



Using centennial changes in plant, butterfly and bird diversity to inform restoration targets

Ane Kirstine Brunbjerg¹ · Kevin Kuhlmann Clausen¹ · Emil Blicher Bjerregård² · Rasmus Ejrnæs¹ · Camilla Fløjgaard¹ · Hans Henrik Bruun²

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Abstract

Historical records reveal significant biodiversity loss, but over such long timespans that human minds gradually adjust to depauperated biotas. We used 19th and early 20th -century Danish records (100–180 years old) to address this blind spot and enhance our understanding of flora and fauna changes beyond mere richness gains or losses. By analyzing species' traits, habitat affinities, and environmental indicators, we identified lost habitat types. Compared to the present, 19th-century Danish landscapes were more heterogeneous, featuring open, wooded pastures, now largely replaced by dense plantation forests. Historical data demonstrated that dark diversity is easily underestimated when based on contemporary data. Historical butterfly faunas were much more species-rich and had a stronger affinity for grazed ecosystems than current communities. Declining plant species of conservation interest were more light- and moisture-demanding and less nutrient-affiliated and competitive than persisting species. Declining butterfly species were linked to host plants with restricted national distribution. Declining bird species were typically carnivorous, migratory, and associated with open habitats, particularly grasslands, coastal areas, and freshwater wetlands. Our findings may guide the ambition level and direction of restoration efforts. The results suggest a restoration focus on open, heterogeneous woodland, grassland and wetland ecosystems with low nutrient status and natural disturbance regimes, including populations of large herbivores near carrying capacity. This contrasts sharply with today's timber-focused plantation forests and conservation area management governed by agricultural subsidies.

Keywords Biodiversity loss · Ecological restoration · Biotic homogenization · Land-use change

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✉ Ane Kirstine Brunbjerg
akb@ecos.au.dk

¹ Department of Ecoscience, Aarhus University, C.F. Møllers Allé 4-8, 8000 Aarhus, Denmark

² Department of Biology, University of Copenhagen, Universitetsparken 15, Copenhagen, Denmark

Introduction

Human activities dominate Earth's climate systems and biodiversity in the 'Anthropocene' (Crutzen 2002), obliterating the traces of past extinction (Johnson et al. 2017). Some researchers consider the Anthropocene epoch to have commenced around 1784, nearly two and a half centuries ago (Crutzen 2002). Since then, pervasive industrialization of agriculture and silviculture, plus urbanization and infrastructure development, have severely impoverished the integrity of ecosystems, both in terms of ecosystem processes and biota (Johnson et al. 2017). Today, we are confronted with a biodiversity crisis driven by human exploitation of natural resources, with species extinction rates up to 100 times higher than natural background rates (Turvey and Cries 2019). Land-use changes, particularly habitat conversion, play a crucial role in biodiversity loss (IPBES 2019). Recognizing the urgency, habitat restoration efforts are gaining momentum. The incentive for successfully restoring European habitats has recently increased with the adoption of the EU Nature Restoration Law, in which member states are obliged to restore at least 20% of the degraded ecosystems by 2030 and all ecosystems in need of restoration by 2050. However, planning and implementing efficient and successful restoration is not an easy task and suffers from a shortage of evidence-based solutions, insufficient pre- and post-restoration monitoring, and preconceived restoration goals (Suding 2011; Cooke et al. 2018). Most importantly, proper restoration must be assessed against natural reference conditions or, at least, historical states, when most ecosystem processes were much less impacted by human activities. Relevant references include knowledge of site appearance, environmental qualities, and species occurrences before degradation (Klein & Thurstan 2016). However, most biodiversity monitoring programs began long after the acceleration of major anthropogenic pressures (Mihoub et al. 2017; Soga and Gaston 2018). While some historical sources, such as diary notes and landscape paintings (Fig. 1), provide fragmentary evidence of the past, they are often subjective or qualitative human perceptions. The gradual degradation of ecosystems (Klein & Thurstan 2016) and our tendency to underestimate historical biodiversity or misinterpret natural processes due to limited awareness of past conditions challenge restoration ambitions. Without accurate records of past near-natural states, restoration goals may be unambitious (Papworth et al. 2009; Vera 2010).

