCA) takes into account the presence of all species and the mean trait values for each time period. Time period (decadal from 1830-2019, midpoint displayed in red) moves chronologically along axis 2. Each parish here moves along that time axis, and individual parishes maintain a chronological trajectory in individual CCAs (**Appendix C**).

Extinctions and Introductions

In total there were 1709 local extinctions within the 10 parishes by the year 1980 (Fig. 11). 797 of those extinctions correspond to unique species. 414 unique species went extinct from at least two parishes and were considered for general trait analysis (Fig. 11).

Only 12 species were locally extinct from more than 6 parishes: *Eleocharis quinqueflora* (9), *Antennaria dioica* (8), *Bromus secalinus* (8), *Cuscuta epilinum* (8), *Pinguicula vulgaris* (8), *Blysmus compressus* (7), *Bromus secalinus* (7), *Carex pulicaris* (7), *Epipactis palustris* (7), *Gentianella campestris* (7), *Parnassia palustris* (7), and *Sparganium natans* (7).

A total of 2197 local introductions occurred after 1989 in the ten parishes (Fig. 10). Of these, there are 898 unique species. 488 unique species were introduced to 2 or more parishes and were therefore included in a general analysis of species trait values (Fig. 11).

51 unique species were introduced to 7 parishes or more:

10: *Heracleum mantegazzianum*, *Reynoutria japonica*, *Tulipa gesneriana*

9: *Brassica napus*, *Helianthus tuberosus*, *Lactuca serriola*, *Lupinus polyphyllus*, *Lysimachia punctata*, *Prunus cerasifera*, *Rubus laciniatus*, *Salix x fragilis*, *Scilla luciliae*, *Verbascum speciosum*

8: *Berberis thunbergii*, *Centaurea montana*, *Cornus sericea*, *Cotoneaster divaricatus*, *Crocus vernus*, *Digitalis purpurea*, *Dipsacus fullonum*, *Eranthis hyemalis*, *Galanthus nivalis*, *Galinsoga quadriradiata*, *Helianthus annuus*, *Larix x marschlinii*, *Lonicera tatarica*, *Othocallis siberica*, *Picea pungens*, *Solanum tuberosum*, *Spiraea x billardii*, *Veronica filiformis*

7: *Caragana arborescens*, *Dasiphora fruticosa*, *Epilobium ciliatum*, *Hyacinthoides italica*, *Laburnum anagyroides*, *Lactuca macrophylla*, *Ligustrum vulgare*, *Lychnis coronaria*, *Mahonia aquifolium*, *Nicandra physalodes*, *Phacelia tanacetifolia*, *Populus x canadensis*, *Populus balsamifera*, *Quercus palustris/rubra*, *Rheum rhabarbarum*, *Robinia pseudoacacia*, *Rosa glauca*, *Rubus armeniacus*, *Scilla forbesii*, *Tilia platyphyllos*

Local extinctions vs. Local introductions

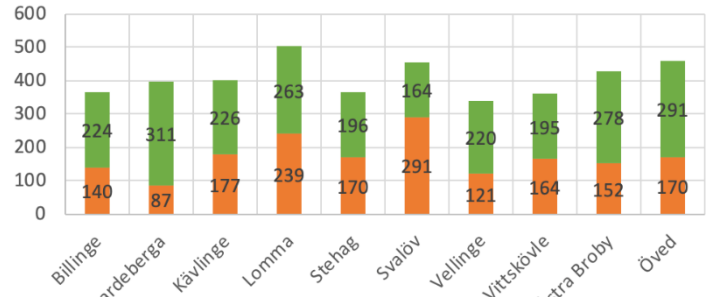


Figure 10 Local extinctions and introductions for each parish



Figure 11 The mean values from the selected unique species that went extinct (orange) or were introduced (green) are compared with the mean trait values for all parishes over all decades. Because the scales of the Trait List (Table 2) vary quite a lot, these traits should not be directly compared, but rather used as an indicator for comparison and direction of mean trait shifts between introductions and extinctions, in relation to the “average” flora. Note that the scale is adjusted for a break in invasive species concern, as introductions greatly exceed the general scale, reaching a mean trait value of 6.

Community Analysis

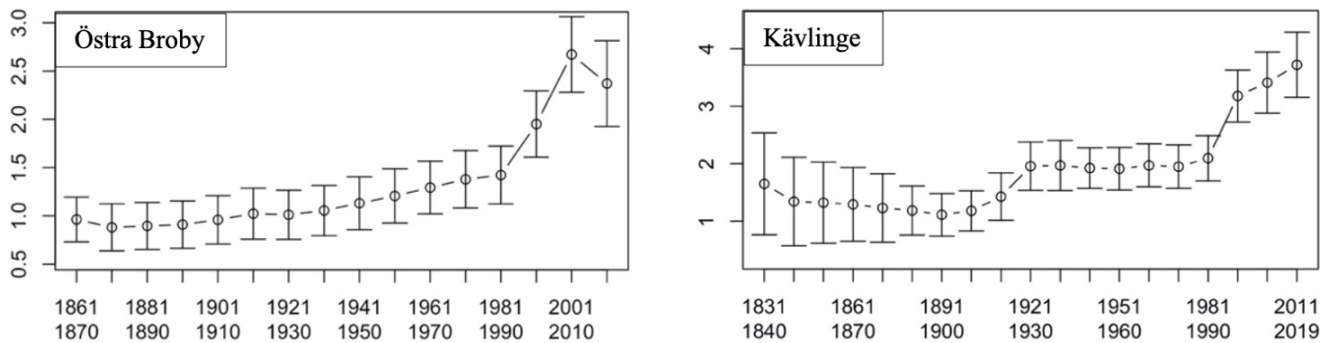


Figure 12 Mean trait value comparison for Östra Broby and Kävlinge/Lackalänga combined parishes for the trait value index of invasive concern show increases at different rates and time periods.

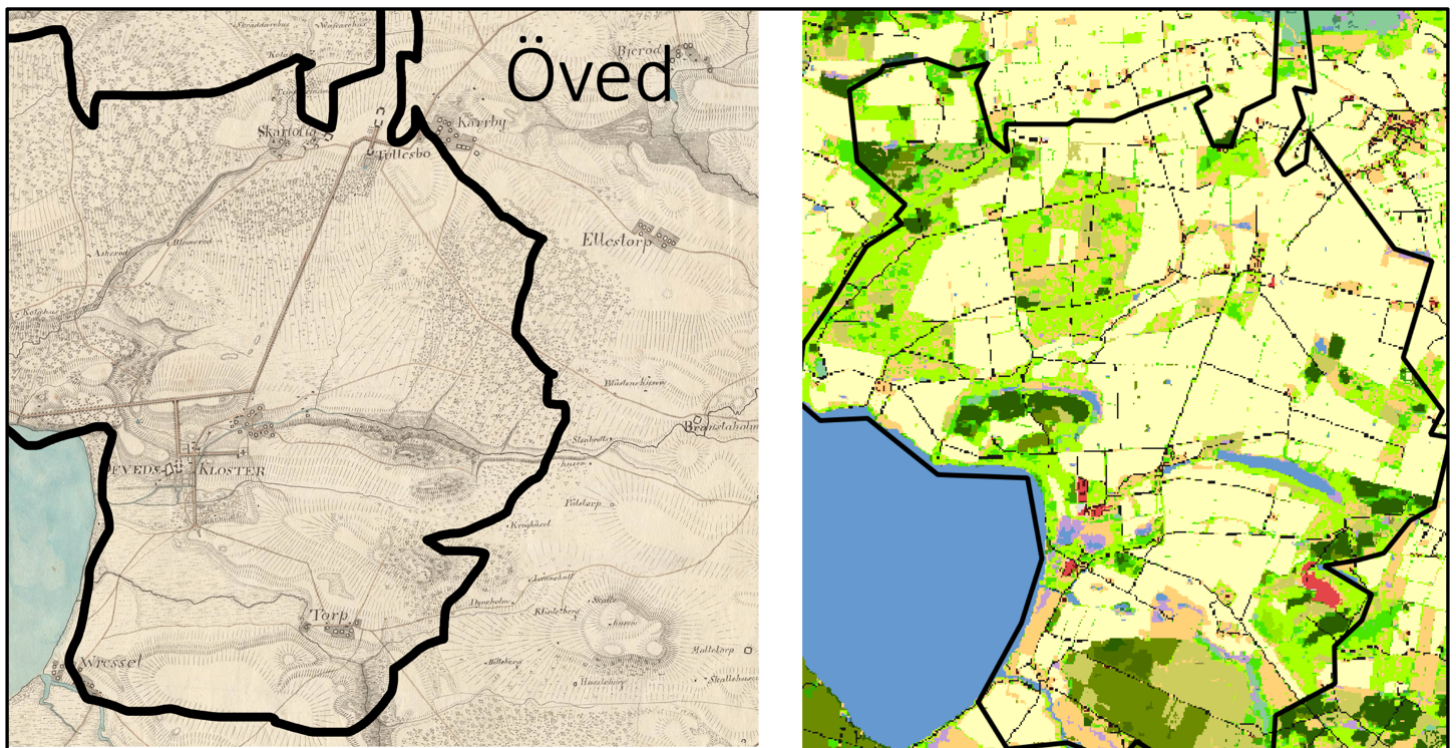


Figure 13 Land use was visually compared between reconnaissance maps from 1812-1820 (left) and modern land-use data (Nationella Marktäckedata). Comparisons for other parishes are found in **Appendix D**.

Discussion

Since the first half of the 19th century there has been a steady shift towards the prevalence of species whose inherent traits favor N and P availability, a milder climate, decreasing grazing/mowing, sunlight, and disturbance regimes, drier habitats, seeds with longer dormancy periods, a more persistent seed bank, and a perennial growth habit. In addition, there have been accelerated shifts since 1980 towards species which favor extreme climate warming, the lengthening of the growing season, increased nectar production, and which are of greater concern for invasive ability. These trends reflect an overall shift towards plant species which are more competitive and resilient. Additionally, the landscape of Scania has become more homogeneous over time. Individual findings are

discussed in the same order they were presented in the results. This is followed by the discussion of local extinctions and introductions, community analyses, the validity of the data used, and conservation implications.

Mean trait values over time

Heat and cold requirement trait values correspond well to national records compiled from 35 meteorological stations which indicate cooler average temperatures in the 19th century, a warm period in the 1930s, a relatively colder period from 1961-1988, followed by an accelerated warming from 1988 onwards (SMHI open data 2019). The trait mean values for heat requirement (**Fig. 4b**) correspond well to a relative cool period around 1970. As heat requirement indicator values from the Trait List are correlated to true climatic conditions (Tyler, Herbertsson, Olofsson & Olsson, in prep.), it is not surprising that a similar trend is represented in meteorological data. Trait mean values for cold requirement (**Fig. 4a**) are also well-reflected by national climate data records which indicate most winters from 1988 and onwards being warmer than average. Values show a slow warming through the 1800s, an increased warming around the 1930s warm period, a short trend reversal following the colder period from 1961-1988, and an accelerated warming thereafter.

Although there is a presumed lag associated with the response of local plant species to climatic and environmental conditions, there is a strong relationship between climate records and the observed flora. For instance, a warmer period is observed starting around 1930 in the meteorological data which corresponds to a plateau and then a shift towards high heat requirement values beginning around 1940. This may indicate a connection between the response time of the local flora to climatic change and should be studied further. Similar trends favoring a warming climate have been observed within several comparable surveys using the Trait List measures of temperature optimum, cold and heat requirements, continentality, and phenology (Tyler et al. 2018, 2020).

Trait mean values for temperature optimum (**Fig. 4c**) may reflect the accumulation of more “generalist” species over time, which would trend toward a median optimal value. Additionally, this may indicate a loss of warmer grassland species and the gain of closed-canopy forest species over time. The increased introduction of exotic species and the acceleration of climate warming are also relevant, the effects of which are likely compounded. As this is a fairly general trait and a combination of the heat and cold requirement scales, interpretation is limited.

Average yearly rainfall in Sweden was below 600 mm from 1860 to 1920, stabilized around 600 mm from 1920-1980, and increased after 1980 to averages of about 700 mm (SMHI open data 2019). Combined with the aforementioned increases in temperature over time, it would be expected to see a shift away from continental species and towards oceanic species, which is well reflected by the continentality (**Fig. 4d**) trait mean values measure.

From defined normal periods of 1860-1900 to 1991-2019 southern Sweden has warmed on average by 1.7 degrees Celsius, and most warming has occurred in the spring season (SMHI 2019). Additionally, the growing season in Sweden has lengthened by two weeks over the past several decades, mainly affecting the spring season (SMHI open data 2019). Trait mean values shifting towards an earlier phenology (**Fig. 4e**) may therefore be expected given patterns for climatic warming. Additionally, as winters have been milder in southern Sweden (SMHI open data 2019), many native and non-native species have expanding climate niche envelopes. Many recent immigrants come from warmer climates and may show earlier phenology or have an understudied phenology in northern Europe, which will likely influence the mean trait values. This corresponds as well to the mean trait values for extreme phenology (**Fig. 4f**) and to the expansion of the growing season in either direction, and therefore may be closely tied to the introduction and spread of neophytes. While phenology values show a steady decline, extreme phenology values show a sudden increase in recent times, indicating that earlier and later flowering (extreme) species may be canceling each other out in the overall phenology trend during the past 50 years. These trait values should be considered in tandem with descriptions of locally introduced species, which indicate many horticultural escapes have spread through the landscape, including many early-flowering ephemerals which may lower phenology trait mean values over time.

Literature regarding trends of woody encroachment and increased forest cover in Scania in the 20th century is extensive and is due in large part to traditional hay-making and grazing lands being abandoned or converted to forest for economic purposes (Cousins et al. 2015). However, extensive reduction in the seminatural disturbance patterns of animal grazing and the harvesting of hay and crops with non-mechanized tools have dramatically altered the landscape of Scania starting as early as the 1800s (Atlas Över Skåne 1999). From pollen analyses, total tree cover was estimated to increase by 65-84% from 1800-2008, with most of this change occurring from 1880-1940 (Fredh et al. 2012). Additionally, the number of farmers, farming businesses, and dairy operations have decreased steadily since the beginning of the 20th century (Atlas Över Skåne 1999). Despite recent, extreme changes in climate and woody encroachment which likely accelerate shifts away from higher sunlight (**Fig. 5a**), soil disturbance (**Fig. 5b**), and grazing/mowing (**Fig. 5c**), species requirements, the mean values for these traits reflect the steady shift away from traditional land uses toward industrial and intensified practices beginning in the early 1800s.

Though average rainfall has increased since 1980, significant land use changes occurred during the mid-1800s as the desire to increase agriculture, grazing, and forestry led to the draining and diminishing of water sources and wet areas. Though most ditches in Sweden were dug prior to modern mapping techniques (Hasselquist et al. 2018), draining of lakes and wetlands was most extensive at the end of the 19th century and the beginning of the 20th century (Hoffman et al. 2000). The climatic data contradicts the moisture trait mean values (**Fig. 5d**) which shift from wetter-growing species toward drier species. That plant species with affinities or tolerance for drier habitat can increase while rainfall in the region is increasing is counterintuitive and may indicate that historical land use changes have played a larger role than changes in rainfall.

Because land use patterns have been acting for centuries, it is not surprising that the mean trait values for light, grazing/mowing, disturbance, and moisture requirements have been shifting steadily over almost 200 years, in contrast to the rapid recent changes observed for several other traits.

Mean trait value for N (**Fig. 6a**) and P (**Fig. 6b**) affinity have increased and soil pH (**Fig. 6c**) realized niche has decreased since the early 19th century. N leach rates and N gross load in the landscape of southern Sweden have been extensive from as early as the mid-1800s, about 100 years before industrial fertilizers were introduced. High levels of early N deposition have been traced to the practice of leaving fallow fields, the tilling of previously unfarmed land, and low yields (Hoffman et al. 2000). This steady N load from the 19th century is reflected by the linear increase of mean trait affinities of the flora in the parishes toward nitrophilous species. N deposition has the potential to reduce local plant diversity by decreasing species richness and evenness in temperate forests, acidifying seminatural grasslands, and increasing population densities of highly productive, nitrophilous species which outcompete existing species (Bobbink et al. 2010). P flow in landscape is also tied to agriculture. Though inputs were much lower in the mid-19th century, more P was needed to increase agricultural productivity as the Swedish population grew, eventually leading to the heavy application of chemical fertilizers from the 1950s to the 2000s (Schmid Neset 2008).

Increasing N and P trait mean values correspond to the general acidifying deposition from industrial processes and emissions. Long term studies of soil pH in southern Sweden find acidification across habitat types starting in 1949, likely due to nitrogen and acid deposition, and these chemical changes have specific effects on the frequencies of vascular plant species (Falkengren-Grerup 1986, 1987). N, P, and soil pH mean trait values are in this way interrelated and reflect historical milestones. The relatively consistent acidification and nitrification of Scania is well-reflected by shifts in the flora over the past 200 years.

Though seed dormancy (**Fig. 7a**) has been associated with various ecological factors such as phylogenetic group, longevity, and seed weight, the strongest association is to harsher and more variable environments (Jurado and Flores 2005). The increase of seed bank mean values (**Fig. 7b**) may therefore indicate a shift toward unstable and more extreme conditions associated with climate change. Seed dormancy and seedbank are not directly

correlated, and combinations of persistence and dormancy of seeds span biological strategies (Thompson et al. 2003). That seed bank and seed dormancy show similar trends towards a more resilient strategy due to turbulent climate conditions strongly indicates that hardier species may have been favored over the past 200 years and will likely continue to be favored under climate change models. Hardiness is additionally selected for by the loss of disturbance from traditional agriculture and grazing practices, as many species would benefit from being able to survive in the seedbank for an extended period of time and as intervals between grazing or mowing become longer, enabling woody encroachment to degrade habitat.

Trait mean values for longevity (**Fig. 7c**) further support this shift in land use, as the loss of disturbance patterns combined with woody encroachment favors perennial strategy. Annual plant species are likely to be disfavored over the past 200 years, and this is reflected by a steady shift towards perennial behavior mean trait values. Studies of semi-natural grassland connectivity in Sweden in the latter half of the 20th century found increased strategies for clonal reproduction and persistence of seeds in the soil to be favored under conditions of landscape fragmentation (Lindborg 2007). That these shifts appear to have been initiated much earlier than expected indicates yet again that landscape-level changes have been strongly influencing species distributions from the early 19th century.

An increasing trend of trait mean values for biodiversity relevance (**Fig. 7d**) indicates a shift towards vascular plants with a higher number of associated non-plant species. Small plants support less associated species than larger plants in general, and larger plants are usually woody and often perennial. In Sweden, trees, shrubs, and woody plants have been found to harbor many insect, fungi, and cryptogram species (Sundberg et al. 2019). The biodiversity relevance trait mean scale (**Table 2**) may therefore measure a shift from smaller, herbaceous, possibly more specializing species, towards larger, perennial, competitive, possibly more generalist species that support a larger number of non-plant species overall. This conclusion cannot be reached with the current data, but this Trait List metric should be investigated in other settings and with other datasets to explore additional uses and possible correlations to the increase in woody plant species over time. Additionally, this increase towards larger and more long-lived species lends well to the gestalt that the flora has shifted in favor of more competitive species during the last 200 years.

Increased nectar production has been associated with environmental as well as heritable factors and has been linked to pollinator response and plant fitness, specifically regarding resource acquisition (Parachnowitsch et al. 2019). Additionally, pollinator-mediated natural selection for nectar traits lacks evidence. The evolution and ecology of nectar production within plant-pollinator interaction has eluded researchers for some time and warrants further research. Trait mean values for nectar production lend well, again, to the continued shift towards species which are more competitive across several metrics and habitats. Although it may seem counterintuitive for mean trait values (**Fig. 7e**) to shift toward higher nectar production in the past 50 years given recent studies outlining insect decline (Hallmann et al. 2017), these traits may indicate overall biological fitness more than an intricate relationship with the pollinators themselves. In this way, it would be possible for insect populations to decline while nectar production in plants increases, in a way decoupling this often closely held interaction.

Trait values for both time of immigration (**Fig. 8a**) and the level of invasive concern (**Fig. 8b**) are derived in large part by the historical arrival of species. Therefore, these coupled traits are assumed to show an increase from a zero value (resident species = 0 in the Trait List, **Table 2**) to some increased rate dependent upon local introduction of certain species. This quantifies introduction rates at a regional level, but is potentially more informative when comparing parishes or regions to one another (see **Appendix B** for individual trait mean values over time). Because non-native invasive species threaten to displace and outcompete native species, it is important to understand introduction patterns and timelines, many of which have occurred long ago and long before the negative effects on biodiversity have become apparent. Likewise, a slow increase in potentially invasive plant species, combined with climate changes that expand niche envelopes for many non-native species, can lead to exponential increases of ecological damage on the landscape-level. Therefore, even lower-level indications for invasive species concern, as defined by the Trait List, should be taken seriously by regional land managers and mitigated before climate change accelerates their spread and impact.

The Canonical Correspondence Analysis of trait means values and species presence (**Fig. 9**) reveals an overall movement of the ten parishes over time from disparate planes to a centralized point and thus indicates a likely homogenization of the regional landscape. There is an effect of nearly all individual traits included, with weaker associations to moisture and extreme phenology traits. N, P, invasive concern, and immigration traits correspond to more recent changes and to unilateral effects. Temperature metrics, pH, and biological strategy metrics show more variation in their effect and have a stronger effect in earlier decades. Billinge, Svalöv, Vittskövle, and Östra Broby parishes form a cluster which do not seem to correspond to geographical or historical land-use divisions. Hardeberga/Södra Sandby, Öved, and Stehag parishes are more spread out across time but are loosely in the same plane. Vellinge has the most outlying spread, which is not unexpected as it is southernmost, coastal, and strongly affected by intense agriculture. Lomma travels along a similar plane as Vellinge parish, although it not as outlying, and is also southern and coastal. Because the most recent decades of this analysis are related to immigration and invasiveness measures, neophytes can be inferred as a driver of the homogenization of the landscape. These species are often weedy generalists and can be found in a variety of different habitats and therefore do not reflect the geologic, climatic, or historical history of the individual parishes. This can result in a deadening effect on unique patches across the landscape, as local diversity is masked.

The following descriptions of local extinctions and introductions are concordant with trait mean values and CCA analyses. In summary of the habitat descriptions from the Flora of Scania (Tyler et al. 2007), the twelve species with the highest proportion of local extinctions within the parishes have a high sunlight requirement, a high preference for disturbance regimes of varying types, several prefer wetter sites, and most prefer nutrient-poor soils. Several of the locally extinct species were associated with traditional agriculture and field margins. A mix of habitats for these locally extinct species may indicate once again that there was more variation in traits and habitats for the flora of the past. In general, as is indicated by the trait means (**Fig. 11**) locally extinct species had a much lower preference for N and P, were more favored by disturbance regimes, and had less competitive biological strategies (less perennial, less seed dormancy, shorter-lived seed bank). Both cold and heat requirements were higher than average, which may indicate a preference for continentality.

Being that these species have disappeared from 70% or more of the study area, they can be inferred to have been well-spread in the landscape at some point, due to suitable habitat and geography. Their declines may have begun long before this study, as the effects of draining the landscape, N deposition, and land use changes in favor of more intensified agriculture and forestry have been sustained for centuries.