In this study, we present targets for ecological restoration based on historical data on plants, butterflies, birds, and their ecological indicator values and habitat affinities. Denmark, like many European countries, has undergone radical land-use change over the past 100–200 years (Levin and Normander 2008; Finderup Nielsen et al. 2021). The agricultural area has remained relatively constant, even slightly decreasing to around 60% of the total land area (excluding forest plantations) since a peak around 1935. Non-arable lands have been affected by increasing intensification of farming and forestry, implying both spill-over from intensified arable farming (drainage, fertilization, pesticides) and conversion of near-natural or set aside areas to plantation forest and cultivated grass-clover ley (Fig. 1). Official statistics tell that the total forest area has increased from 3 to 4% in 1805 to 11% around year 2000 (Levin and Normander 2008). However, what used to be semi-open woodlands grazed by livestock have been converted to dark plantations. The area of open habitats, such as grasslands and fens, has decreased from 25% in 1888 to less than 10% in 2000 (Levin and Normander 2008) due to cessation of extensive livestock grazing and subsequent encroachment (Eriksson et al. 2002), and the lack of conservation grazing on the remaining open

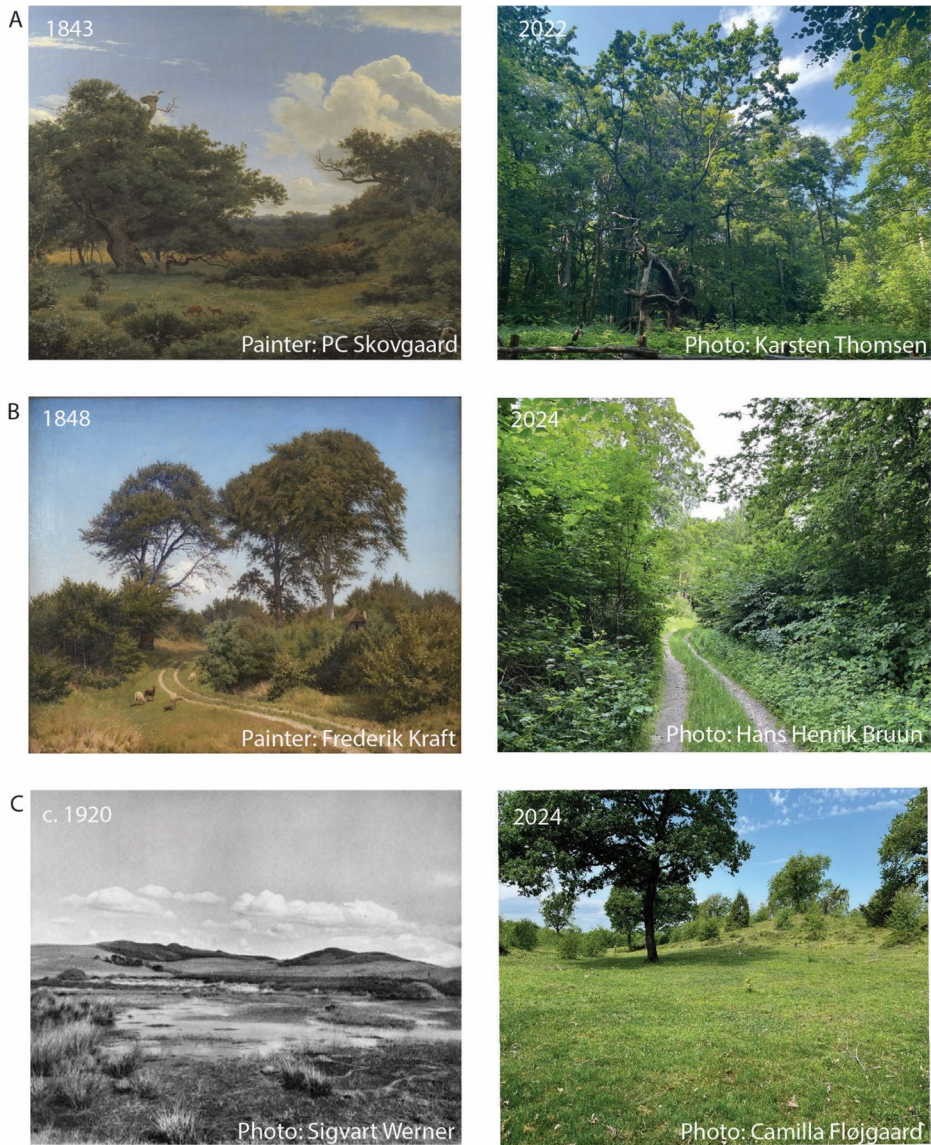


Fig. 1 Historical paintings/photographs and current photographs of selected localities: **A:** Storkeegen in Jægerspris Nordskov (locality 5, Fig. 2), **B:** Færgelunden (locality 6), **C:** Hverrestrup Bakker at Simsted (locality 1)

habitats. Previous studies on historical species data have shown that early 19th -century butterfly, plant, and bird communities were radically different than those of today (Eskildsen et al. 2015; Finderup Nielsen et al. 2019, 2021; Møltøfte et al. 2021; Bjerregård et al. 2023).

Our aim is to demonstrate the magnitude of biotic changes over the past 100–180 years. We have selected plants, butterflies, and birds as focus groups primarily because reliable historical data exist for these groups; their complementarity across trophic level, mobility,

and body size is an advantage and corresponds to sensitivity to complementary aspects of habitat change (Newbold et al. 2020). Moreover, plants are important and widely used indicator species (Brunbjerg et al. 2018), while birds and butterflies are some of the most well-studied species' groups (Gregory et al. 2008; van Swaay et al. 2008). By examining these three groups, we aim to gain a comprehensive understanding of historical conditions, although our knowledge is still limited by the lack of data on the response of understudied taxonomic groups to land-use changes (Davison et al. 2021). Through species traits, habitat preferences, and changes in land use, we seek to answer the following critical questions:

1. How can historical occurrence data from multiple sources, of variable quality and quantity, from contrasting species groups, and historical land-use statistics be collated to exemplify how restoration targets can be informed?
2. What characterizes (winner and) loser species during the past 100–180 years, considering differences in habitat requirements and dispersal ability?
3. What landscape-scale changes in habitat quantity and quality can we infer from the observed changes and how can this information be used to inform current restoration efforts?

Methods

Plant localities

Based on historical data availability for plants in Denmark (see Finderup Nielsen et al. 2019), we chose 11 focal localities in which reasonably thorough surveys had been conducted 1835–1915 (Fig. 2). These varied in size (range: 1.2–55.2 km²) and habitat composition but generally had high habitat heterogeneity (Supplementary Information S1).

Plant data

We retrieved historical presence-only data for the selected sites from published literature and from unpublished diary notes (Supplementary Information S2). We aimed for thorough, unbiased species lists for well-defined, well-investigated areas sampled by distinguished botanists. These were supplemented with stray records from somewhat earlier and later times but still representing the state of ecosystems before the industrialization of agri- and silviculture. Thus, occurrences spanned 1790–1947, with the bulk of records dating to 1835–1915 (c. 74% of records; 41 of 58 sources), and many post-1915 records representing rediscoveries of species already known from the site (Supplementary Information S2).