Species with the highest proportion of local introductions in the ten parishes correspond almost exclusively to escapes from horticulture or the forestry industry. Many species are woody, although early spring ephemerals are also well-represented. Many of these species have existed in the landscape for some time, and have only recently begun reproducing or spreading due to milder climate conditions. Comparison mean values (**Fig. 11**) for immigration and invasive concern metrics are expectedly high for recently introduced species. Heat requirement, N tolerance, nectar production, and extreme phenology traits are higher than average species, which corresponds to competitive species as well as many invasive species. Moisture requirement and grazing/mowing requirement were lower than average species, indicating increased suitability to drainage and woody encroachment in the landscape.

Community analyses

This description corresponds to **Figure 13** and **Appendix D**. As generally described in the literature, population growth and demographic shifts have led to development in all regions, with Lomma, Kävlinge/Lackalånga strongly affected, Vellinge and Hardeberga/Södra Sandby moderately affected, and the remaining parishes relatively mildly affected. In the early 1800s, there were no notable coniferous forest stands shown on the reconnaissance maps for the region, except coastal Vittskövle which is presumed to be scots pine forests (*Pinus*

sylvestris) planted from the early 1700's to combat sand drift. Although pine is now planted as well throughout southern Sweden, increases in Norway Spruce (*Picea abies*) plantation has decreased biodiversity and led to extensive habitat loss for many species (Pettersson et al 2019). Also of note is forest cover in general, as Hardeberga/Södra Sandby and Kävlinge/Lackalänga had little to no forest cover in the landscape 200 years ago, while today a significant portion of the parish is forested, almost always as plantations. Areas that were indicated as forested in the 1800s were almost certainly grazed during this time and more open-canopied, while closed-canopy industrial plantations are the norm today.

Pollen analyses indicating a shift from deciduous to coniferous species during a vegetative transition period from 1880-1940 (Fredh et al. 2012), in combination with general woody encroachment and increased forest cover, may have resulted in many of the trends presented. The shift from Scots Pine (*Pinus sylvestris*) to Norway Spruce (*Picea abies*) in the landscape can have a significant effect on regional biodiversity, as *Pinus* supports more understory species than *Picea* in the region (Pettersson et al. 2019).

To illustrate the value of comparing mean trait values for individual parishes or regions, values for invasive concern are described. Kävlinge/Lackalänga combined parishes show a relatively high starting point for invasive concern species trait average (~2 in the mid-1800s). The presence of industrial wool production facilities here introduced many non-native seeds which had been embedded in wool arriving from regions as far away as Australia and South America (Lange et al. 1954). These seeds often germinated and could persist for some years before dying out due to unsuitability for local conditions. Though the rare alien species were not included in analysis, the wool industry likely brought some seed that would eventually be included as resident in the flora and which appeared early on in this parish. Comparatively, Östra Broby parish, which is isolated and sparsely populated, has an average mean value around 1 for invasive concern in the mid-1800s. A significant portion of Sweden's species of invasive concern have resulted from the introduction of exotic plants from the horticulture industry (Tyler et al. 2015). Regionally underpopulated Östra Broby parish has been possibly insulated from such introductions. While direct comparison of these parishes cannot be quantified in regard to potentially invasive species, it does show an early indication of a higher potential for future risk, and does in fact result in a much higher average trait value in Kävlinge (3.5) when compared to Östra Broby (2.25) in present-day.

Validity of the data used:

Availability of herbarium material decreases farther back in time due to degradation and lost collections and historically fewer botanical resources. To compensate for this, all observations prior to 1800 were condensed to a "-1800" category, although early decades represent a fairly small portion of total records. Even Carl Linnaeus contributed several data points from his travels in the region in 1749, though this marks the lower boundary in time from which species-level observations are available. Herbarium data are highly influenced by the individual collector, the localities they choose to focus upon, the decades they are active, specific groups of interests, and many other factors (Rich & Smith 1996, Daru et al. 2018). By allowing for presence/absence data instead of frequency data, the bias of frequently sought after or recorded ("botanically interesting") specimens and habitats is somewhat minimized, as an individual observation of a species per decade is weighted equally. Although frequency data is often preferred in ecological studies, the bias towards (or against) certain species or genera by human interest can be particularly stark farther back in time (Daru et al. 2018).

Although selected for early botanical completeness, each parish shows a clear increase of observation over time, due in large part to the chosen cumulative nature of data compilation (**Appendix A**). Despite efforts to compile data prior to 1800, there are scant observations leading up to the mid-1800s. Billinge parish, after the complete inventory of Lilja (1846), displays a fairly stable number of species over time. Vittskövle and Östra Broby show a similarly stable number of observations due to the work of Brown (1870) and several residing botanists. Hardeberga/Södra Sandby combined parishes show a conspicuous jump starting in the 1960s, which is due to the realization of many botanists that a southeastern portion of the parish was previously neglected and subsequently

added to the future inventories. Lomma, Stehag, Kävlinge/Lackalänga, and Öved parishes show a steady increase of observations per decade over time, which is expected as botanical knowledge increases regionally and as Weimarck's inventories are enacted, starting in 1938. Vellinge and Svalöv parishes also reflect the trend towards more species over time, but have far fewer observations prior to 1900. This limits its utility for this type of study, where regions without an abundance of older observations cannot be effectively investigated.

Fragmented and mix-source data provide many challenges for analysis. As the level of botanical knowledge ebbs and flows across centuries (as it will likely continue to do), data oscillates on a continuum of presence-only and presence/absence data, wherein an increase in observations and overall completeness of a local inventory nears true presence/absence data. For this reason, it is unrealistic to expect data collected through citizen science to ever reflect presence/absence data at the level provided by a standardized survey method. Given the increase in citizen science globally over the past decades (Geldmann et al. 2016) it is highly relevant to explore the application and limitations of these data sources on multiple scales. Additionally, there are likely to be a few false observations across the compiled databases and even several human errors when working with many large files filled in by hand from various sources. This is presumably counteracted by the sheer magnitude of the data included in the analyses, such that several false observations will have little to no effect on the results or to the overall mean values. This study can hopefully provide a template for similar studies in other regions which have an extensive historical collection of species or a flora which is well-documented through publications from the past two centuries or so.

One potential issue within the project is to control for common species. Over the past centuries, and still today, many botanists are more interested in (and therefore more likely to document) unusual or rare species than those which are more common across the landscape (Isaac & Pocock 2015). Because species may fluctuate between rarity and commonness over time, the attention they may receive from botanists will also change. Over several hundred years, even many common species are considered to be threatened or red-listed by the IUCN. The number of species across groups with endangered status have increased significantly according to the 2020 red-list (SLU Artdatabanken, open data 2020).

The importance of common species in historical studies is thus two-fold: correcting for missing data based on prior exclusion by knowing what was excluded and why, and being able to compare relative commonness over time. Because frequency data will never be widely available for the 1800s flora, these types of estimates and comparisons provide a deeper understanding of change over time, especially when informed by the published work of botanists of the past. Not only does Nils Lilja (1808-1870) supply an abundance of observation records to this study, he invaluablely describes frequency of species in the mid-1800s which provides rare information on how common or rare a particular species was up to 200 years ago. Earlier analytical comparisons of the flora of Billinge based on Lilja's prolific works indicate that an overall increase of species does not correspond to an increased local diversity. Many species common 200 years ago have disappeared or greatly diminished from the landscape, even if there are more species existing temporarily, often in human-made habitat, counted in inventories (Tyler 2008). This is greatly reflected in this study, as species total count increases over time, this does not correspond to a greater diversity of habitats or ecological function. The dynamics of common species have proven to be both a computational challenge and an important reminder as to how historical inventories must be understood and corrected for. It also serves to remind us of the possibility to lose common species and habitat, altering biodiversity in a relatively short time and leading to potentially dire ecological consequences.

Additional future studies may focus on habitat-based analyses, as the combinatorial possibilities of habitat type and species traits is seemingly endless, and the exploratory possibilities of finding relevant trends within presence/absence data for a specific location over time are expansive. The addition of Brunnby, Kullaberg and other parishes with large nature reserves would provide a comparison as to how protected areas have changed with fewer human-influences. The addition of categorical data within the Trait List can be rescaled and optimized for analysis to investigate changes for pollinator dependence and mycorrhizal associations over time.

Conservation implications

Whether a trend which decreases species diversity has been acting for a few decades or for a few centuries is of particular importance to conservation, as this provides context for specific habitat types, the extent of fragmentation, the presence of genetic bottleneck effects, and the effects of extinction debt. Management strategy can be fine-tuned when considering these principles. To illustrate, mean trait values over time indicate that the current negative impacts on biodiversity due to woody encroachment are multi-faceted and layered on top of a very long and steady decline in grazing/mowing, disturbance, and light availability. This continuity impresses that losses from these habitats may not be able to be mitigated without significant action, or that previous efforts have not been effective. Simultaneously, the gene pool for these populations is likely significantly altered and should be taken into account within ex-situ conservation. It is critical to compare and prioritize conservation action given limited time and resources for management. Therefore all available contextual information should be considered in planning.

Traits which show rapid and recent changes, such as increasing invasive concern, should be considered from a different time-perspective within conservation. Sweden, like much of Europe, has introduced new plant species over the course of human movement and trade during the past several centuries, and thus many naturalized species are considered as part of the native flora of Sweden. Out of the 7010 vascular plant species recorded in Sweden, 3841 species have immigrated with human assistance since 1700 (Tyler et al. 2015). Many of these species came from neighboring European countries and may have eventually colonized Sweden at some point as the natural expansion of species after the last ice age. Therefore, they often do not display invasive behavior, as many of the habitats, climate, and associated species they interact with are relatively similar to conditions in their previously native range. This is in stark contrast with the more recent arrival of species from North America (*Solidago canadensis*, *Lysichiton americanus*, *Epilobium adenocaulon*), Asia (*Rosa rugosa*, *Reynoutria japonica*), and continents far removed from Europe which would not have reached Sweden without the aid of modern human transport. For these non-native species introduced within the last 100 years, climate warming may expand their ranges quickly and cause irreversible economic and biological damages. Though criteria for evaluating the invasiveness of these species is arduous and complex, and Sweden may have avoided some ecological damage thus far due to a colder climate and poor soils (Tyler et al. 2015), it can be taken hand in hand with several of the presented environmental changes and floristic shifts that conditions for non-native species are likely to improve in the coming decades. Given the acceleration of environmental and land use changes, it is critical to anticipate the spread to invasive species from a conservation perspective and to expect that many of the barriers that have kept invasive species at bay may be rapidly weakening.

Kew Botanic Garden and associates have utilized a database of seed-bearing plants globally to find extinction rates as much as 500 times higher than the previous estimates (Humphreys et al. 2019). While the quantification and ranking of regional and global extinction rates have always been of great importance, it is increasingly likely that we have entered a phase of widespread biodiversity losses wherein common species are rapidly diminishing in geographical range and overall population size. In this way, a study spanning as far back as 1800 serves as a reminder that many of today's rare and endangered species were not rare 100 or 200 years ago. Likewise, the common species of the previous decades should not be considered safeguarded as the Anthropocene continues.

Limitations of historical data were found to lead to conservative estimates of species declines when compiled databases were used for monitoring biological trends (de Heer et al. 2005). Even in well-documented regions in Scania, this likely has the same effect whereby less early-observed species equates to a less-complete early flora and many missed species which would correspond to local extinctions. It is critical to assume that we have lost more species than which we have counted, that common species and habitats must be accounted for before they end up on the IUCN red list, and that human-influence has been the driving factor for floristic change. It is in our hands to create and allow for biodiverse environments to exist or to allow for their continued diminishment.

Conclusion: The resurrection of detailed documentation of early vegetation composition can inform local variation and regional trends in floristic change. Species-specific trait value analyses coupled to presence-only data over a long time-series both corroborates previously described drivers of floristic change, and indicates whether such trends have been long-acting, fluctuating through time, or rapidly accelerating in recent decades. Overall, this study indicates that many of the most alarming recent trends, such as climate change and N deposition have been acting and affecting vegetation for a much longer period of time than previously assumed, some for at least 200 years. Additionally, the landscape has become more homogenous, likely because species-rich grasslands and meadows have been replaced by unilateral stands of forest and cropland and because recent immigrant species have become ubiquitous in the landscape. Many of the non-native species are weedy generalists which lack the habitat specificity requirements associated with many of the locally extinct species. Further, when considering these traits in unison, there is a stark trend towards a more competitive, tolerant, resilient, and versatile grouping of plants which are well-adapted to anthropogenic practices and the high input of nutrients in the modern landscape. In a way, many of these species were groomed by humans and their behaviors in the centuries prior, as much as they are altered by our changing behaviors in the Anthropocene. Humans have powerfully controlled the landscape of southern Sweden for quite some time. Although some general trends act broadly, the extension of time scale in analysis of biodiversity loss and a deep understanding of the local drivers of floristic change of the region provides much-needed context for targeted and successful conservation.

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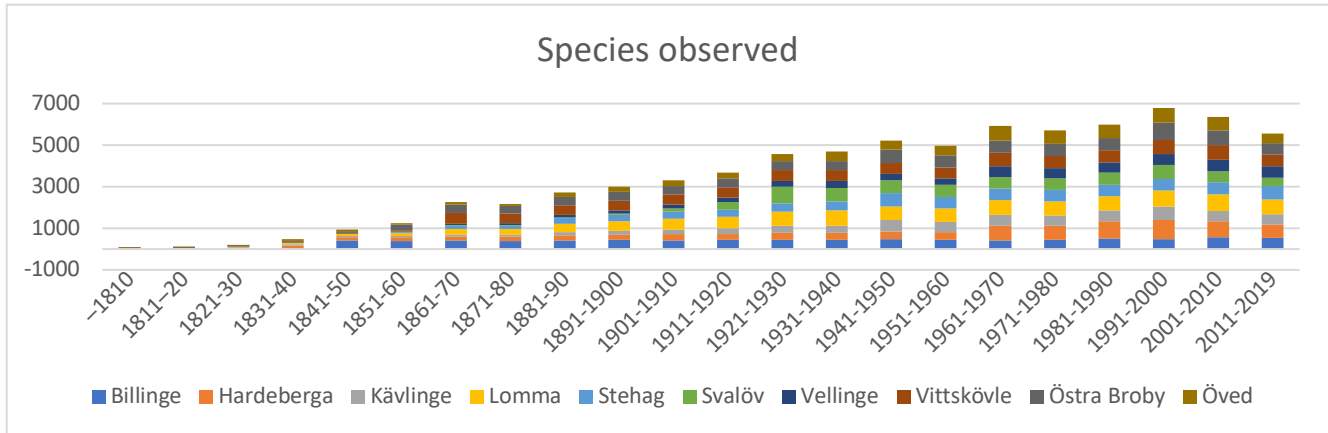
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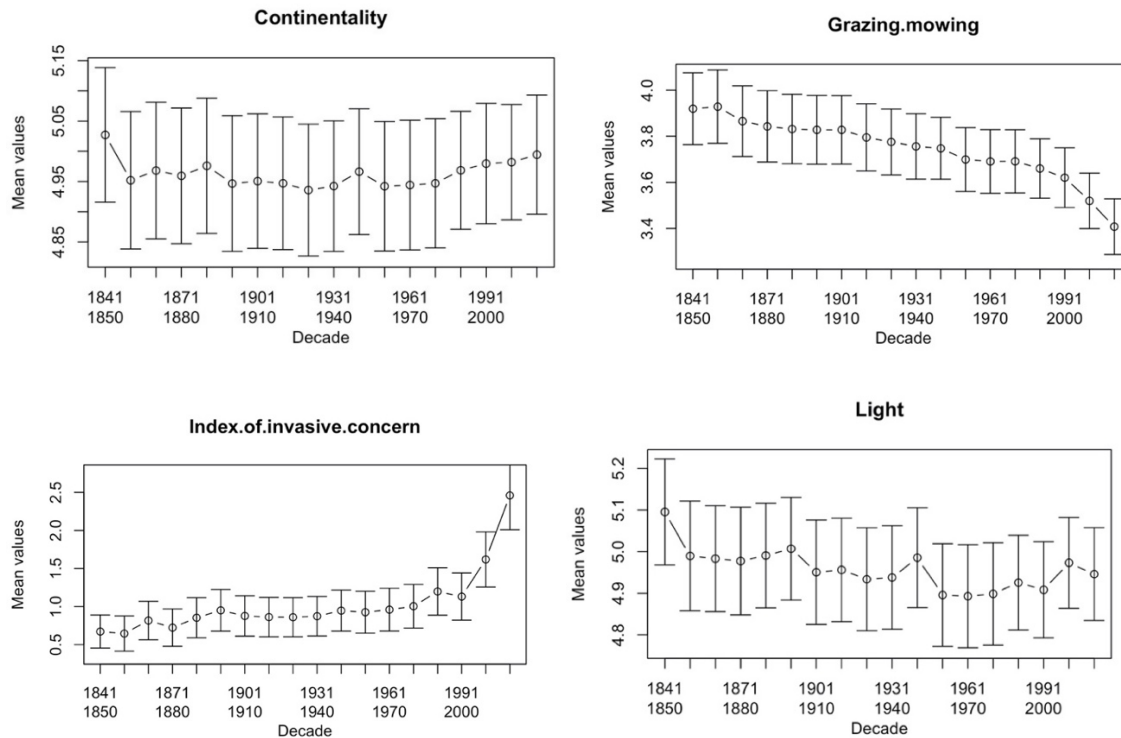
Appendix

A. Unique species observed for each decade for each parish

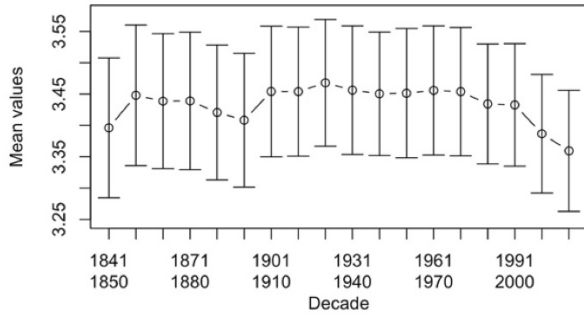


B. Mean trait values for each parish (relevant cutoff of minimum 20% species total)

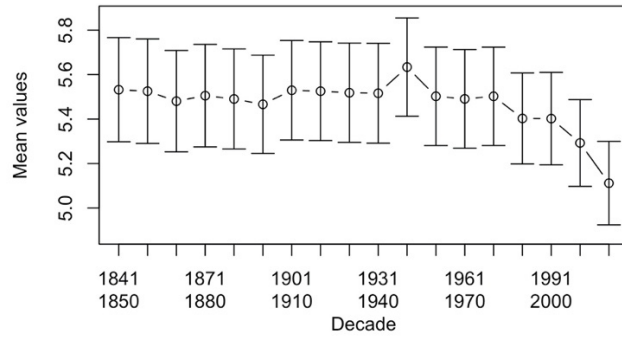
Billinge:



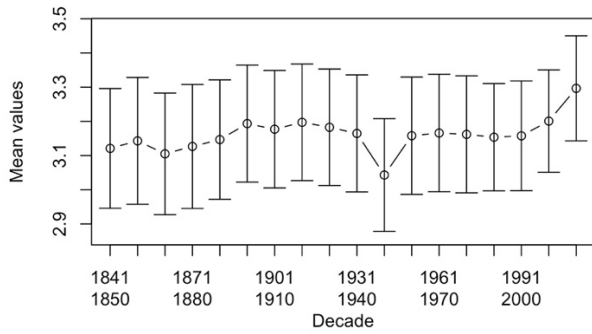
Longevity



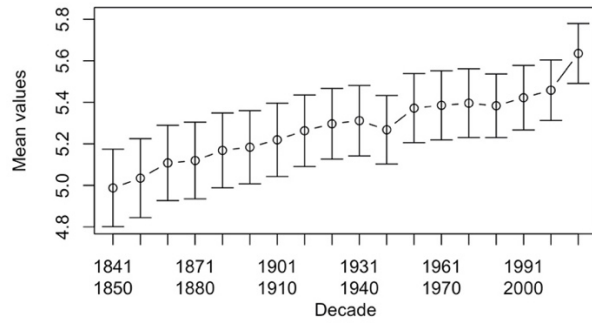
Moisture



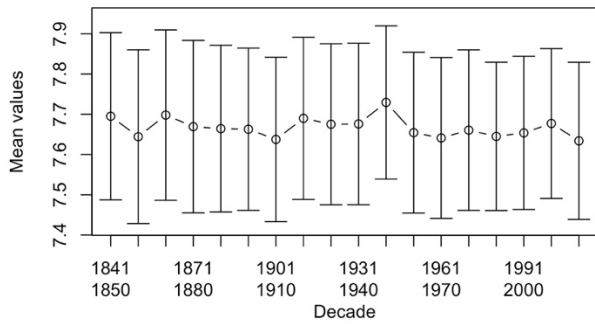
Nectar.production



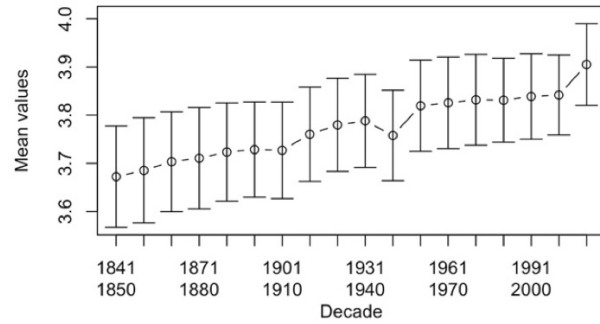
Nitrogen..N.



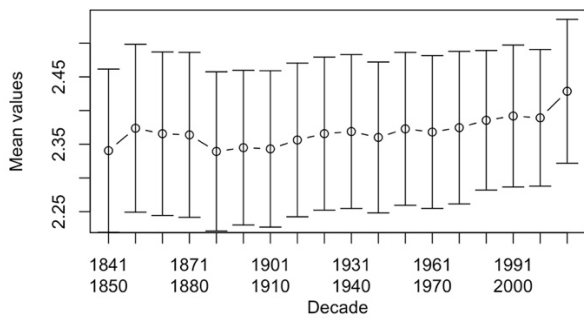
Phenology



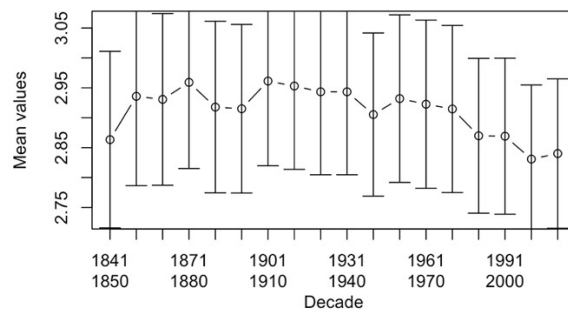
Phosphorus..P.



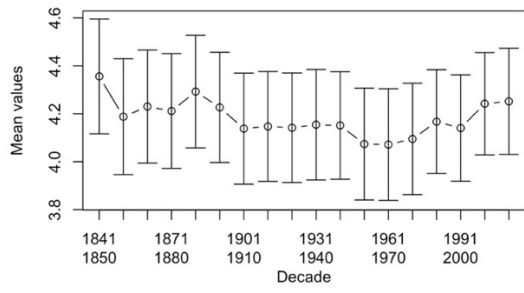
Seed.bank



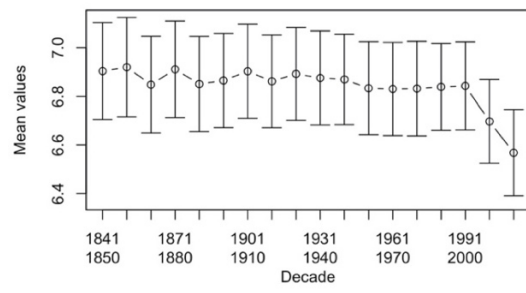
Seed.dormancy



Soil.disturbance

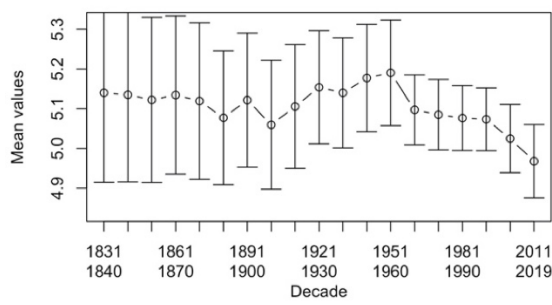


Temp..optimum

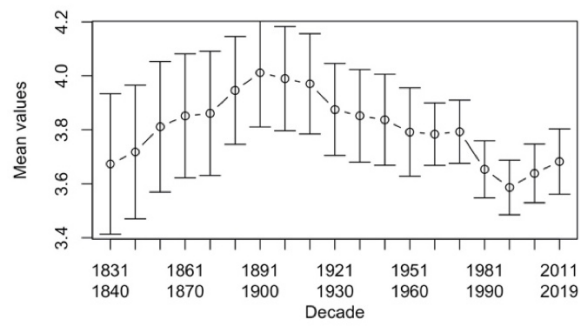


Hardeberga:

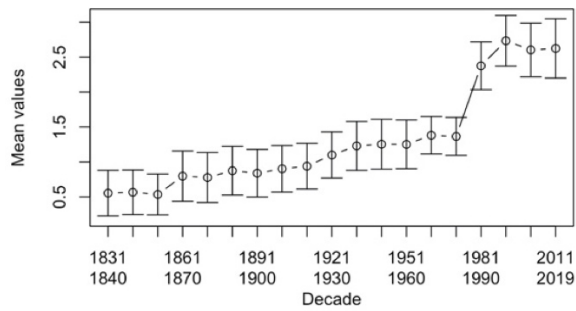
Continentality



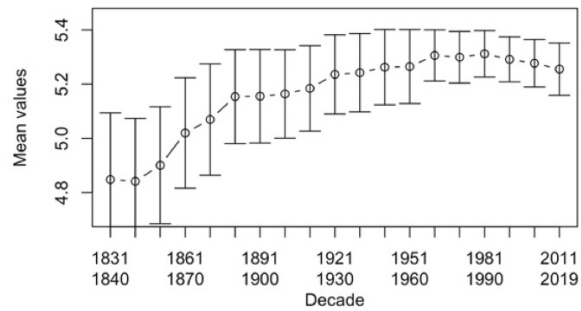
Grazing.mowing



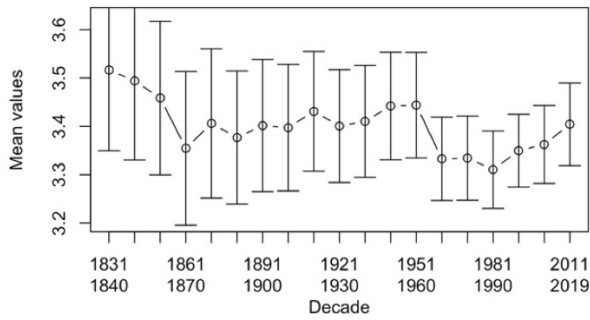
Index of invasive concern



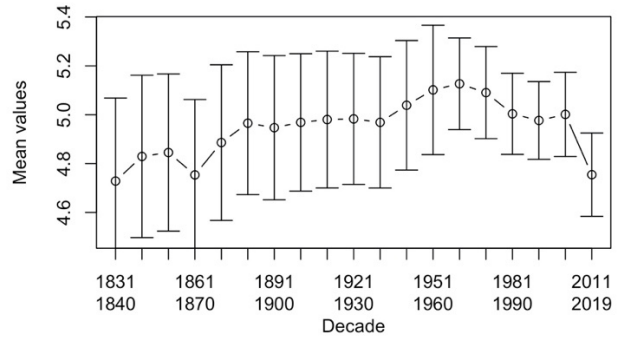
Light



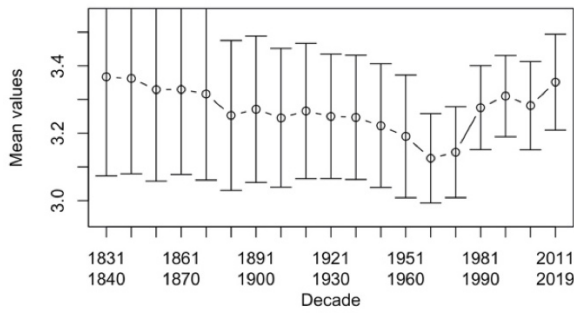
Longevity



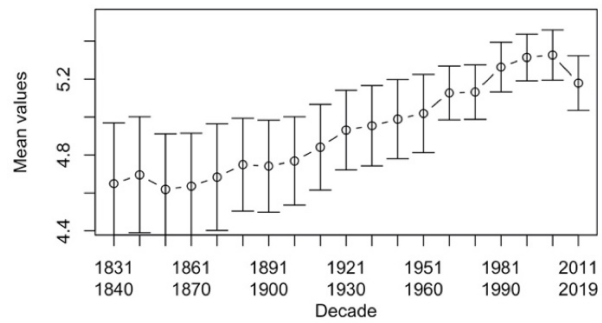
Moisture



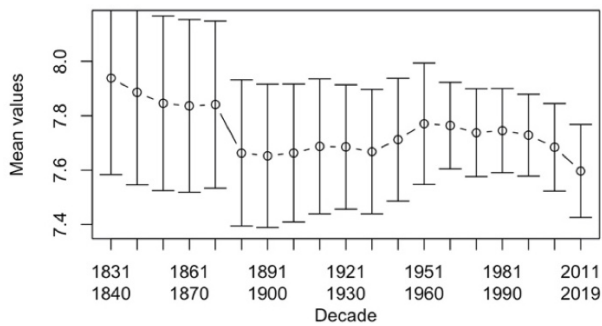
Nectar production



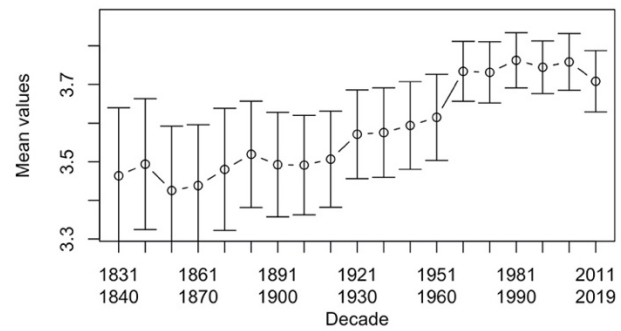
Nitrogen .N.



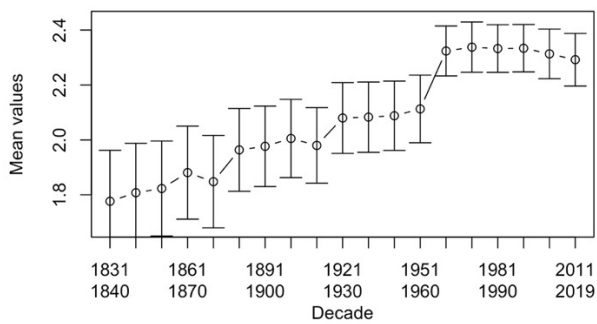
Phenology



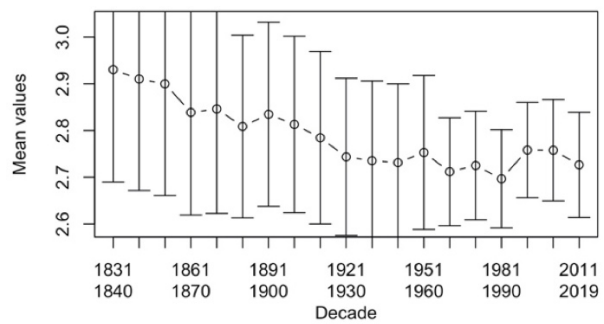
Phosphorus .P.



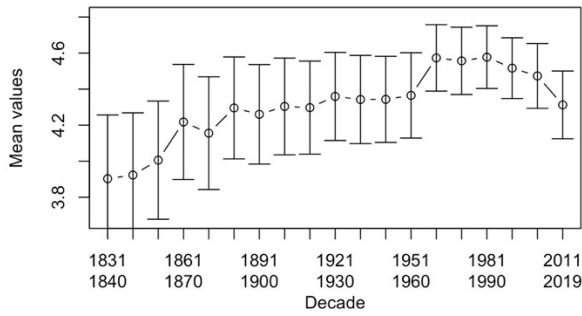
Seed bank



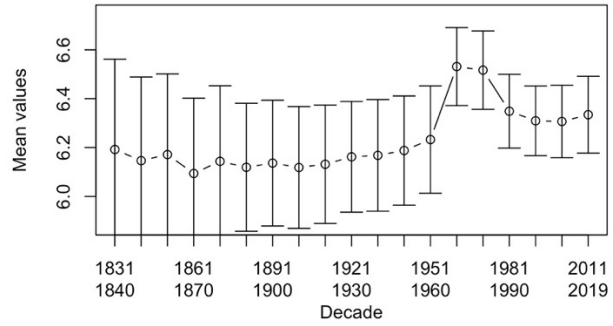
Seed dormancy



Soil disturbance

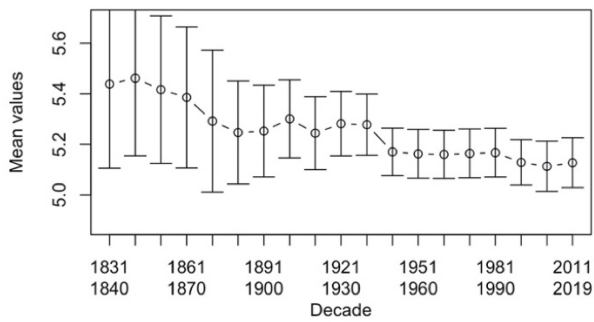


Temp optimum

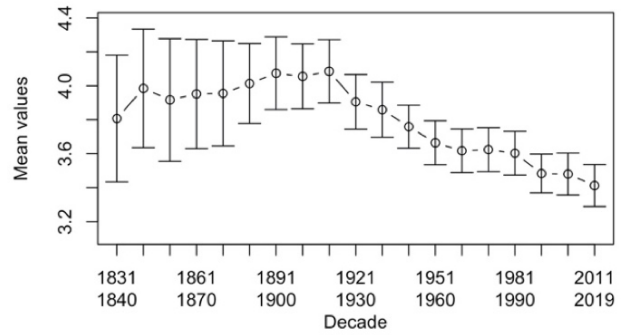


Kävlinge/Lackalänga:

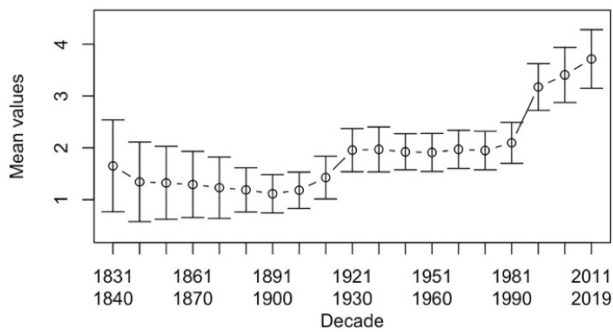
Continentality



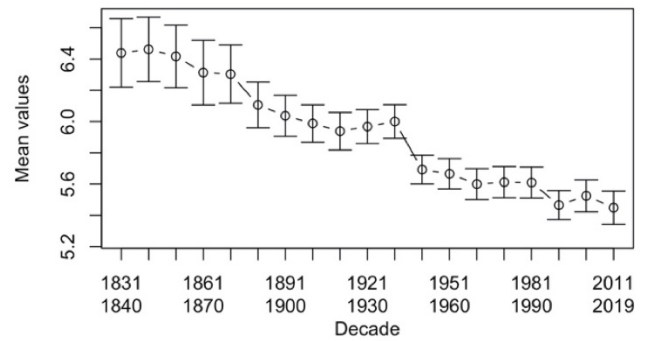
Grazing.mowing



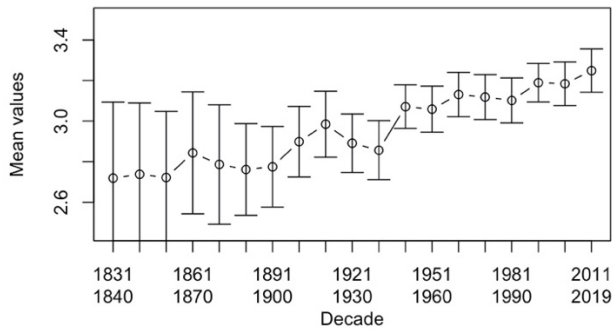
Index.of.invasive.concern



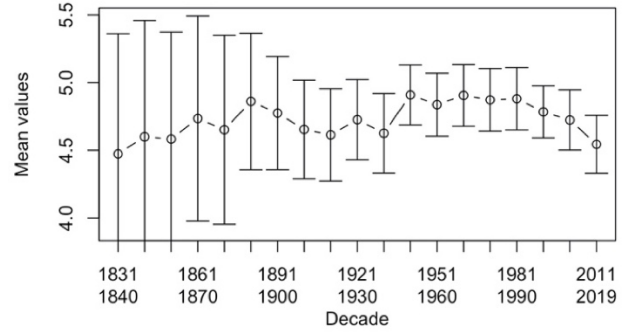
Light



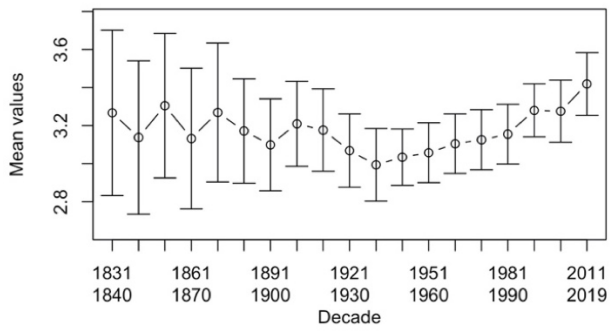
Longevity



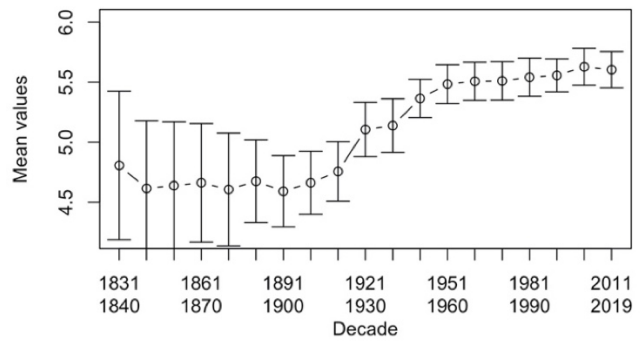
Moisture



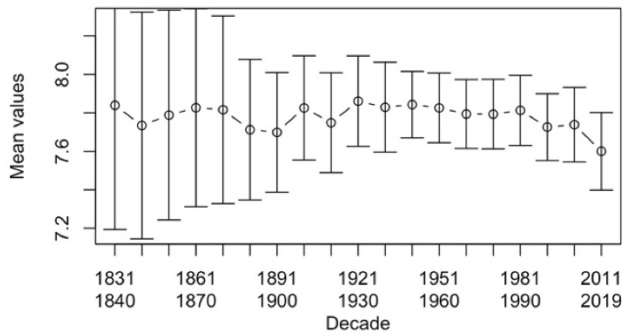
Nectar.production



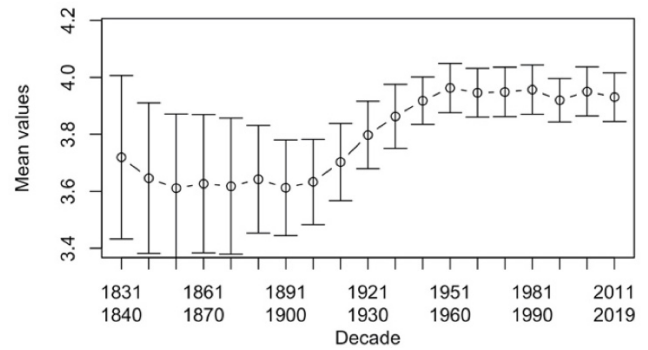
Nitrogen..N.

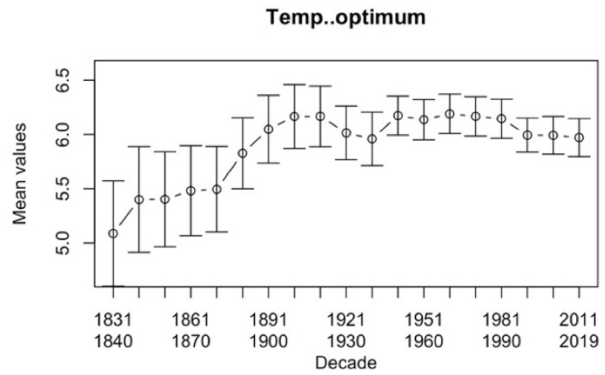
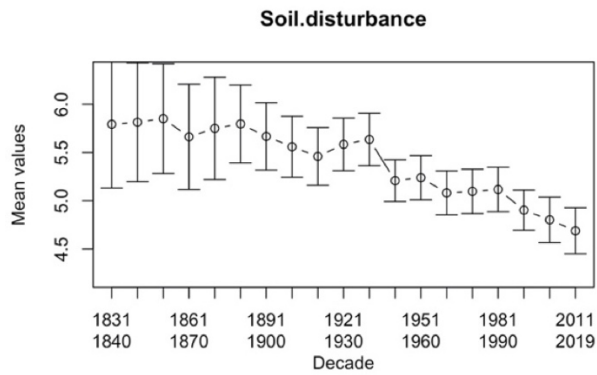
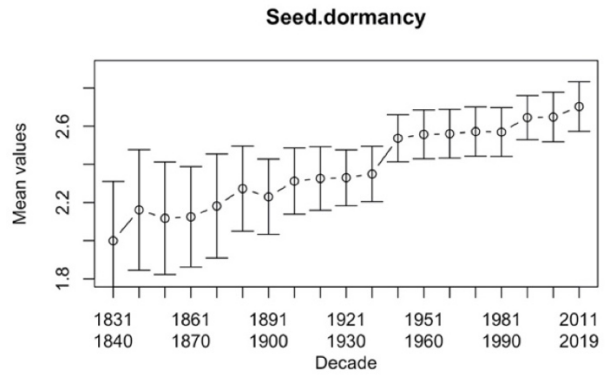
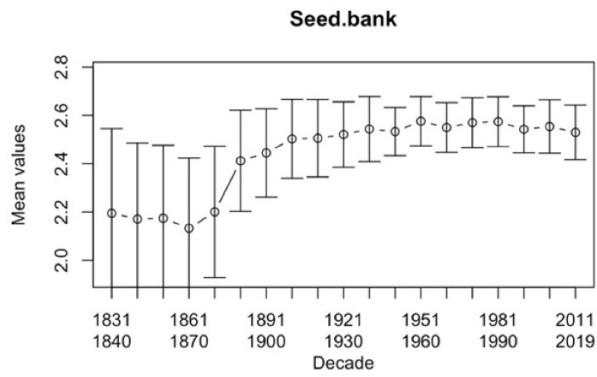


Phenology

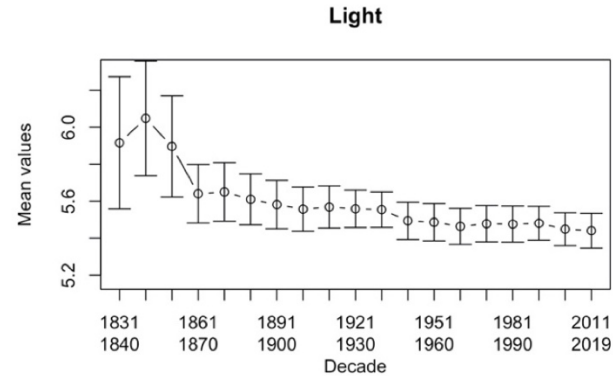
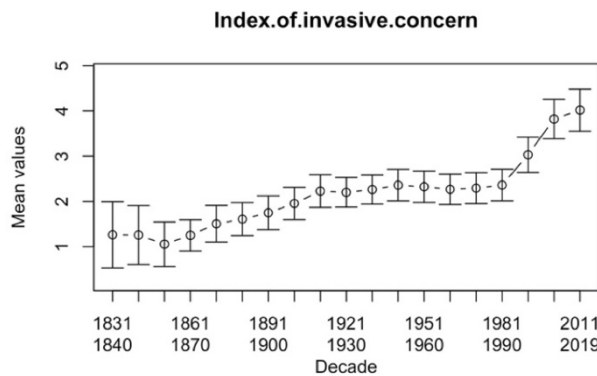
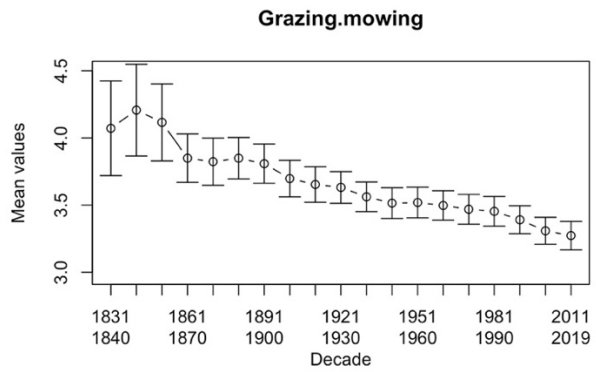
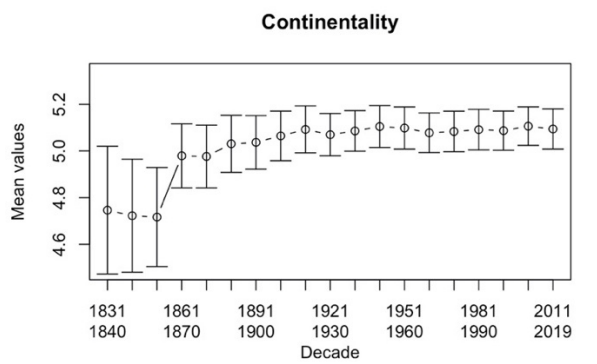


Phosphorus..P.