For these localities, we retrieved current (1992–2023) presence-only vascular plant species data from two databases: A national atlas database (Atlas Flora Danica (AFD) 1992–2014 (Hartvig 2015) and GBIF (1992–2023; GBIF.org (30.03.2023) GBIF Occurrence Download <https://doi.org/10.15468/dl.q6vpsm>). We used data with geographic uncertainty < 1 km (99% of the data). For both current and historical data, we aligned taxonomy, aggregated subspecies and varieties to species level, omitted genus-level records and hybrids, and merged species lists, omitting duplicates. Aggregated taxa were constructed due to changes in species circumscription between the 19th century and now: *Carex muri-*

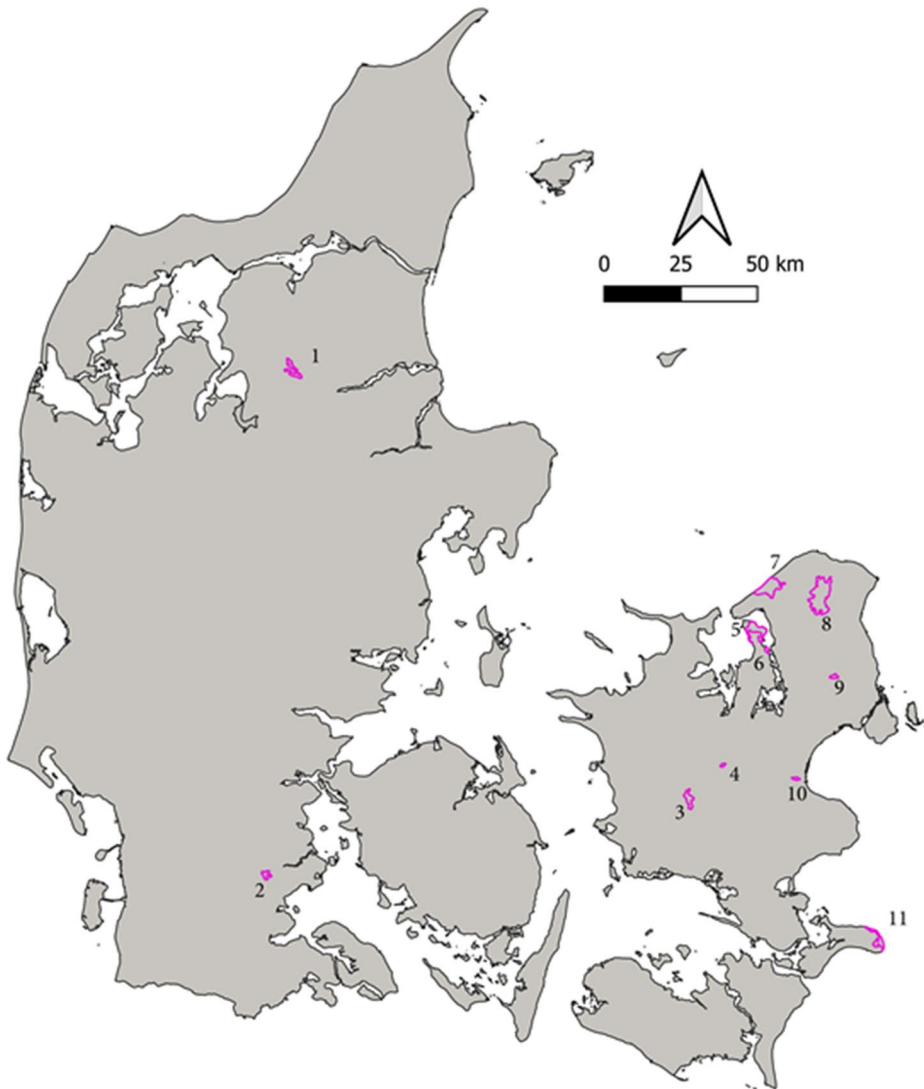


Fig. 2 Focal localities for plant and butterfly analyses (pink). 1: Simsted, 2: Pamhule Skov, 3: Sorø Sønderskov, 4: Allindelille, 5: Jægerspris Nordskov, 6: Færgelunden, 7: Tisvilde Hegn and Melby Overdrev, 8: Gribskov, 9: Jonstrup Vang, 10: Køge Ås, 11: Høje Møn incl. Klinteskoven