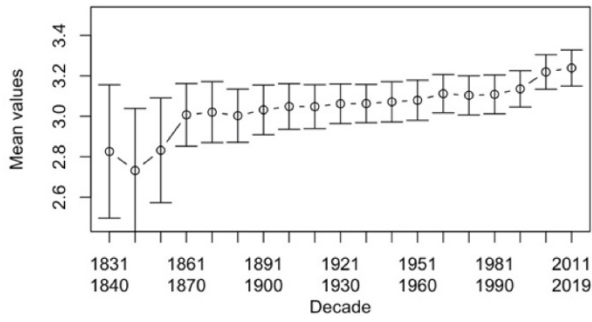




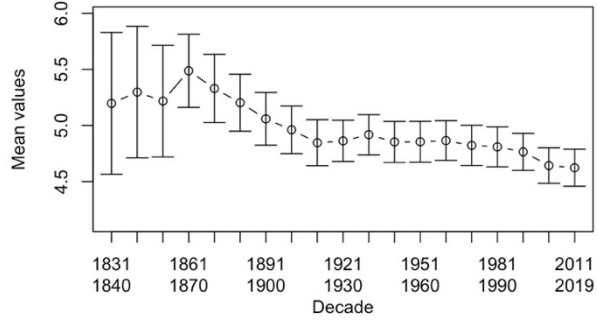
Lomma:



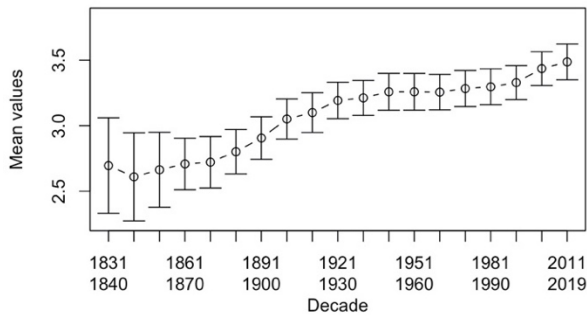
Longevity



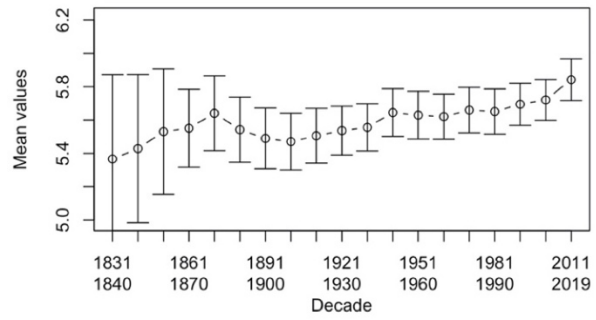
Moisture



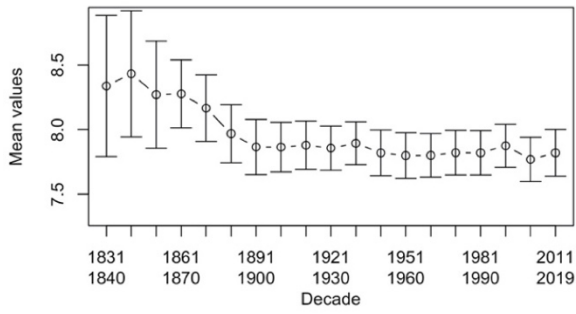
Nectar.production



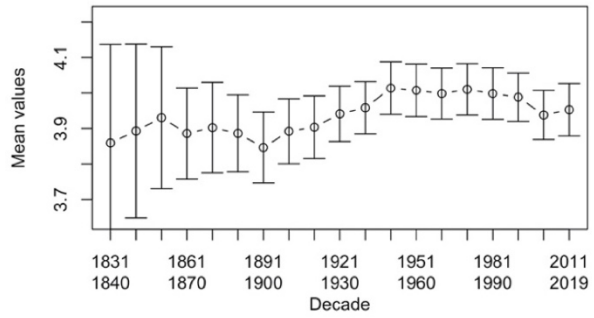
Nitrogen..N.



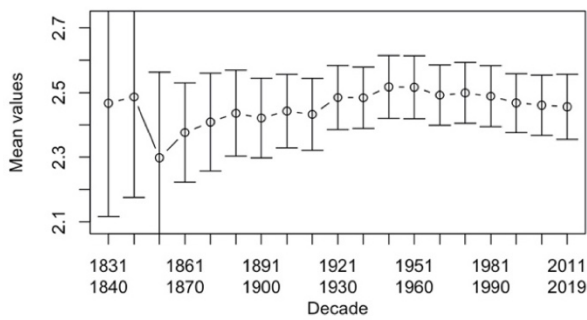
Phenology



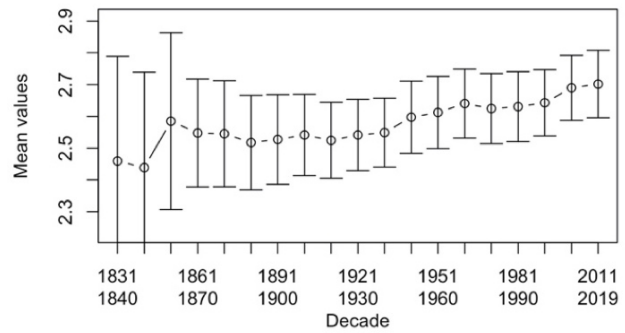
Phosphorus..P.

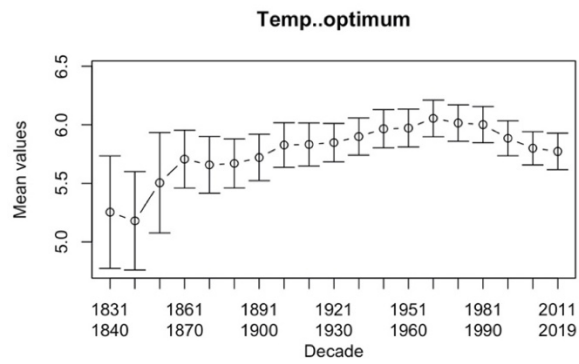
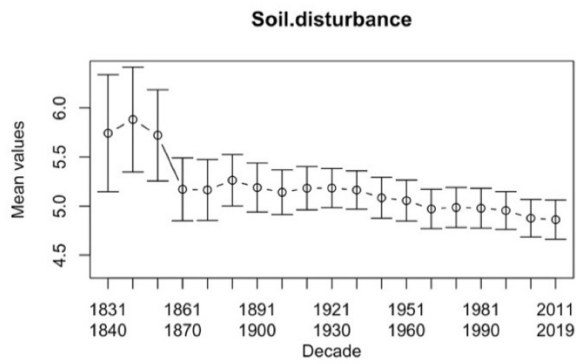


Seed.bank

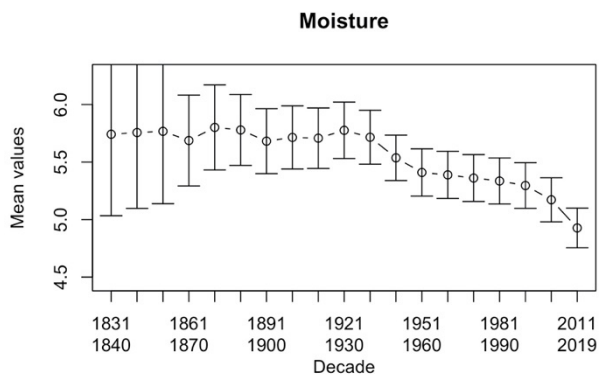
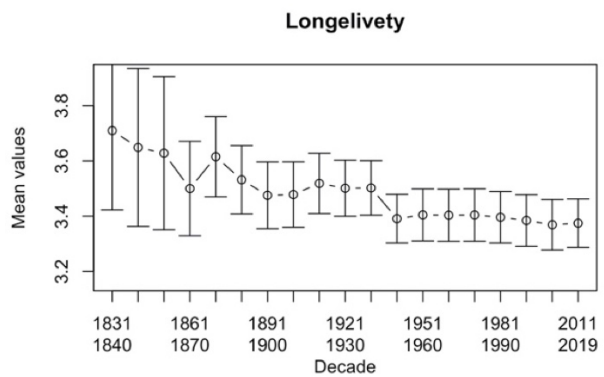
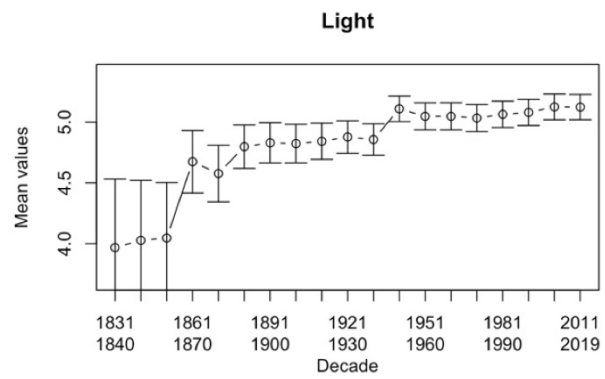
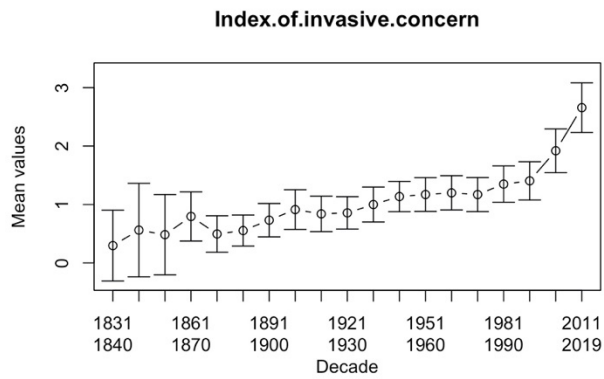
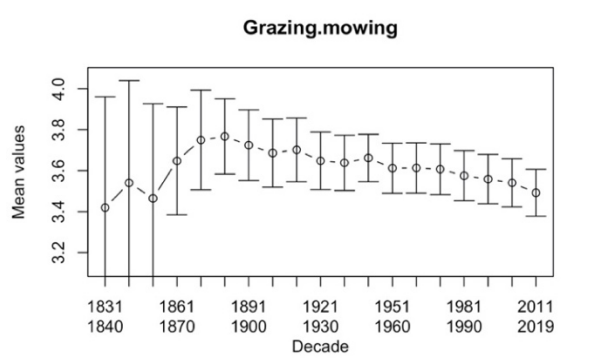
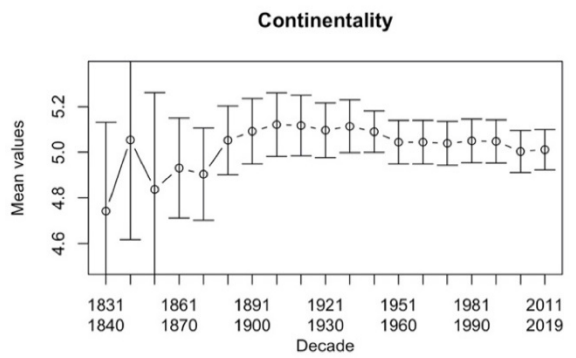


Seed.dormancy

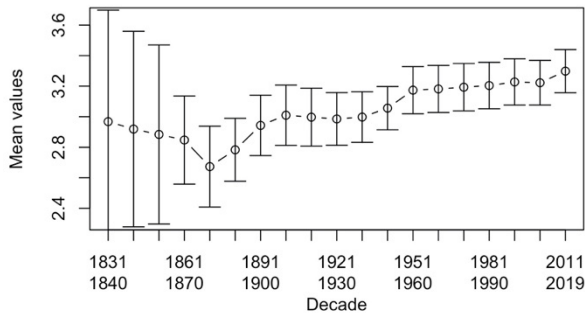




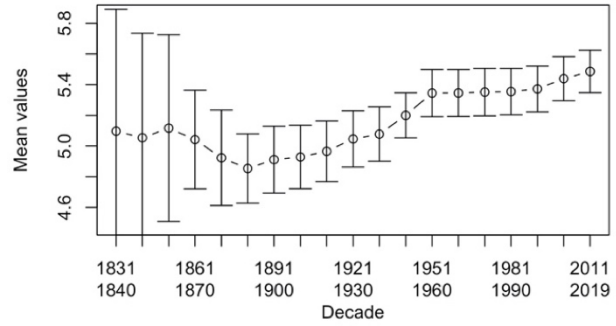
Stehag:



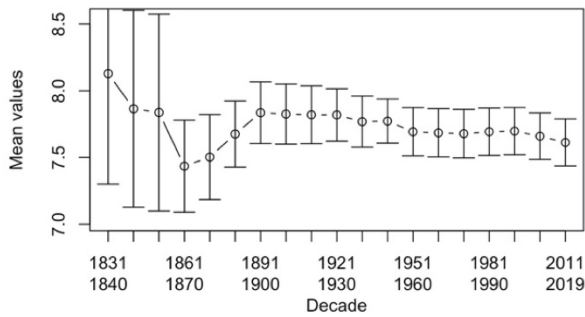
Nectar.production



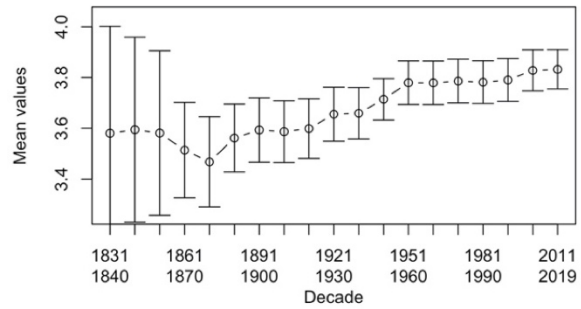
Nitrogen..N.



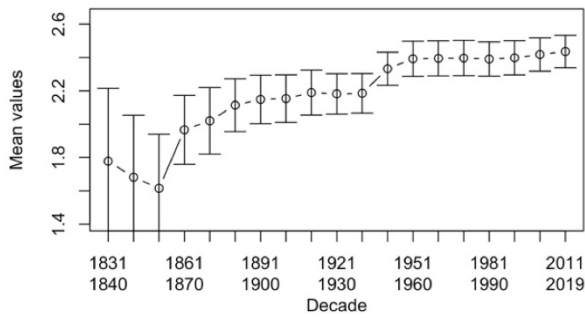
Phenology



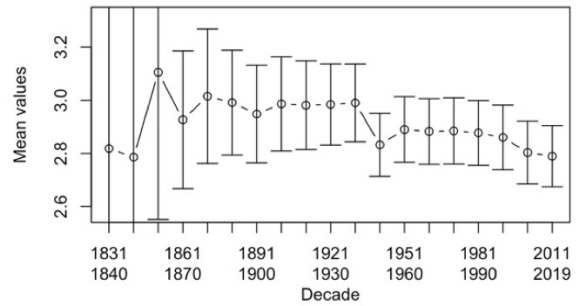
Phosphorus..P.



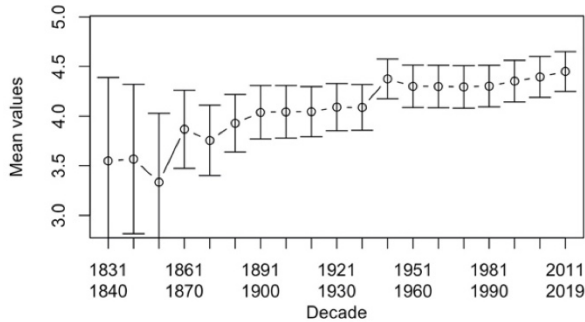
Seed.bank



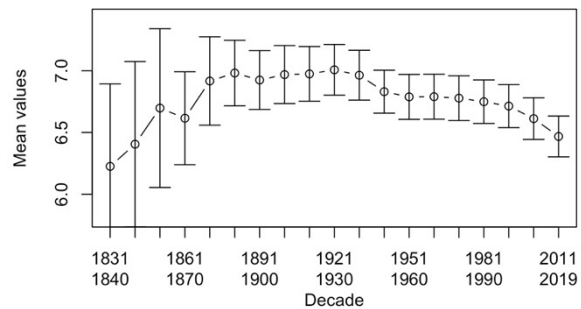
Seed.dormancy



Soil.disturbance

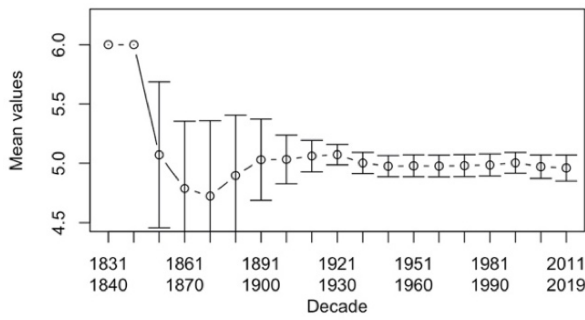


Temp..optimum

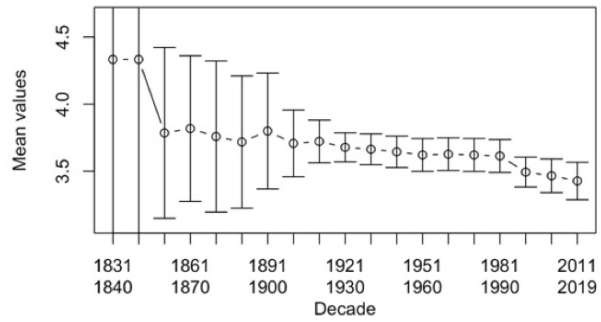


Svalöv:

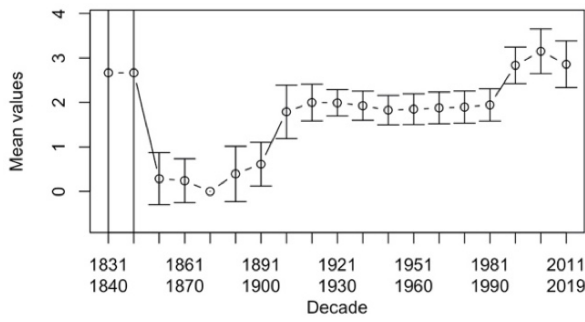
Continentality



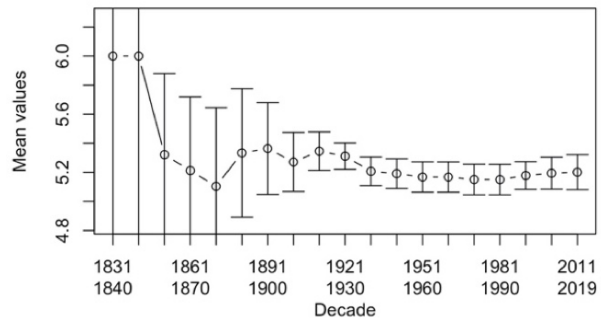
Grazing.mowing



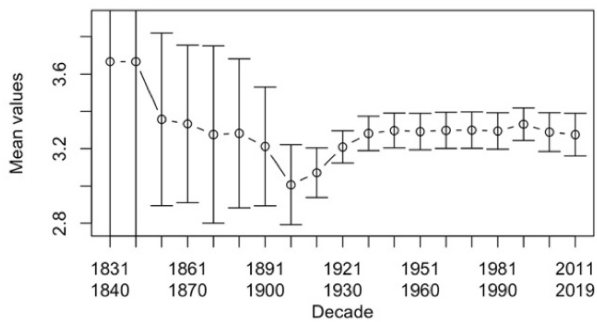
Index.of.invasive.concern



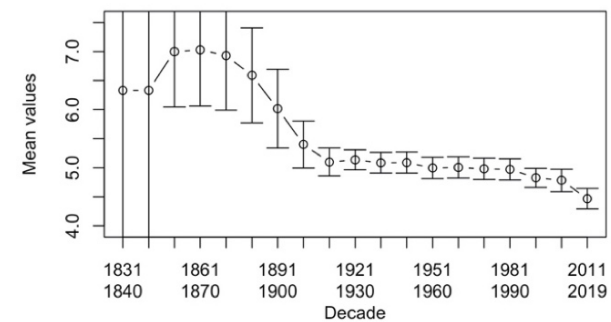
Light



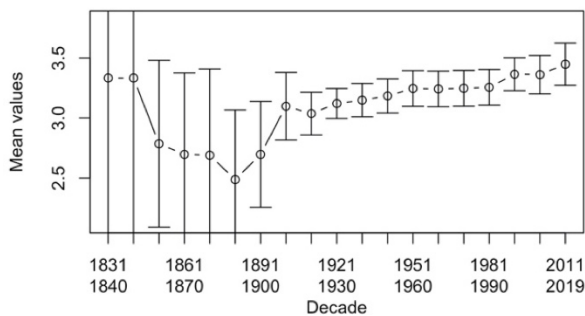
Longevity



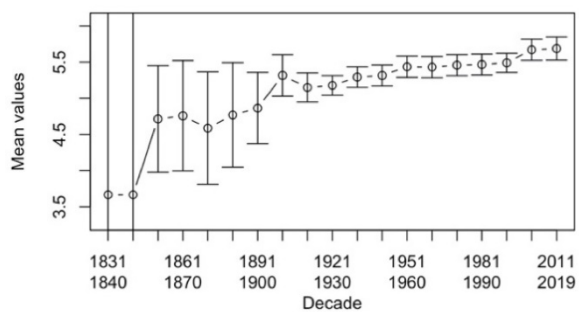
Moisture



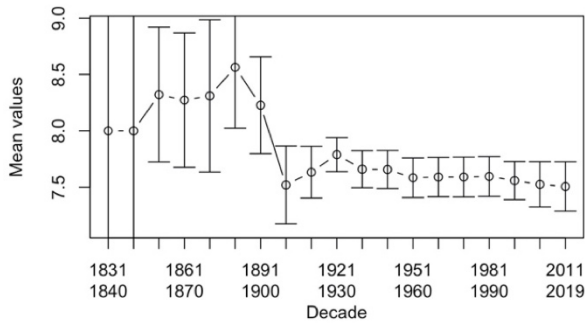
Nectar.production



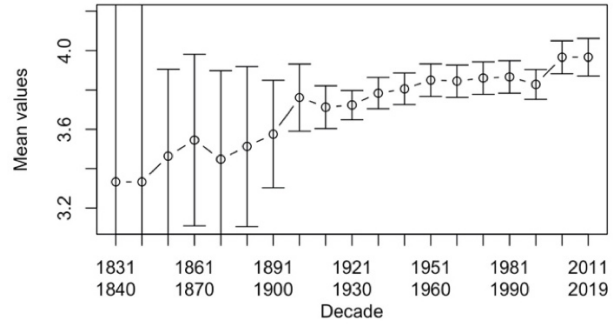
Nitrogen..N.



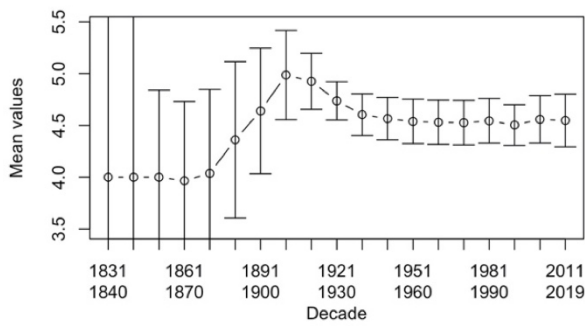
Phenology



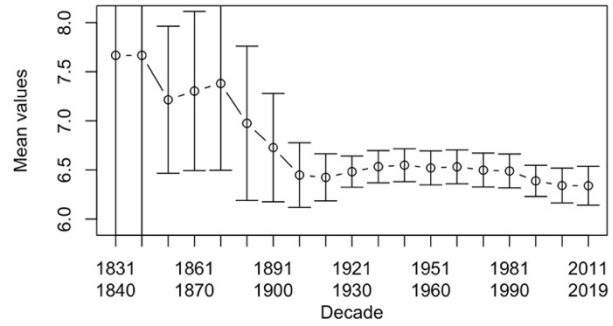
Phosphorus..P.