cata group (*C. spicata* Huds., *C. pairaei* F.W. Schultz, *C. divulsa* Stokes), *Glyceria fluitans* L.+*G. notata* Chevall.+*G. declinata* Bréb.; *Malva neglecta* Wallr.+*M. pusilla* Sm., *Nuphar lutea* L.+*N. pumila* Timm; *Polypodium vulgare* L.+*P. interjectum* Shivas; *Rorippa nasturtium* L.+*R. microphylla* Boenn.; *Rosa tomentosa* Sm.+*R. sherardii* Davies. *Agrostis canina* L.+*A. vinealis* Schreb., *Dryopteris dilatata* Hoffm.+*D. expansa* C.Presl+*D. carthusiana* Vill.

The final current plant list had 1307 species, while the historical list had 888 species, including aggregated taxa.

Butterfly data

Butterfly localities matched plant localities, except two localities with no historical records (Pamhule Skov and Jonstrup Vang), i.e. nine localities were used (Supplementary Information S1).

Historical and current butterfly presence/absence data were based on all existing databases (www.naturbasen.dk, www.arter.dk, ADD database (Atlas of Danish Butterflies), Bugbase (<https://lepidoptera.dk/>), Zoological Museum of Copenhagen collections, Danish Ornithological Society database (<https://dofbasen.dk/>, bird-focused, with occasional butterfly entries), various private 20th century collections, and extensive field work (Bjerrgård et al. 2023) and aggregated temporally to three time periods: 1900–1949, 1950–1999, and 2000–2019. There were many indications that historical data had false negative records of species that were historically too common to be considered “noteworthy”, but which have since then declined in occupancy. This interpretation was supported by regional faunistic treatises indicating that several species now rare were formerly widespread, making their presence likely at sites where contemporaneous records included other species that were already uncommon at the time. Thus, for sedentary species (according to Eskildsen et al. 2015), large and stable populations of a species at a given locality during the later time periods were assumed as evidence of presence also in earlier time periods ($n=91$ occurrences; Supplementary Information S3). In particular, this was applied to sites, for which historical data came from single excursion reports, giving a seasonal bias. For mobile species, no changes were made. Conversely, stray finds in single years of mobile species were considered false positives and removed ($n=52$ occurrences; Supplementary Information S3). The final data comprised 72 butterfly species.

To interpret temporal changes in butterfly communities within localities and relate them to changes in land use, we retrieved data on butterfly host plant distribution for the 72 species in our study from Eskildsen et al. (2015). Habitat openness preference for each species was extracted from the species’ habitat description in Stoltze (1996) and categorized into four classes: open, forest-grassland ecotone, woodland, and habitat generalist.

Bird data

For the avifauna, we analyzed traits of nationally increasing (winners) and declining (losers) Danish breeding bird species from 1800 to 2018. Meltofte et al. (2021) listed 123 species showing clear trends, either increasing or decreasing (Table 1 in Meltofte et al. 2021; Supplementary Information S4). We used the AVONET database (Tobias et al. 2022) to characterize each species’ properties, including habitat preference, vegetation structure, migration, trophic level, and maximum latitude of range (Supplementary Information S5).

We excluded marine and aquatic bird species from our terrestrial ecosystem study, resulting in 105 species (Supplementary Information S4).

Environmental and land-use data

Ellenberg indicator values (Hill et al. 1999) for nutrients (N), soil moisture (F), light (L) and soil pH (R) were available for 970 of 1298 current species (75%) and 787 of 884 historical species (89%). Similarly, Grime’s life strategy indicators for competition (C), stress (S) and

Table 1 Mantel test results from the analyses on species change (historical (1900–1049) and current (2000–2019) species composition) and environmental variables in the 9 butterfly localities

Mantel	R^2	P
Species change~Ell_L	0.13%	0.607
Species change~Ell_F	0.02%	0.559
Species change~Ell_N	10.60%	0.006
Species change~Ell_R	1.80%	0.105
Species change~Grime S	14.62%	0.002
Species change~Grime R	0.75%	0.775
Species change~Grime C	1.91%	0.069
Species change~BioflorClass	1.13%	0.172
Species change~plant spc rich	0.02%	0.429

Variation (R^2) in species dissimilarity explained by dissimilarity in environmental variables (Ellenberg L (Ell_L), Ellenberg F (Ell_F), Ellenberg N (Ell_N), Ellenberg R (Ell_R), Grime S, Grime R, Grime C, habitat type diversity (BioflorClass) and plant species richness (plant spc rich)). P-values are given (1000 permutations)

disturbance (R) (Grime et al. 1989) were recoded as numeric values for each species following Ejrnæs and Bruun (2000). Species' grazing/mowing affinity was retrieved from Tyler et al. (2021) (Supplementary Information S6). Mean and standard deviation Ellenberg, mean CSR and mean Tyler's grazing/mowing affinity were calculated based on species lists for each locality in each time period.

We estimated current and historical habitat diversity within localities using species-habitat affiliations from the Bioflor database (Kühn et al. 2004). We included all natural habitats listed per species (omitting highly modified agroecosystems (as our objective was to infer near-natural habitat diversity) and alpine classes (not relevant to Denmark), then calculated habitat diversity per locality and period (Supplementary Information S7). Habitat diversity was adjusted by dividing the number of habitats with the log transformed number of species in each locality.

Historical land-use categories from 1881 were retrieved at the parish-level using Danmarks Statistik: Statistisk Tabelværks 4^{de} række, Litra C, Nr. 4. Land-use categories were aggregated (Supplementary Information S8) and summarized for each locality based on the areal share of each parish located in a locality. Current land-use categories were aggregated to match historical data categories (Supplementary Information S9) and summarized for each locality based on Basemap 04 (Levin 2022) which is a national map of land use and land cover for Denmark.

Mean current grazing density (kg large herbivore biomass per ha) for each locality was retrieved from the Danish Nature Indicator (Ejrnæs et al. 2021, <https://naturindikator.dk/>).

Historical grazing densities were estimated from national statistics on horses, cattle and sheep at the parish level in 1864 (Danmarks Statistik: Statistisk Tabelværk ser.3, vol. 3, 1864), recalculated to kg/ha using parish areas overlapping with each locality (Danmarks Statistik: Statistisk Tabelværks 4de række, Litra C, Nr. 4 and Dam 2023) and mean body mass for historically common breeds of cattle, horse and sheep (cattle: Jysk Malkekvæg = 350 kg, horses: Frederiksborghest = 500 kg, sheep: Dansk Landfår = 70 kg). Cattle, horse and sheep were known to graze in most grasslands and forests historically, whereas pigs were disregarded here, as they - by the mid-19th century - were most likely fenced near settlements and no longer roaming freely as pannage pigs. The method assumes that parish-level density

is representative for localities and that 1864 livestock mainly fed on wild plants (either grazing or fed locally harvested hay).

Analyses

Plants

We assessed temporal changes in plant species richness by calculating total species richness for each locality. Similarly, we calculated the number of red-listed species (*critically endangered*, *endangered*, *vulnerable*, *near threatened*, and *data deficient*) based on the Danish National Red List (www.redlist.au.dk). A few species were matched at subspecies level to retrieve the correct red list category. As a supplement to the red listed species, we used a list of indicator species considered moderately to very sensitive towards habitat changes as defined by Fredshavn et al. (2010). We combined red-listed and indicator species to identify sensitive species lost across localities during the study period. Paired t-tests were employed to compare Ellenberg N, F, L, R and N/R (Andersen et al. 2013) values and Grime C, S, R values between species lost and those remaining in the localities throughout the study period.

Butterflies

To test trends in butterfly species richness per locality for pairs of the three time periods (1900–1949, 1950–1999, and 2000–2019), we used one-tailed, paired t-tests and checked normality with Shapiro-Wilk tests.