Soil.disturbance

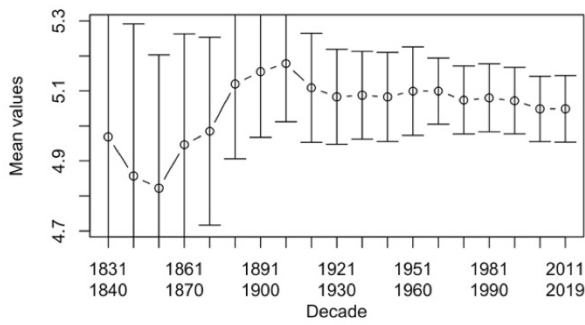


Temp..optimum

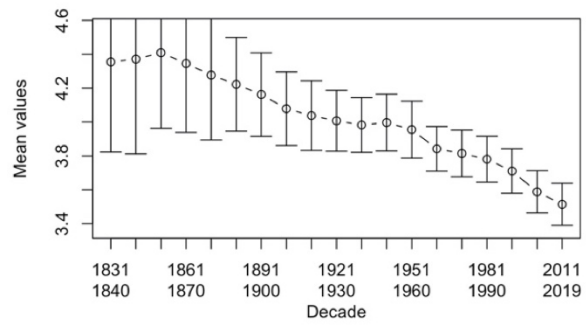


Vellinge:

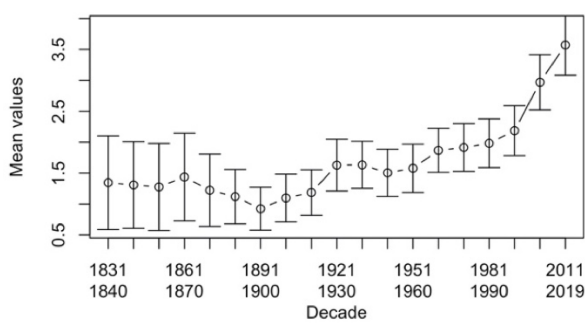
Continentality



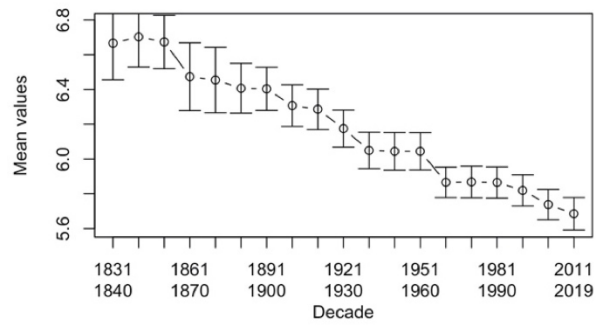
Grazing.mowing



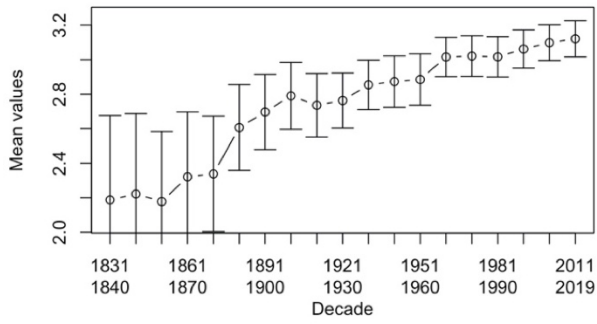
Index.of.invasive.concern



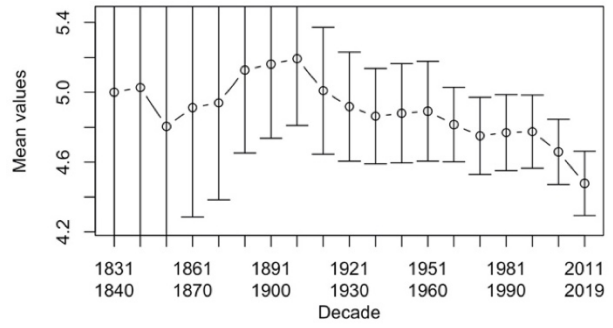
Light



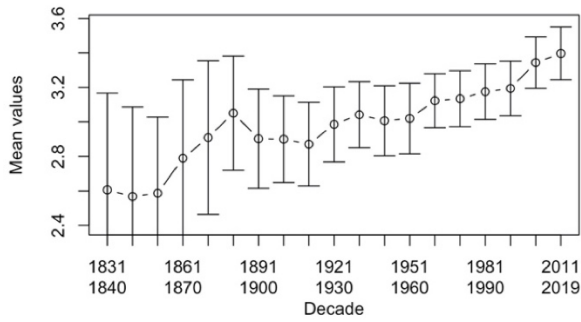
Longevity



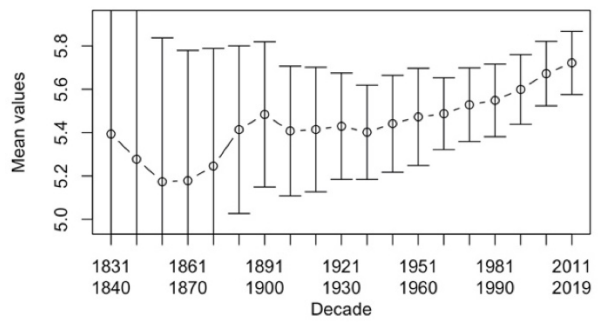
Moisture



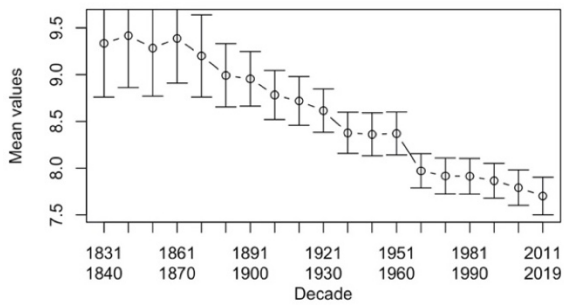
Nectar.production



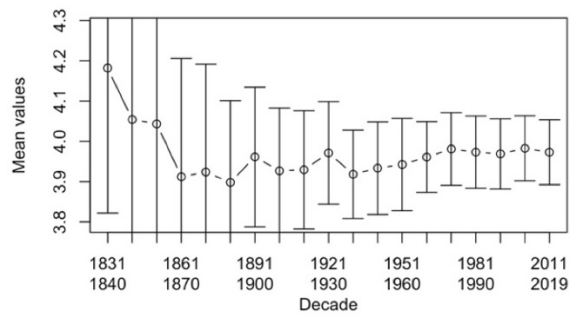
Nitrogen..N.



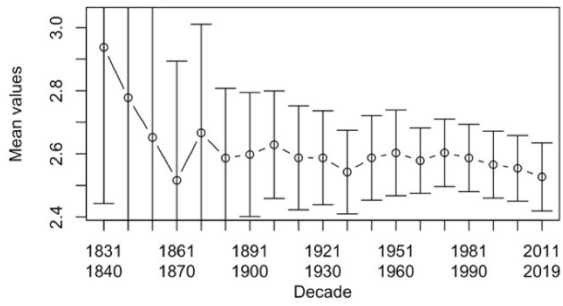
Phenology



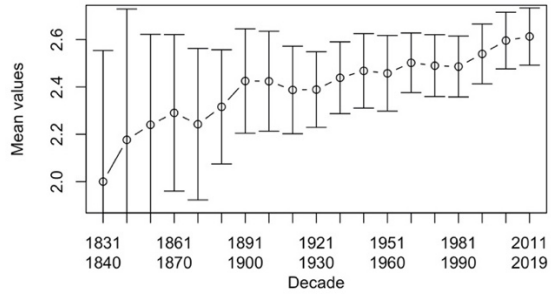
Phosphorus..P.



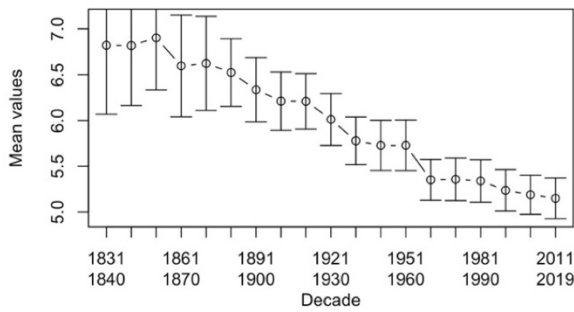
Seed.bank



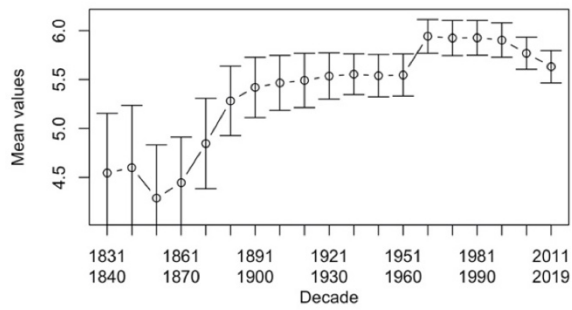
Seed.dormancy



Soil.disturbance

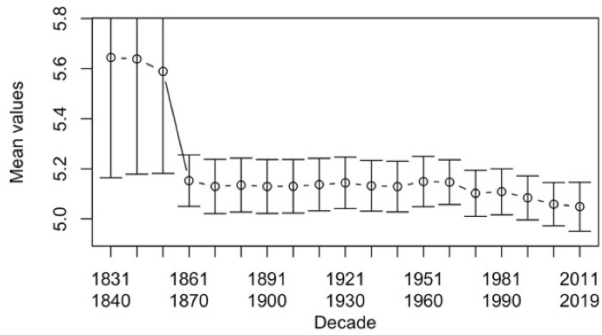


Temp..optimum

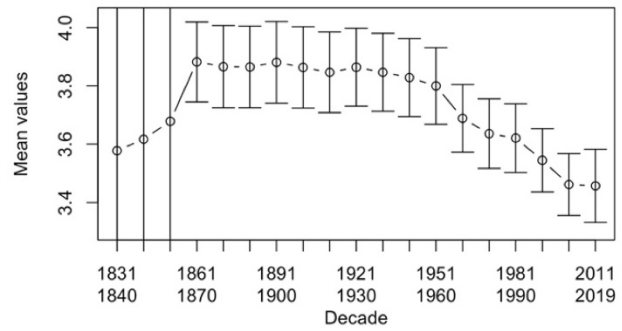


Vittskövle:

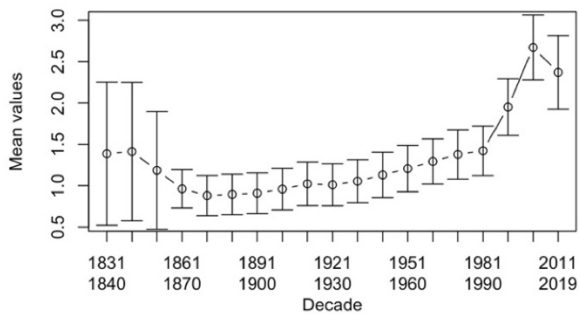
Continentality



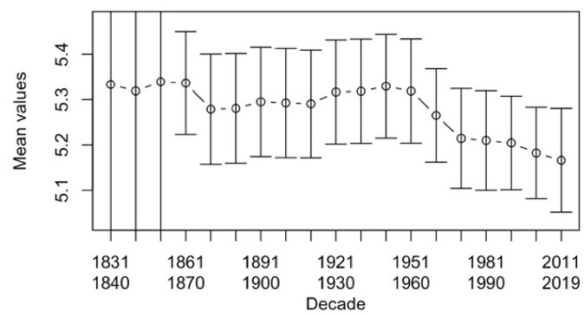
Grazing.mowing



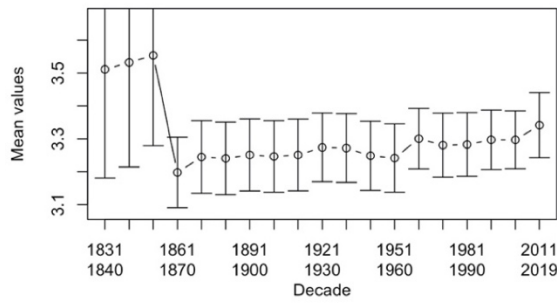
Index.of.invasive.concern



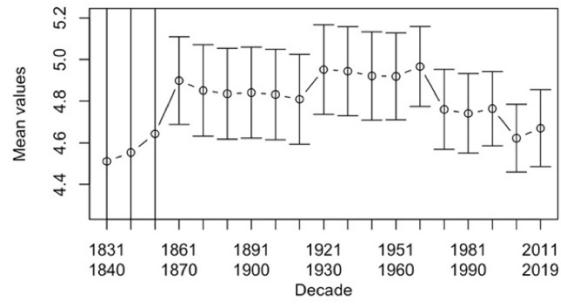
Light



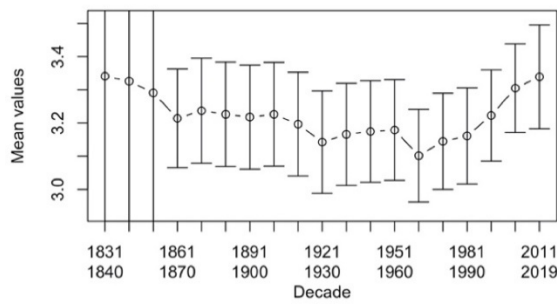
Longevity



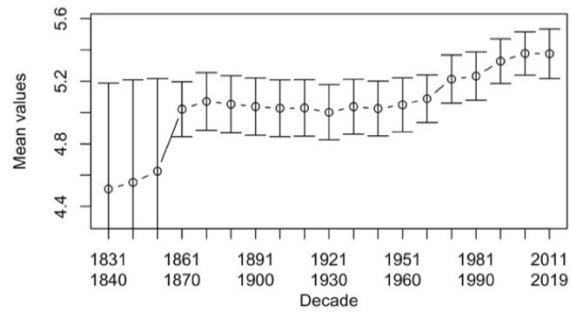
Moisture



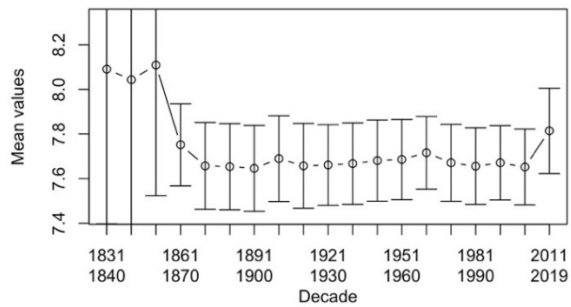
Nectar.production



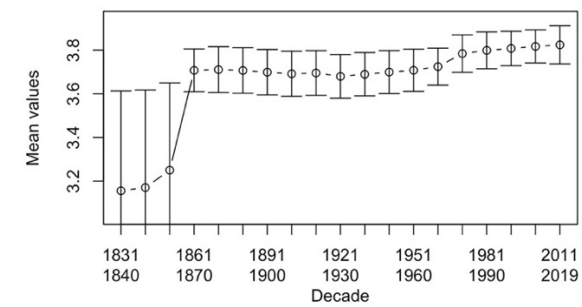
Nitrogen..N.



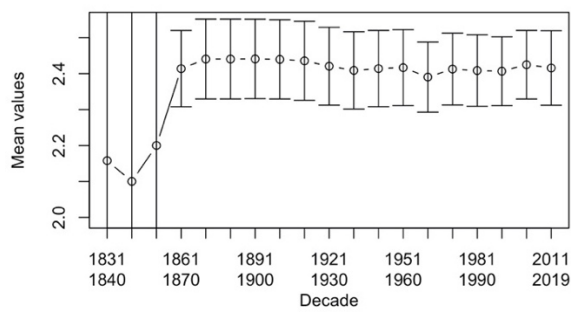
Phenology



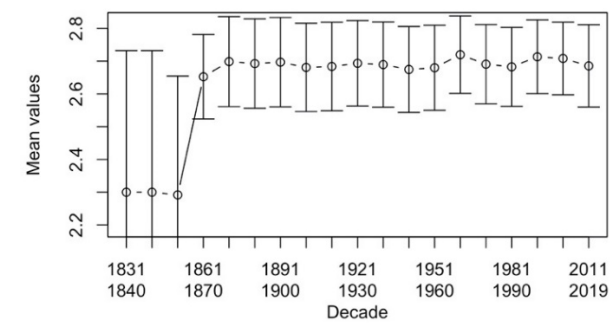
Phosphorus..P.

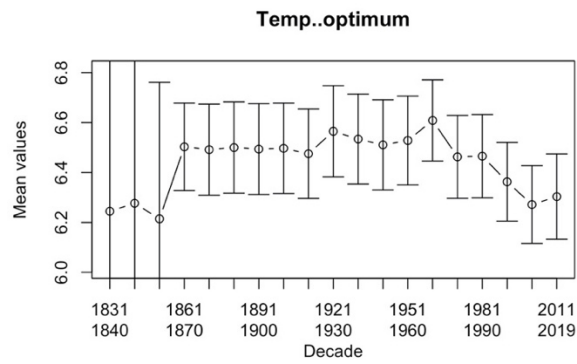
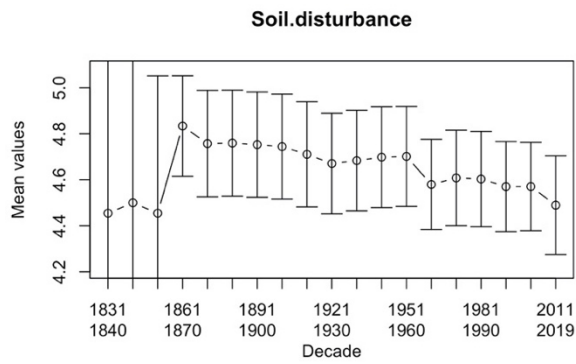


Seed.bank

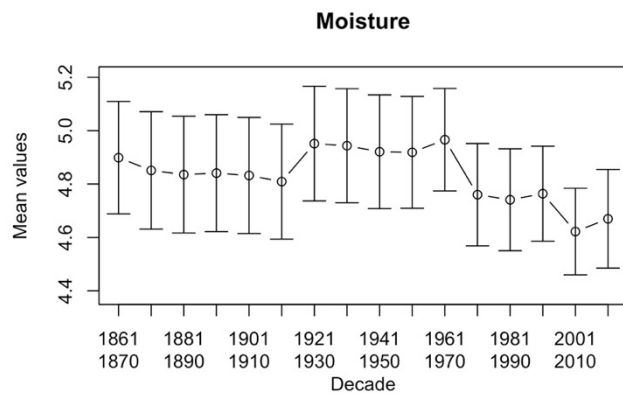
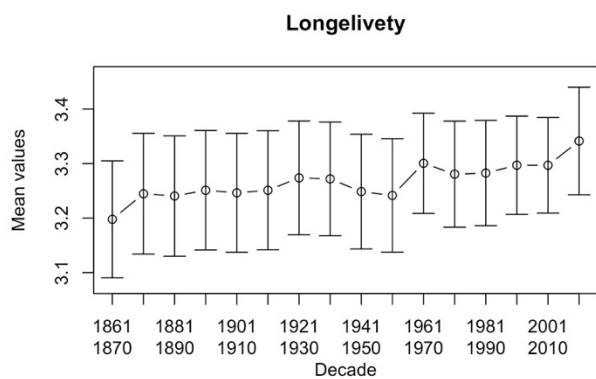
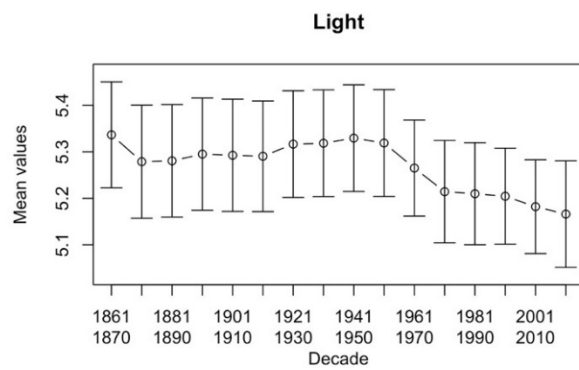
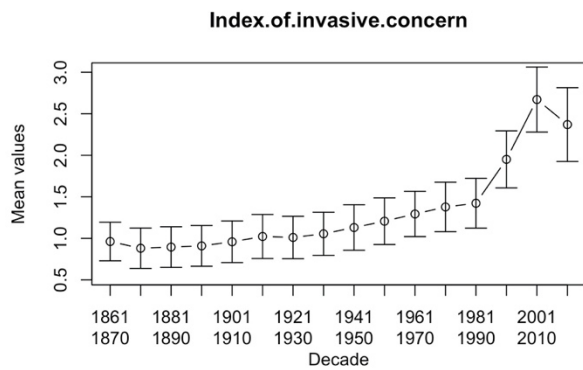
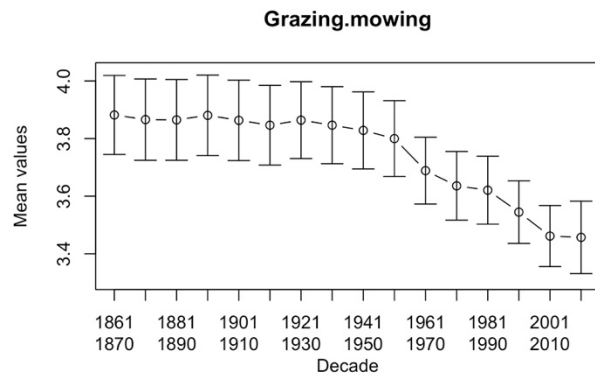
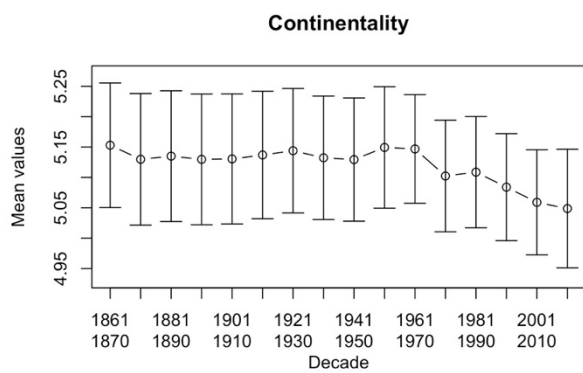


Seed.dormancy

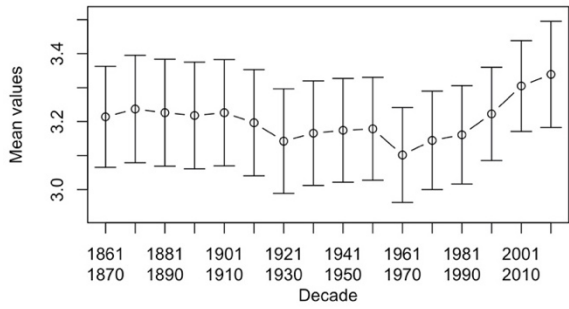




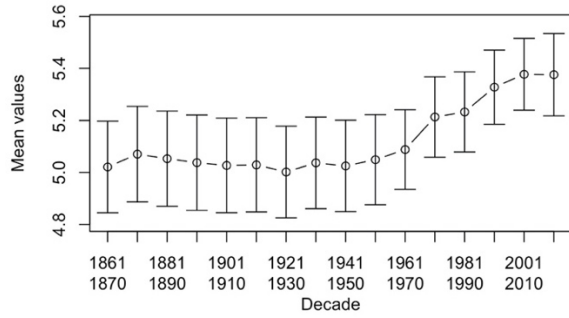
Östra Broby:



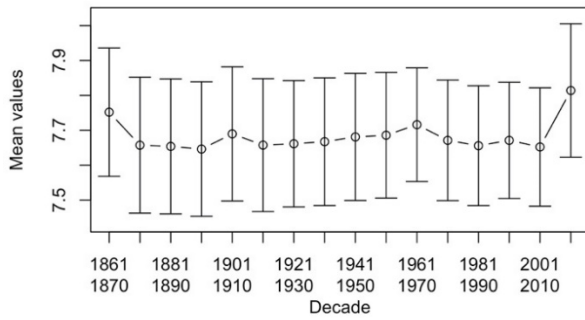
Nectar.production



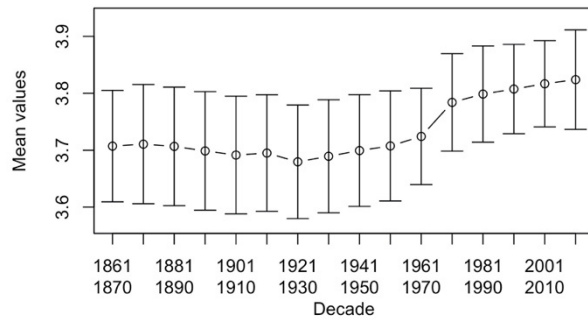
Nitrogen..N.