We assessed changes in butterfly community composition using nonmetric multidimensional scaling (NMDS) on 72 species across 27 time period-locality combinations using the function metaMDS in the vegan R-package (Oksanen et al. 2017). Dispersion ellipses (0.4 confidence on standard deviations) were drawn for each time period (1900–1949, 1950–1999, and 2000–2019).

To relate butterfly species composition to local environmental conditions, we computed dissimilarities in Ellenberg L, F, N, R; Grime C, S, R; BioFlor habitat diversity; and plant richness (Euclidean similarity index), and tested their association with butterfly community dissimilarity (Sørensen similarity index, only using time periods 1900–1949 and 2000–2019 to match the environmental variables) using Mantel tests.

Butterfly species were categorized as winners and losers based on presence/absence of species on each of the localities in two time periods (1900–1949 and 2000–2019) as response variable and ‘time period’ as explanatory variable in a binomial glm. Significant positive estimates indicated winners, while negative estimates indicated losers. The butterfly data set included species found in only a few localities, yet these species are highly important as they may be on the verge of extinction. Because of small sample sizes for some species, we used a significance level of $p < 0.05$ as well as $p < 0.2$ to gain knowledge of the rare species. Because we tested species-level trends across many butterfly species, we also adjusted p-levels according to Bonferroni (Supplementary Information S13). Differences in ecological traits of winners and losers (unadjusted $p < 0.2$) were tested using contingency tables for selected traits (host plant distribution and habitat openness) and two-tailed Fischer’s exact test.

Birds

We used contingency tables to test for associations between “species trend” (increasing or decreasing in Table 1 in Meltofte et al. 2021; Supplementary Information S4) and the variables “habitat,” “vegetation structure,” “migration,” and “trophic level”. For the “habitat” variable, two habitats with <5 species (riverine and rock) were omitted from the analysis. Significance was inferred using two-tailed Fisher’s exact tests.

To investigate the potential effect of global warming and northward range shifts in describing bird species trends, we tested for potential differences in “max latitude” between increasing and declining species using the Wilcoxon signed-rank test (Wilcoxon 1945).

Land-use changes

To investigate the potential temporal change in land-use we used paired t-tests on locality mean-values of Ellenberg (L, F, N, R), Grime’s CSR, Tyler’s grazing/mowing affinity, and Bioflor habitat diversity, number of annual plant species and richness of red-listed plant species as well as density of large grazing herbivores and land-use categories.

All statistical analyses were performed in R version 4.2.2 (R Core team 2022).

Results

Plants

Historical (1790–1947) plant species richness across the 11 localities ranged from 78 to 374 species, while current (1992–2023) richness ranged from 296 to 785 species. Larger localities had more species missing from historical data (estimate = 7.5, $p = 0.03$). The higher number of species in the current dataset suggests more complete inventories and more neophytes (3.8% and 19.6% neophytes in historical and current dataset respectively. Neophyte definition based on Buchwald et al. (2013) and Plants of the world <https://powo.science.kew.org/>). Direct comparison of total richness should be interpreted with caution, and we therefore emphasize composition and trait-based indicators.

The historical and current dataset had 159 and 116 red-listed species, respectively (Supplementary Information S10), and 341 and 301 sensitive species, respectively. Historical richness of now red-listed species ranged from 10 to 51 species per locality. Current red-listed richness ranges from 4 to 42 species. All sites had substantial losses of species sensitive to human land-use intensification, despite being relatively unaltered compared to the landscape at large. Potentially, several now redlisted species could have been lost from the sites prior to the earliest botanical investigation (Fig. 3). Two sites with relatively scanty botanical data (but good butterfly data) deviated from the overall pattern. Moreover, the historical plant communities were more stress-tolerant (Grime S) and had a higher affinity for grazing and mowing than the more competitive (Grime C) current communities (Supplementary Information S12, A, C, D).