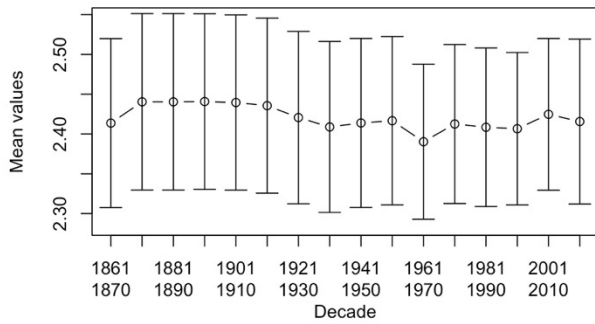
Phenology



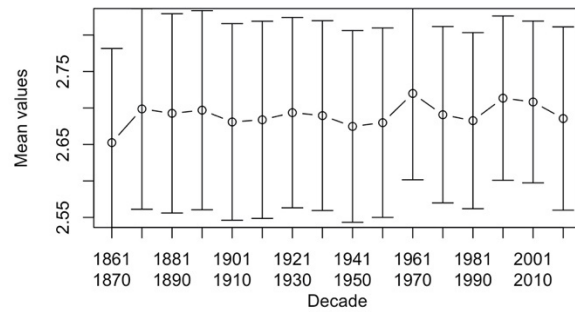
Phosphorus..P.



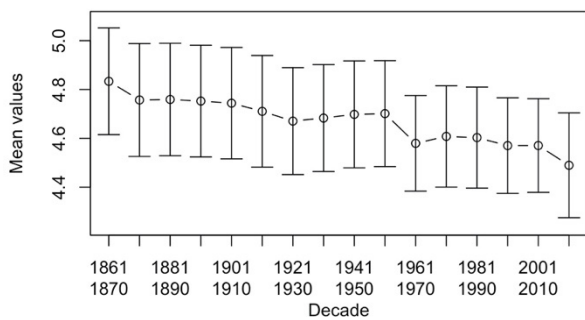
Seed.bank



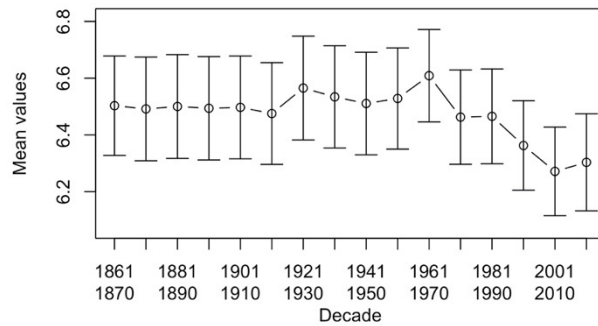
Seed.dormancy



Soil.disturbance

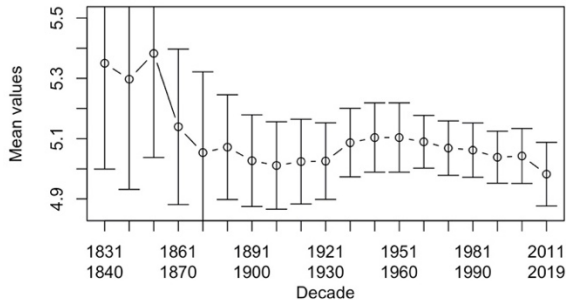


Temp..optimum

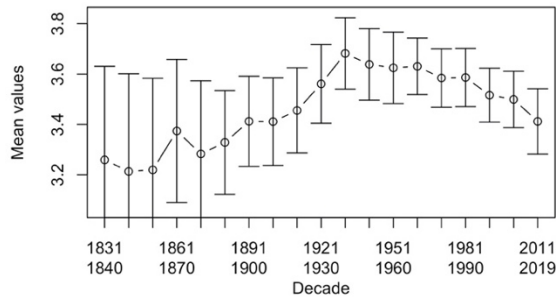


Öved:

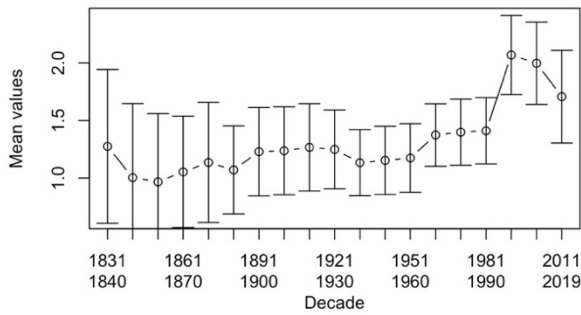
Continentality



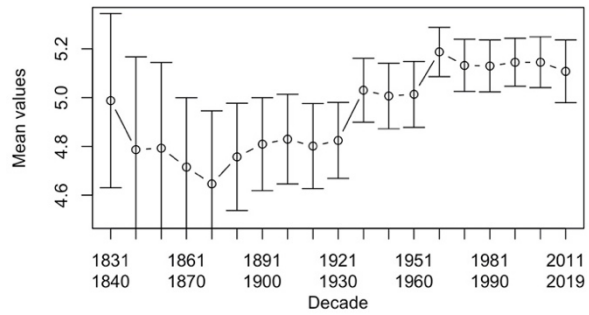
Grazing.mowing



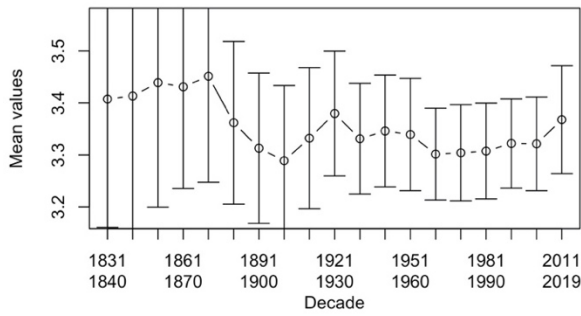
Index.of.invasive.concern



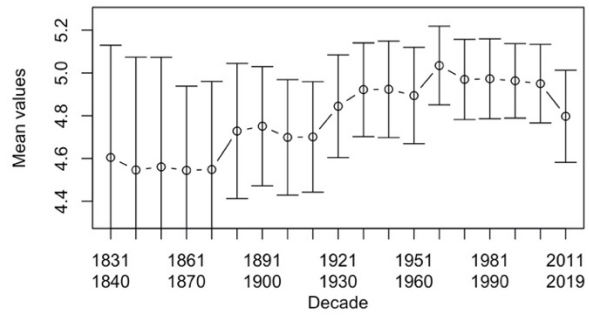
Light



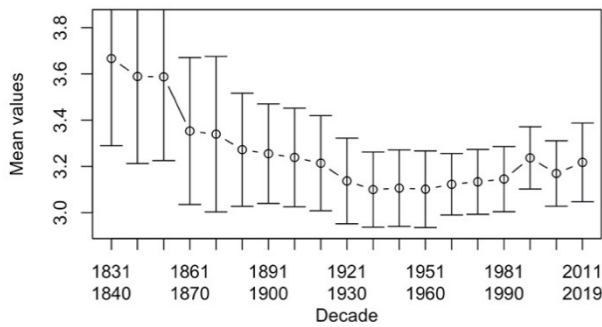
Longevity



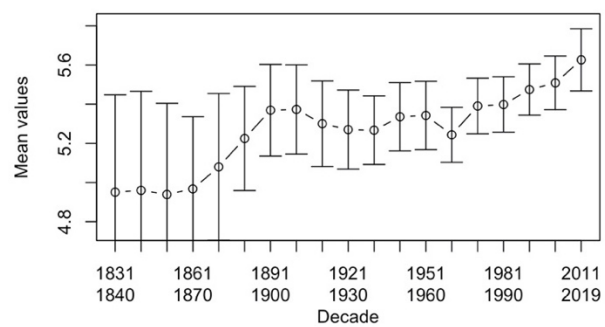
Moisture



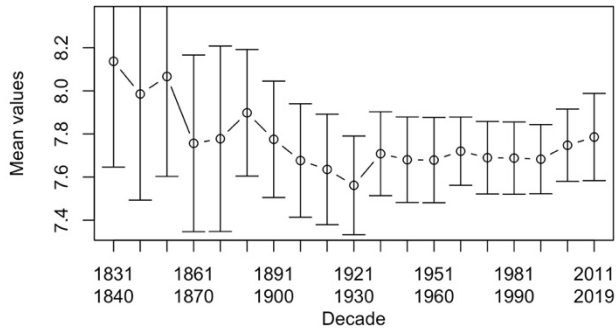
Nectar.production



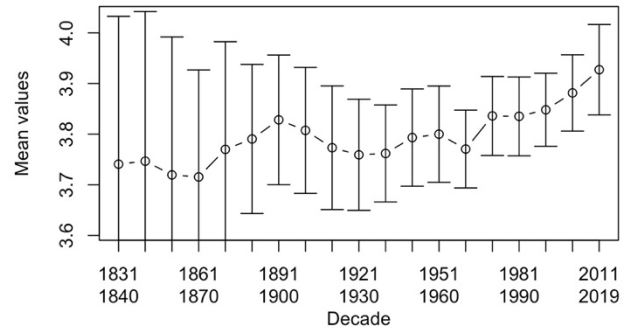
Nitrogen..N.



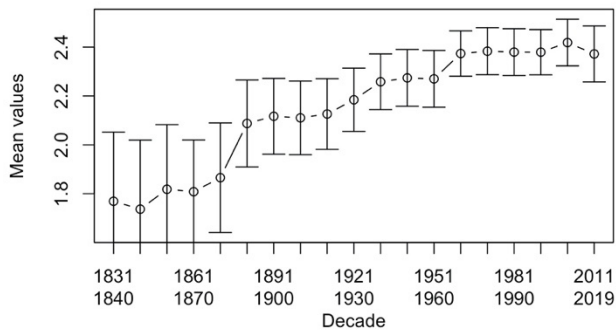
Phenology



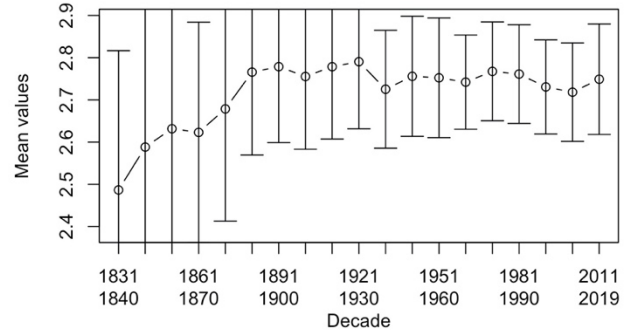
Phosphorus..P.



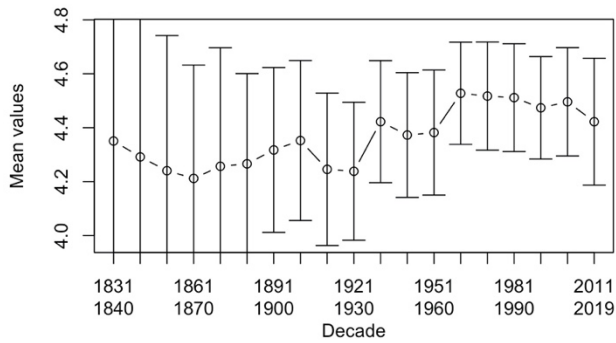
Seed.bank



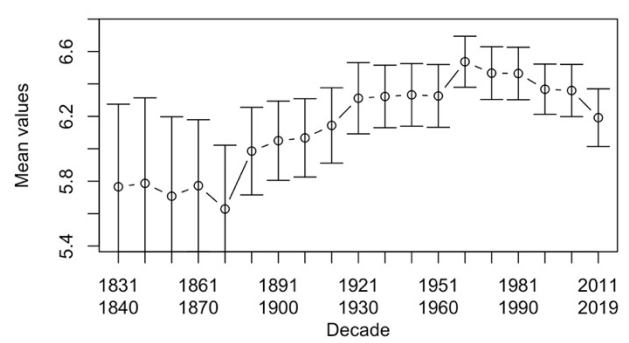
Seed.dormancy



Soil.disturbance

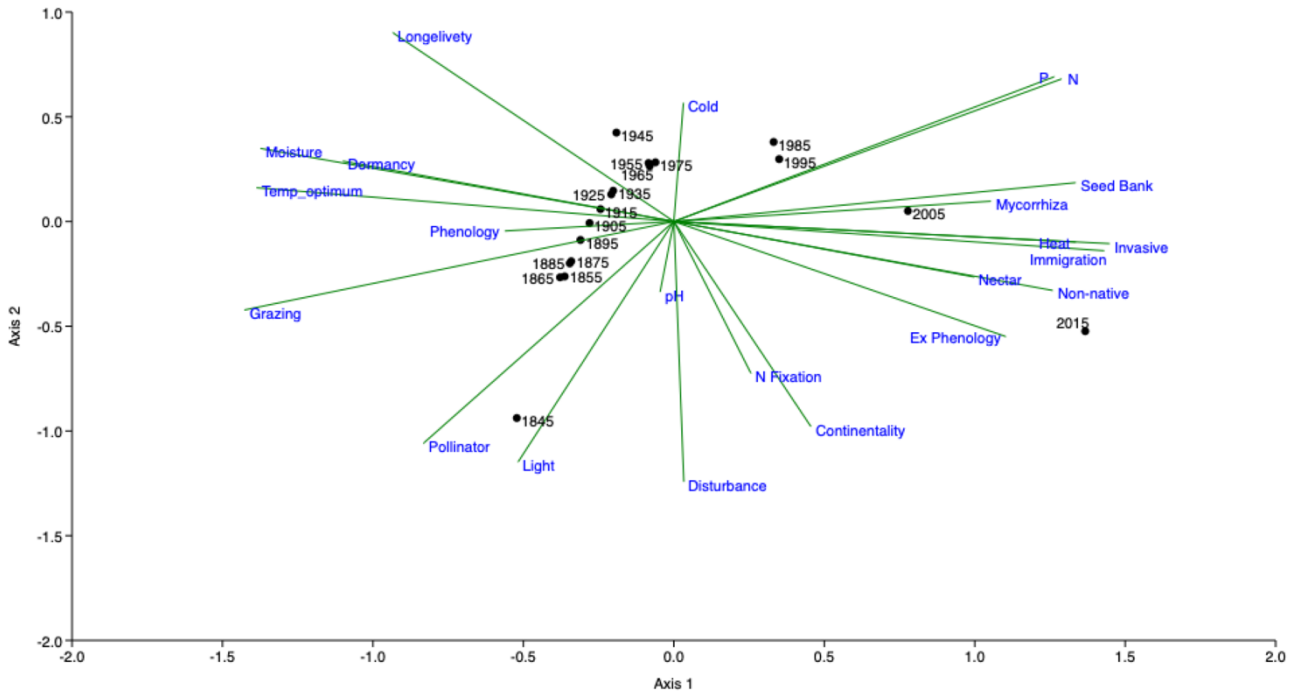


Temp..optimum

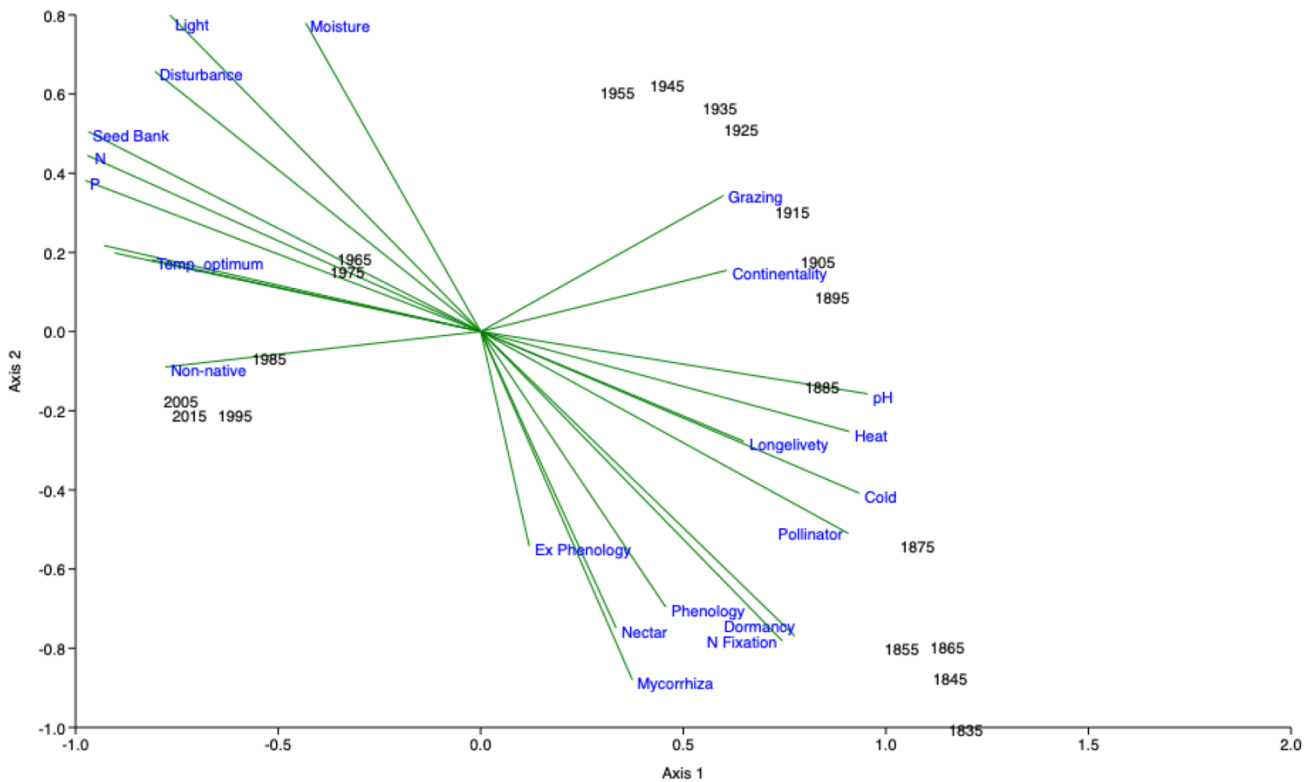


C. Canonical Correspondence Analyses

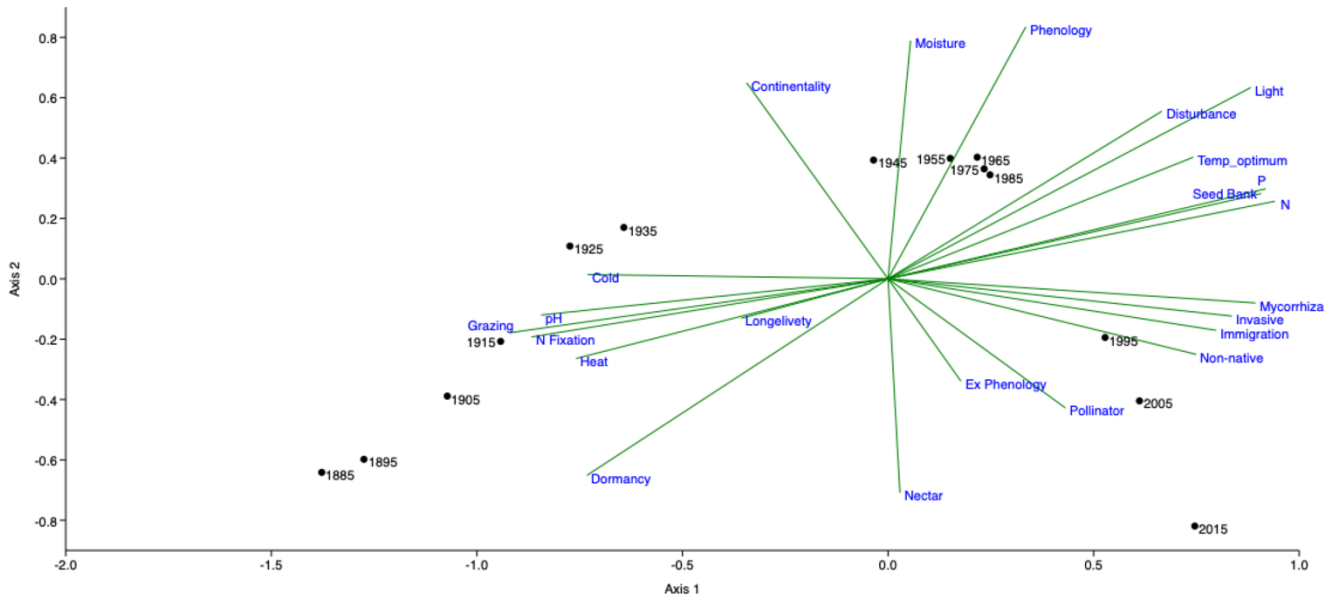
Billinge:



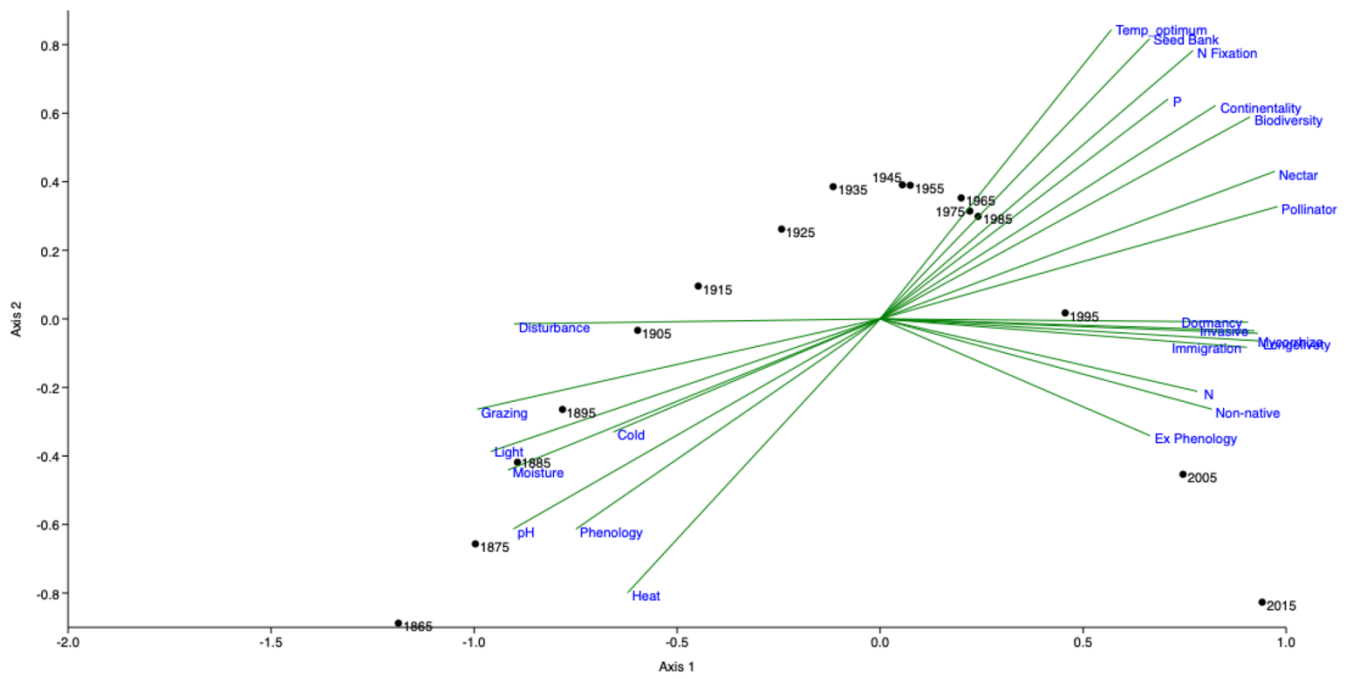
Hardeberga:



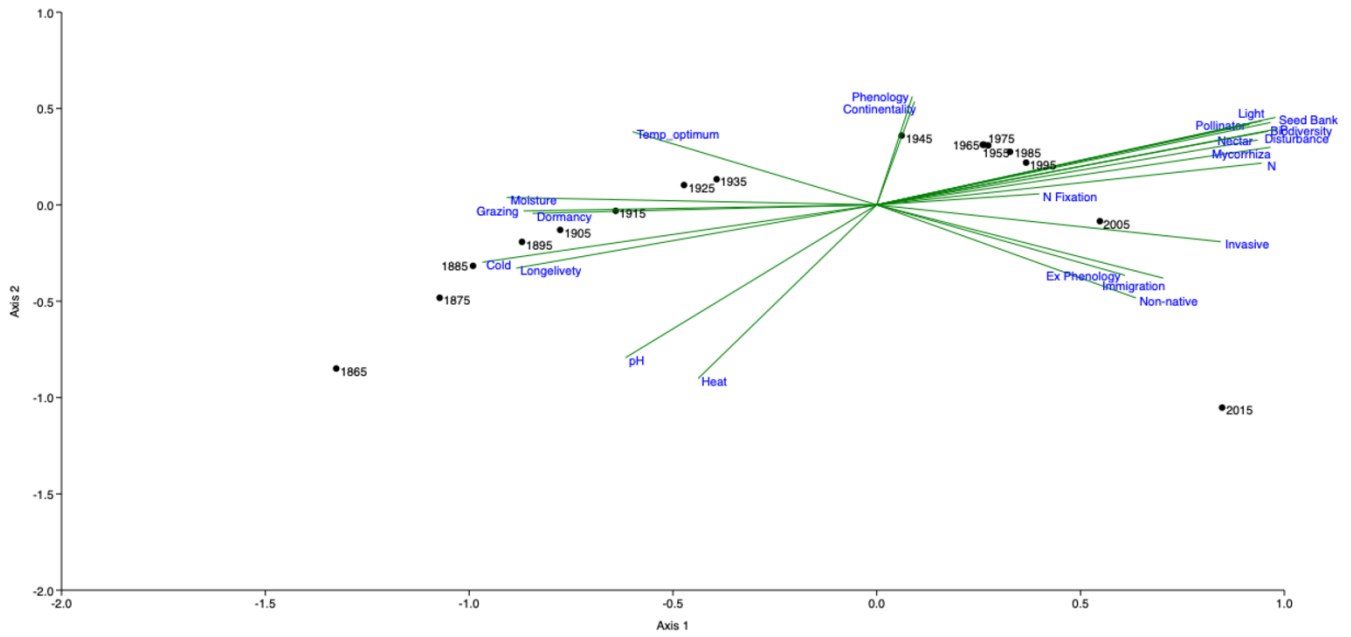
Kävlinge / Lackalänga:



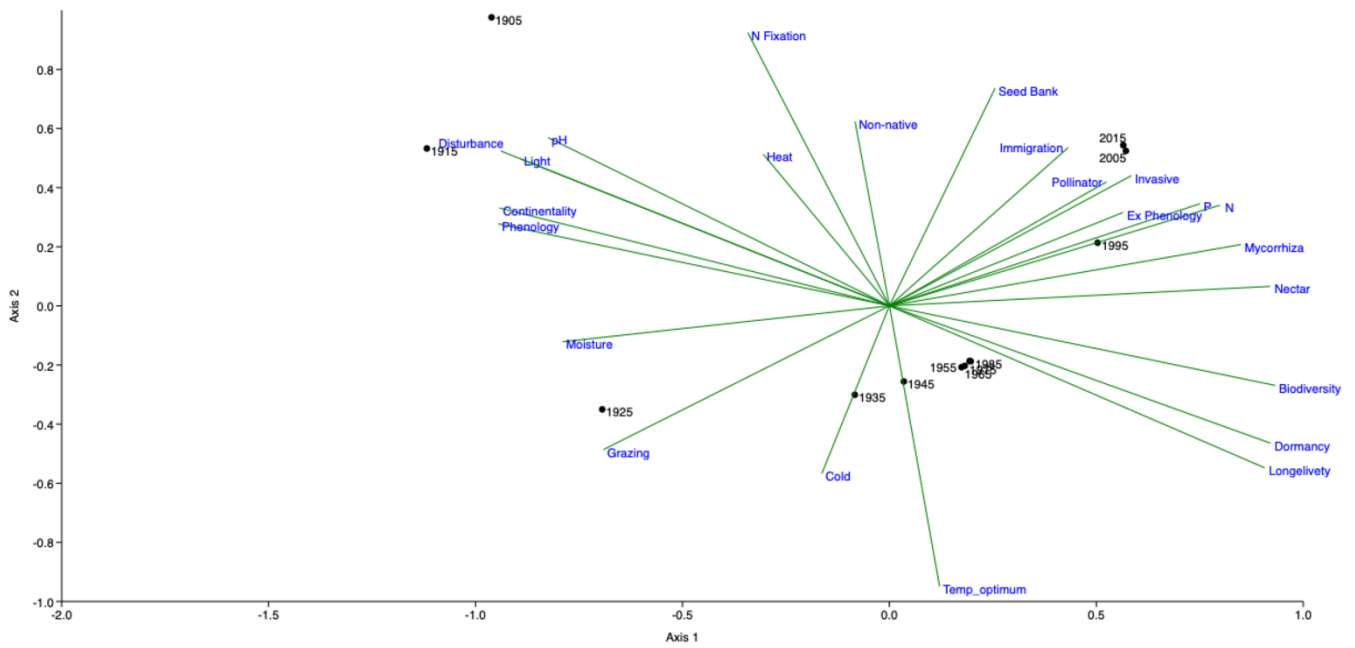
Lomma:



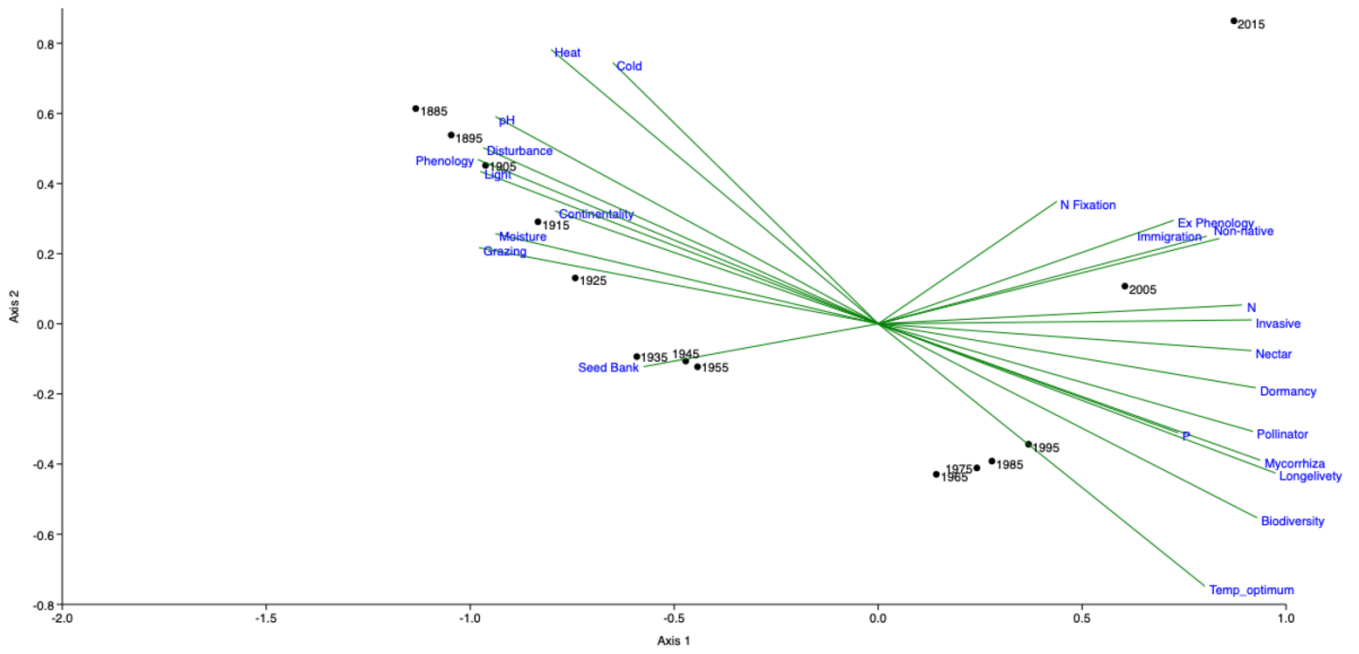
Stehag:



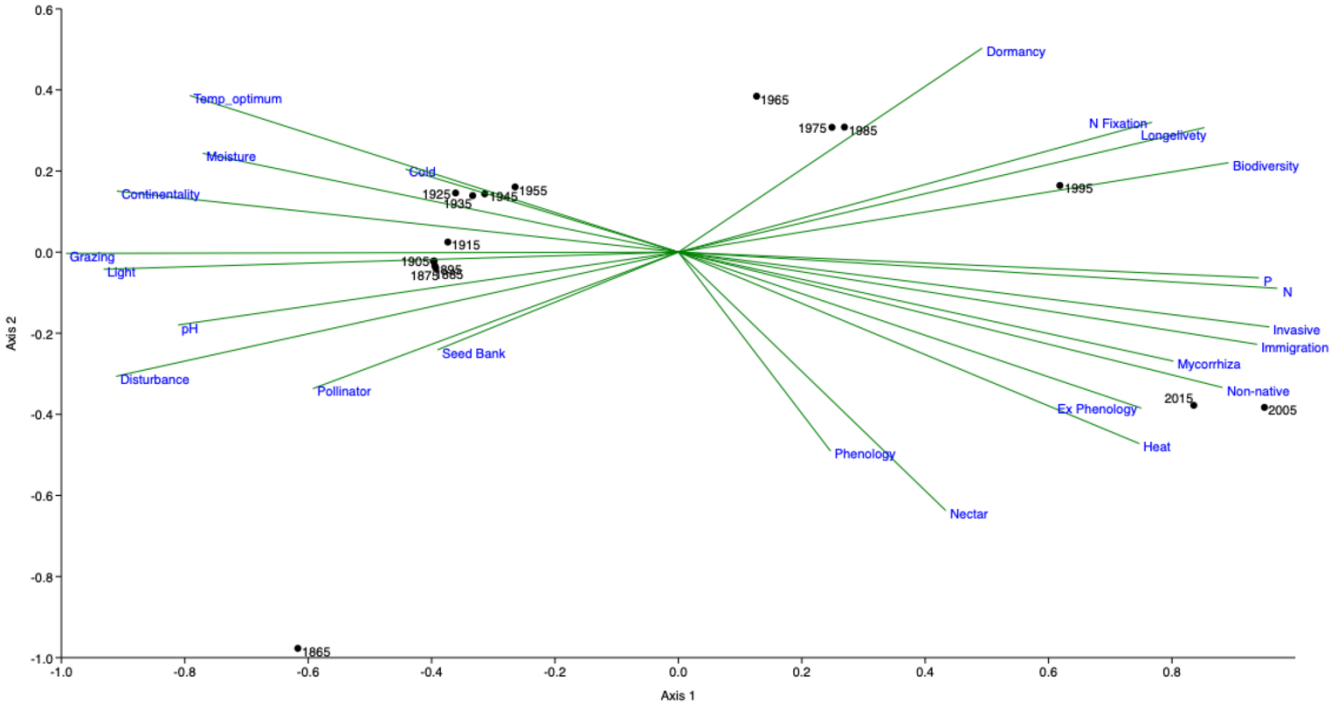
Svalöv:



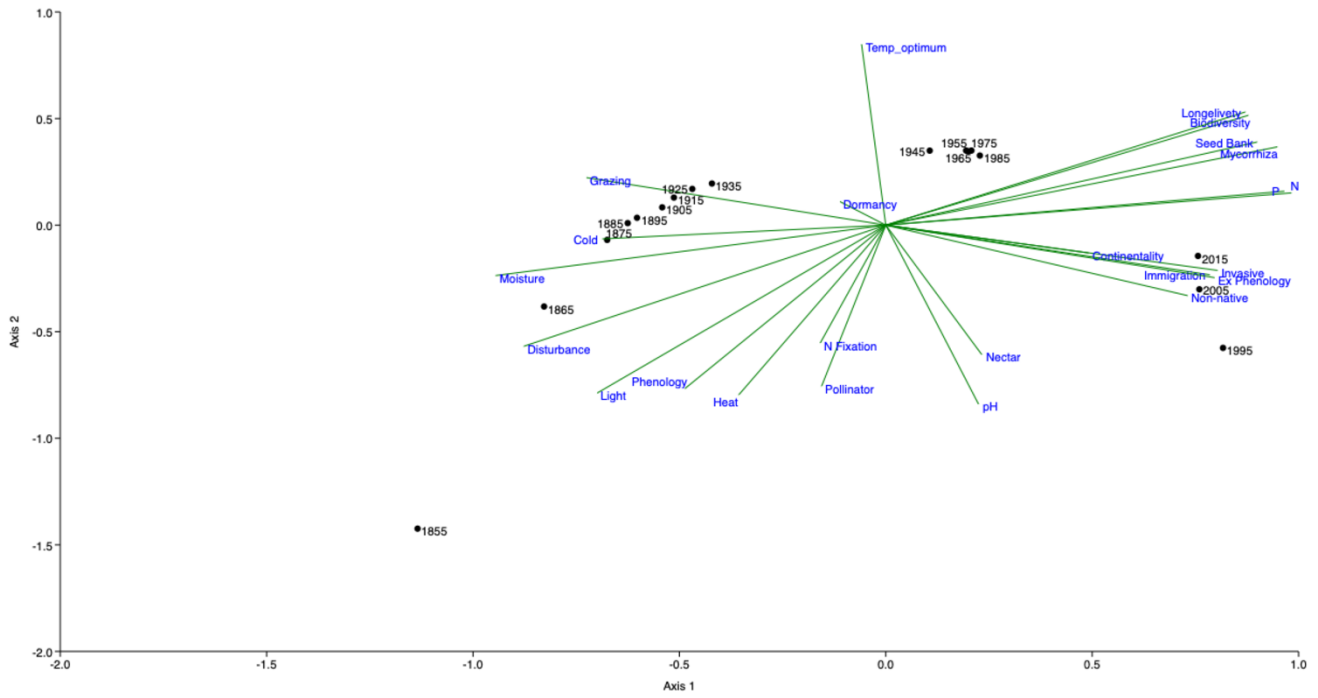
Vellinge:



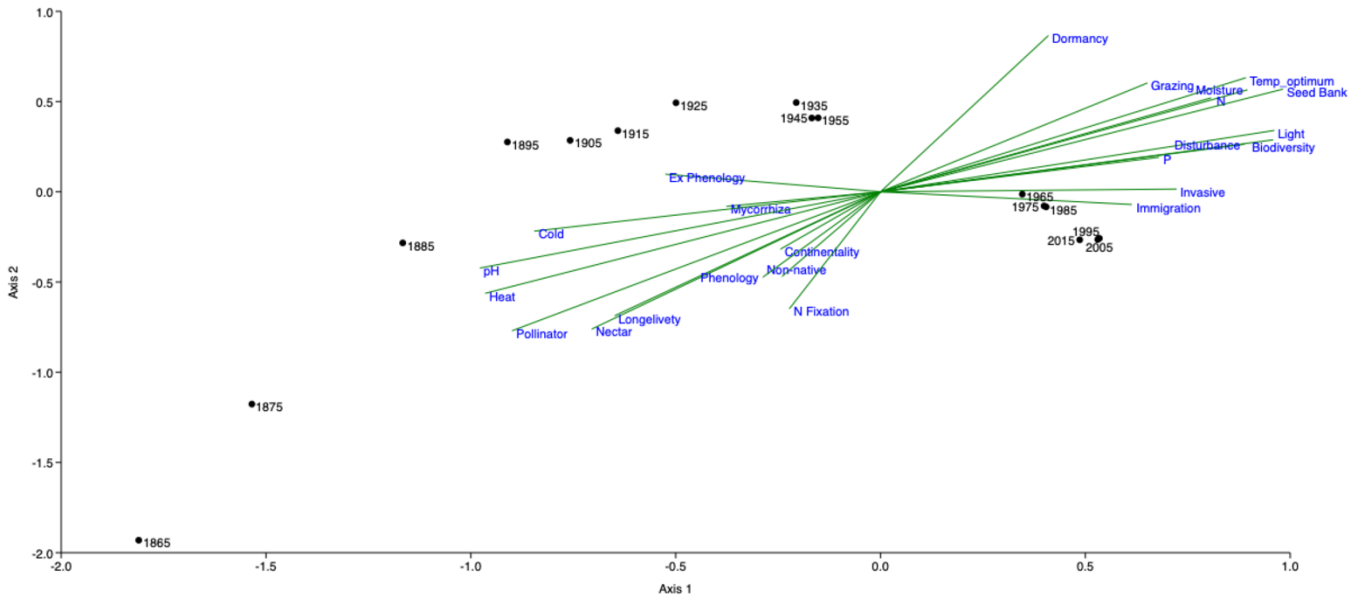
Vittskövle:



Östra Broby:

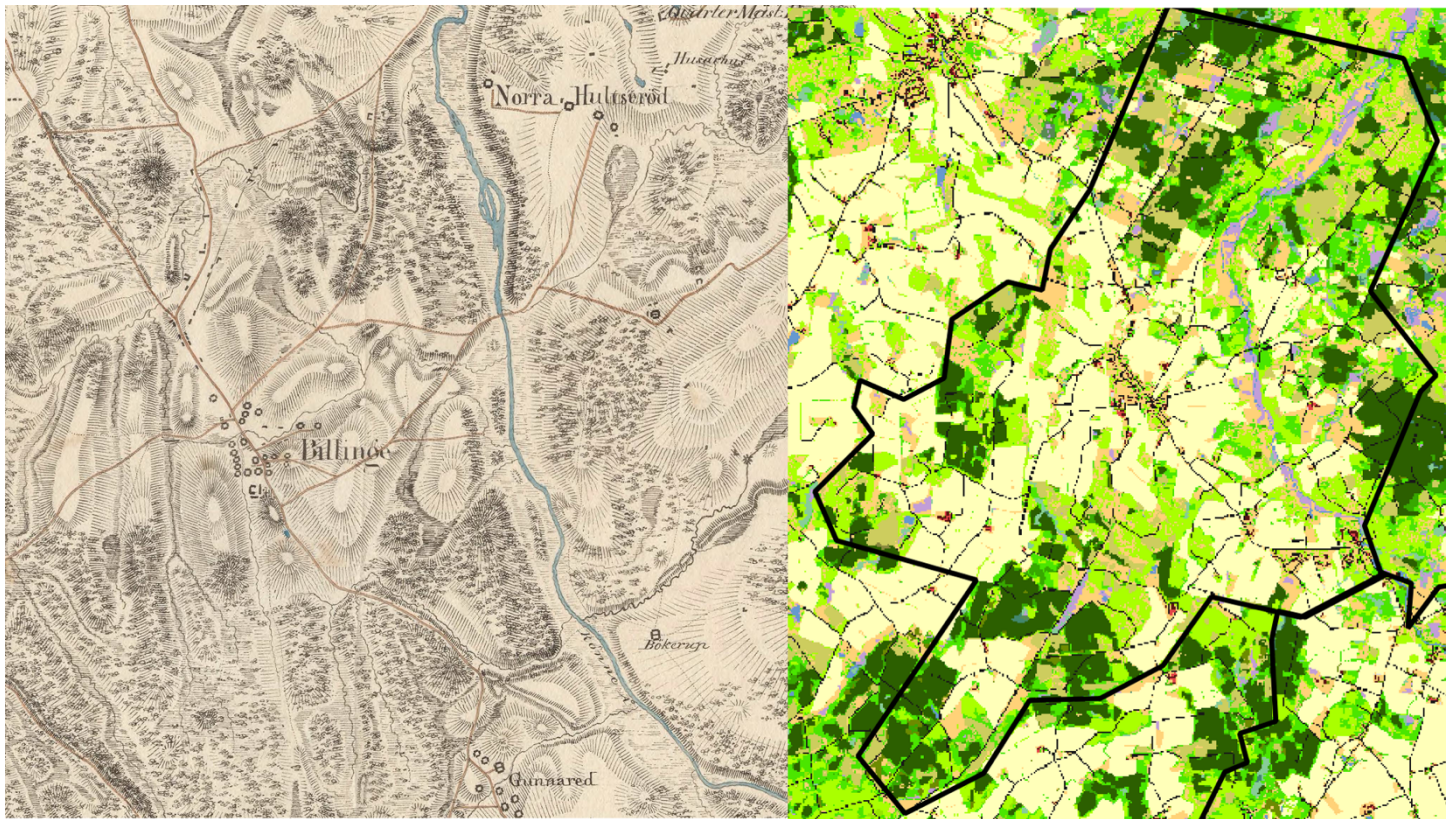


Öved:

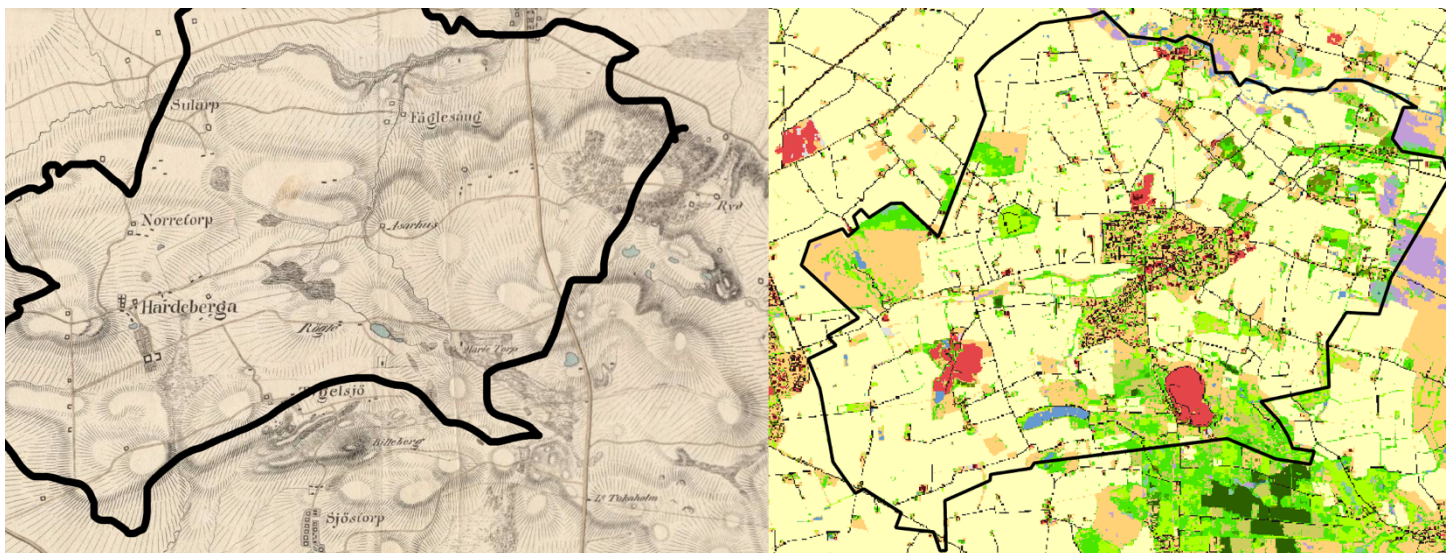


D. Map comparisons

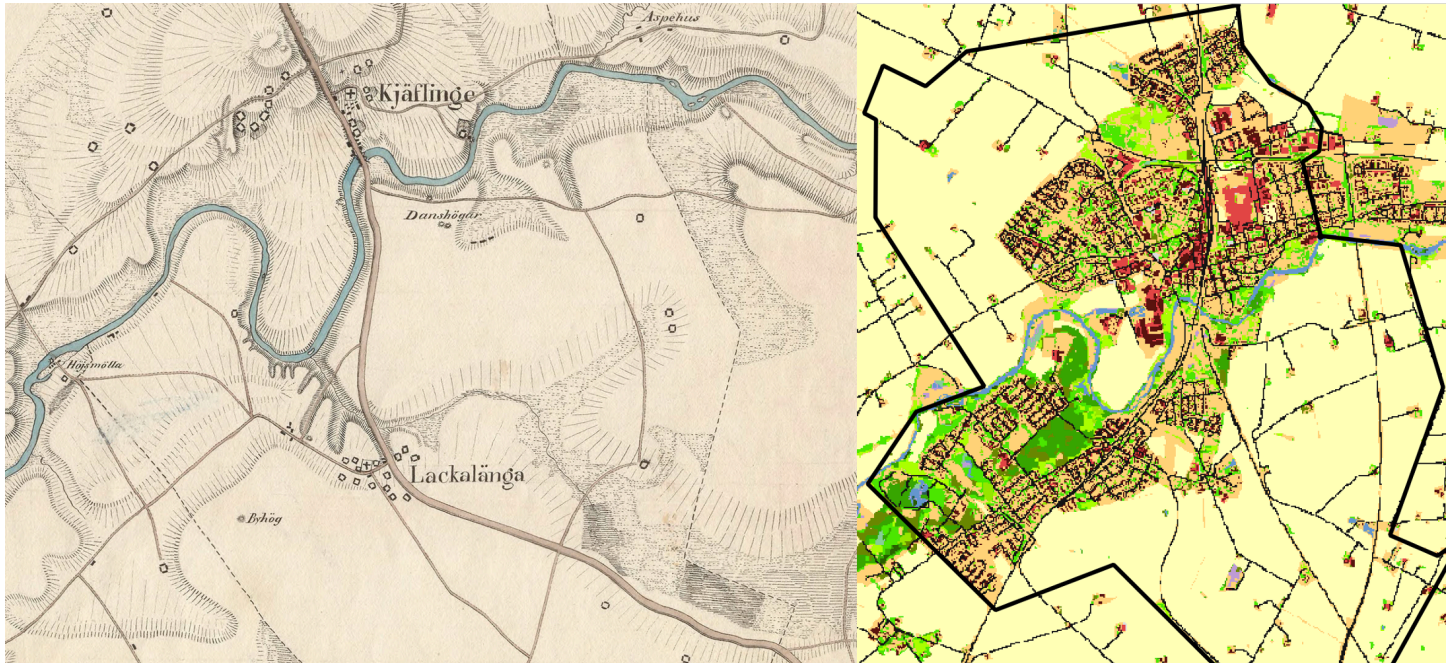
Billinge:



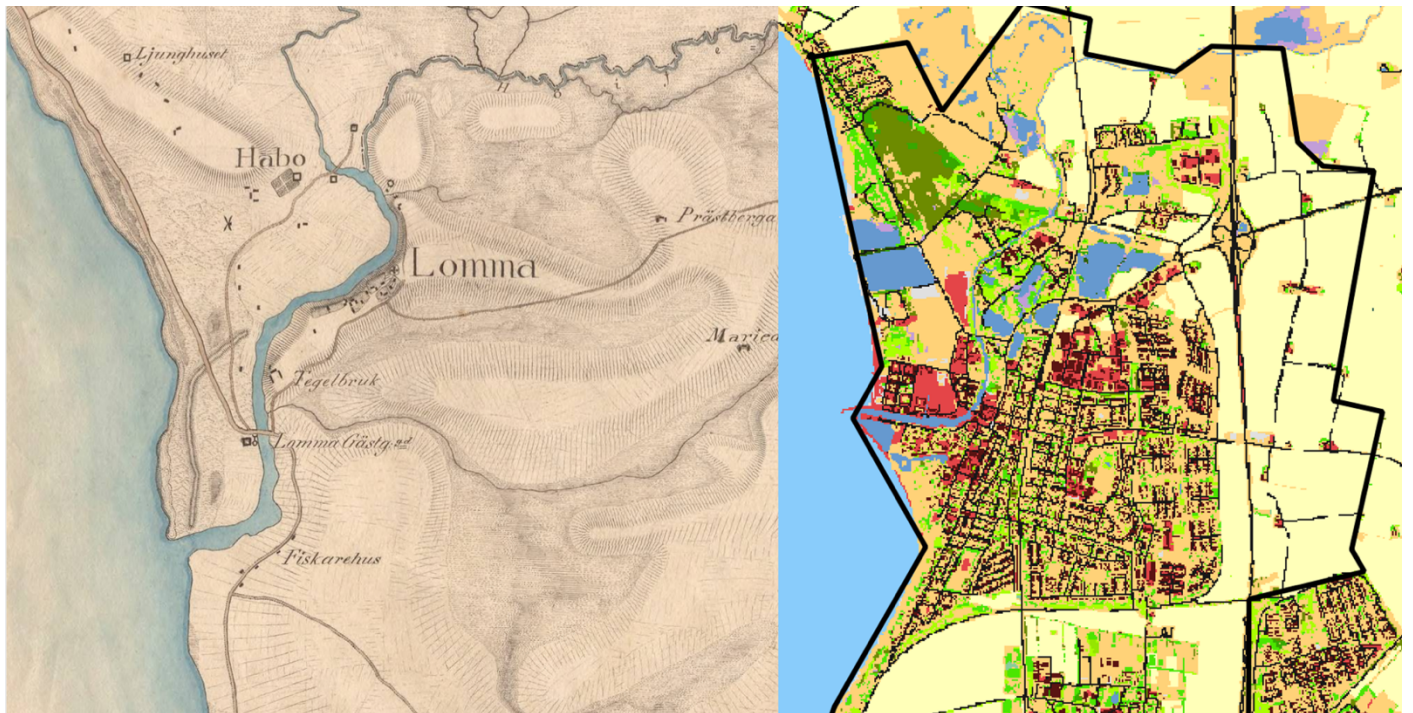
Hardeberga / Södra Sandby:



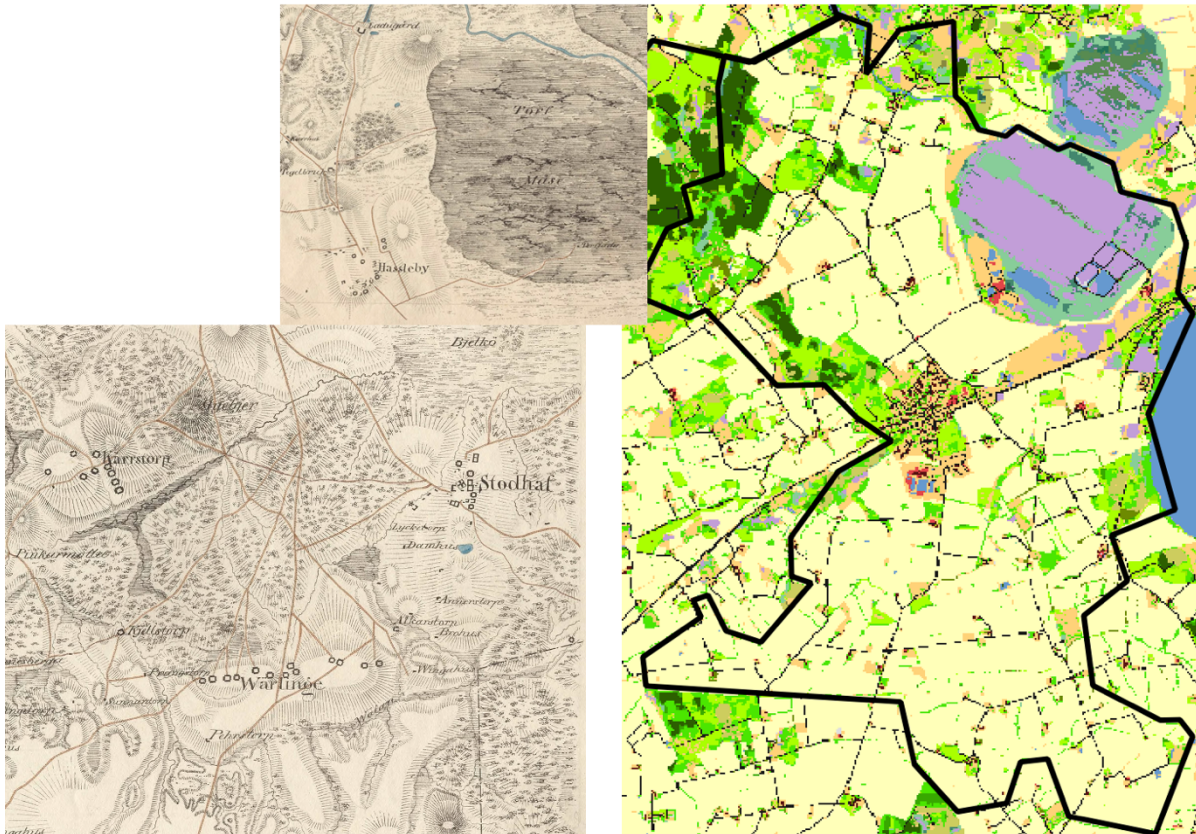
Kävlinge / Lackalänga:



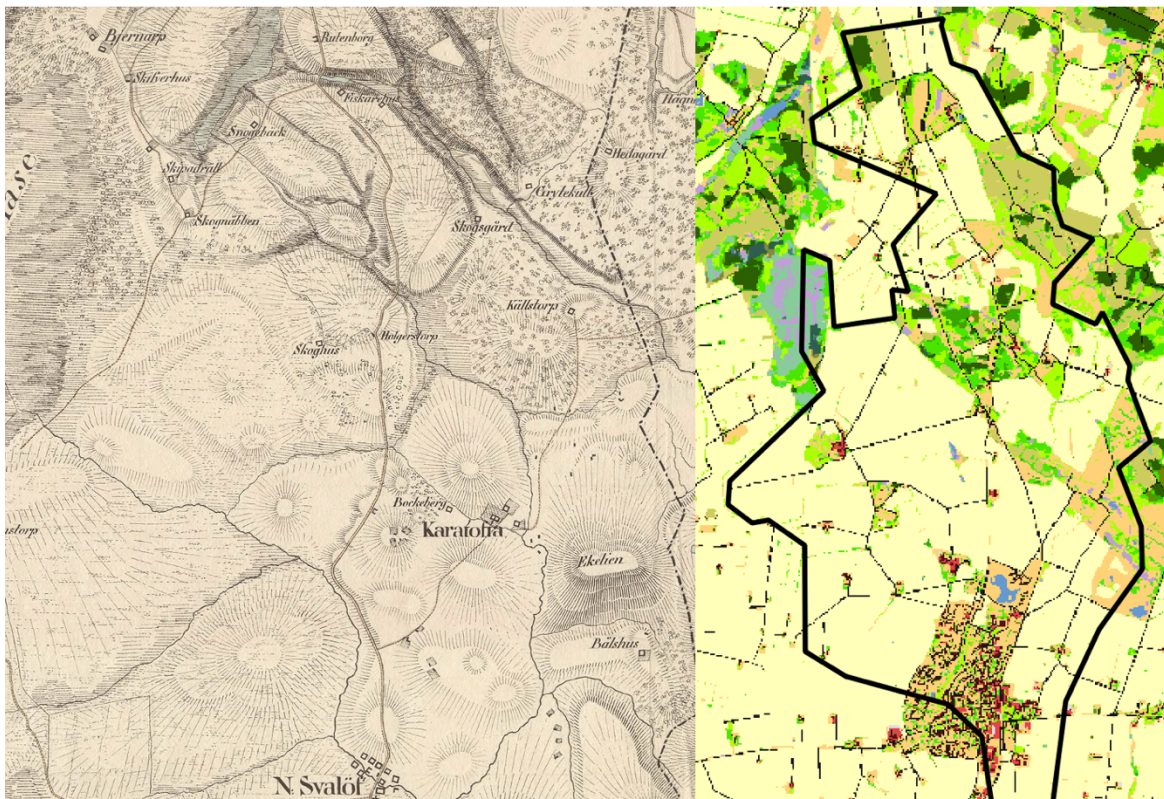
Lomma:



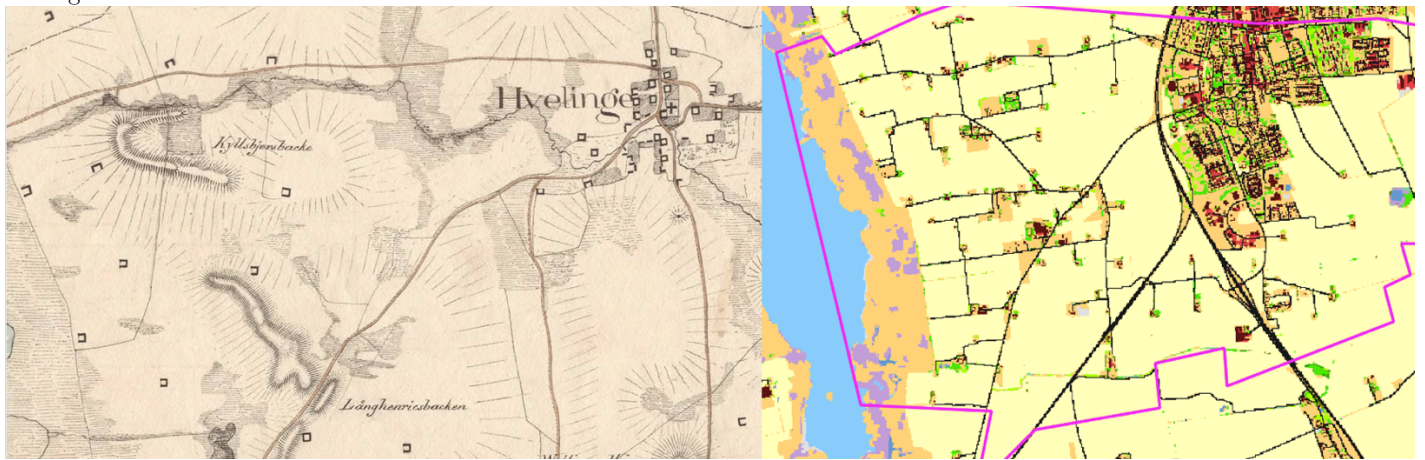
Stehag:



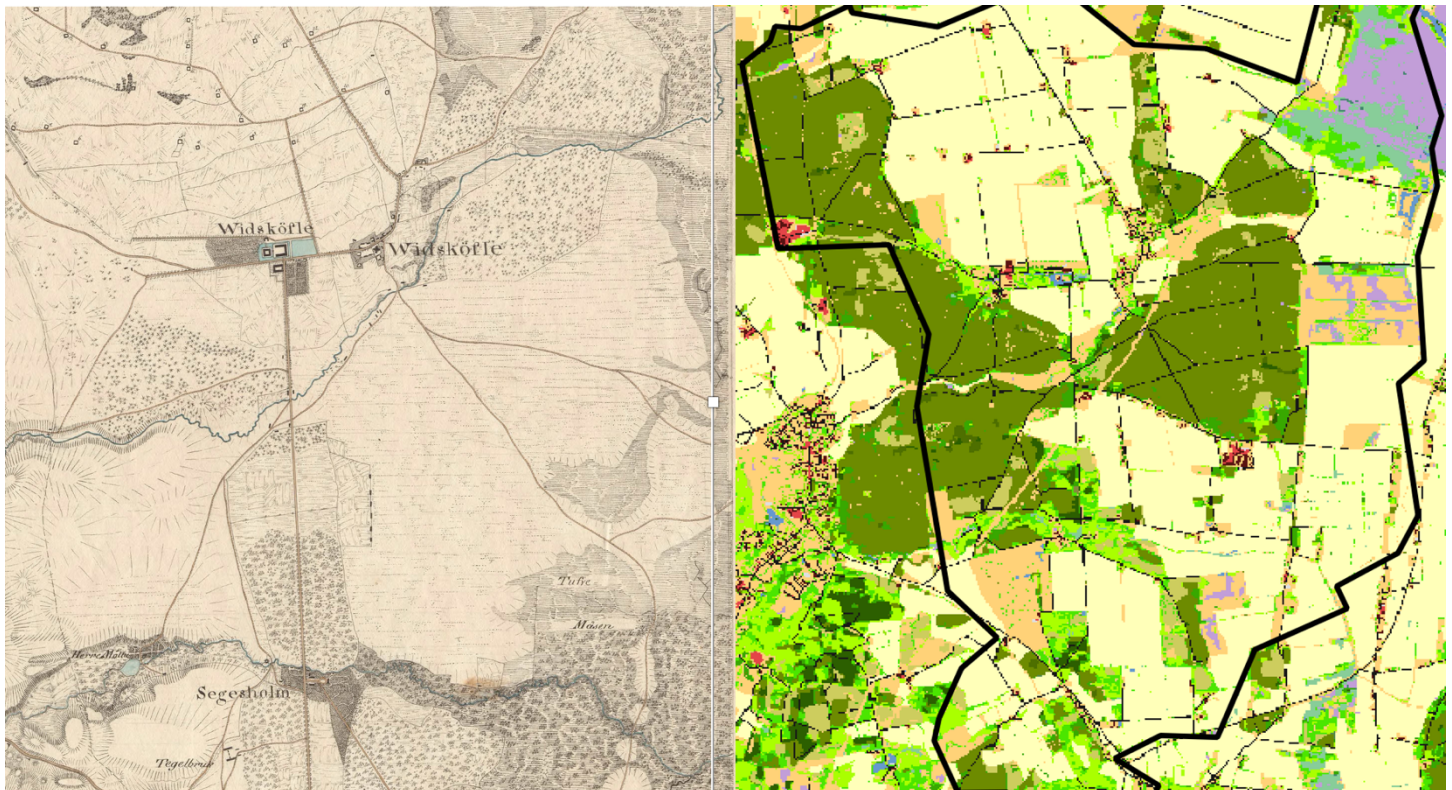
Svalöv:



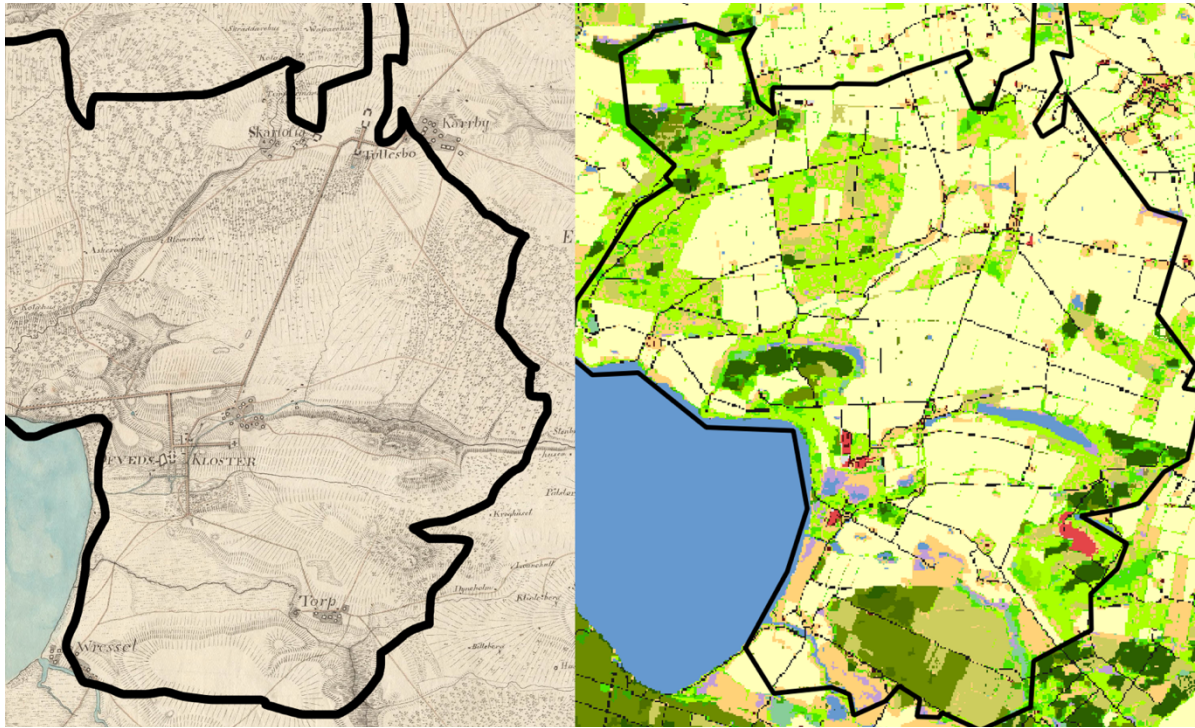
Vellinge:



Vittskövle:



Öved:



(Note: Östra Broby map not made during this time period)