Consistent with expectations, the historical dataset had more red-listed species per locality than current data despite fewer recorded species overall (absolute numbers: one-tailed t-test: mean difference: 10.5 species, t -value = -2.004, $df = 10$, $p = 0.036$; relative numbers:

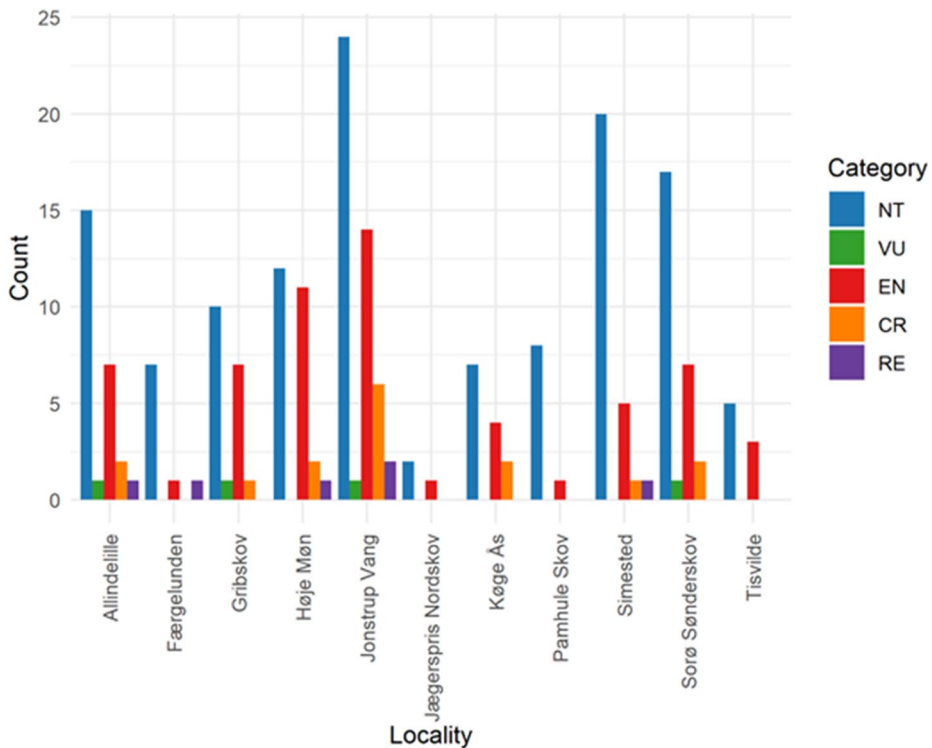


Fig. 3 Number of red listed vascular plant species that have disappeared for each locality per red list category (NT=near threatened, VU=vulnerable, EN=endangered, CR=critically endangered, RE= Regionally extinct)

one-tailed t-test: mean difference: 0.092, t -value = -7.104, df = 10, p < 0.001) and the difference was due to a significant difference in red-listed species belonging to the categories EN (one-tailed t-test: mean difference: 3.5 species, t -value = -2.057, df = 10, p = 0.033) and CR (one-tailed t-test: mean difference: 1.2 species, t -value = -2.137, df = 10, p = 0.029). This pattern emphasizes that losses concentrate among sensitive taxa, even where regional richness has increased.

When comparing Ellenberg and Grime values for red-listed and sensitive species, we found that vanished species were significantly more light- and soil moisture-demanding (Ellenberg L, 7 of 11 localities and Ellenberg F, 5 of 11 localities, respectively), and significantly less nutrient-affiliated (Ellenberg N, 6 of 11 localities, Ellenberg N/R, 5 of 11 localities) and competitive (Grime C, 6 of 11 localities), than species that persisted (Supplementary Information S11).

Butterflies

Butterfly species richness across the nine localities varied from 30 species at Færgelunden to 65 species at Tisvilde (1900–2019). There was a significant decline in species richness across the nine localities from 1900 to 1949 to 1950–1999 (one-tailed t-test: mean difference: 3.33 species; t = 2.673, df = 8, p -value = 0.014); 1950–1999 to 2000–2019 (one-tailed t-test:

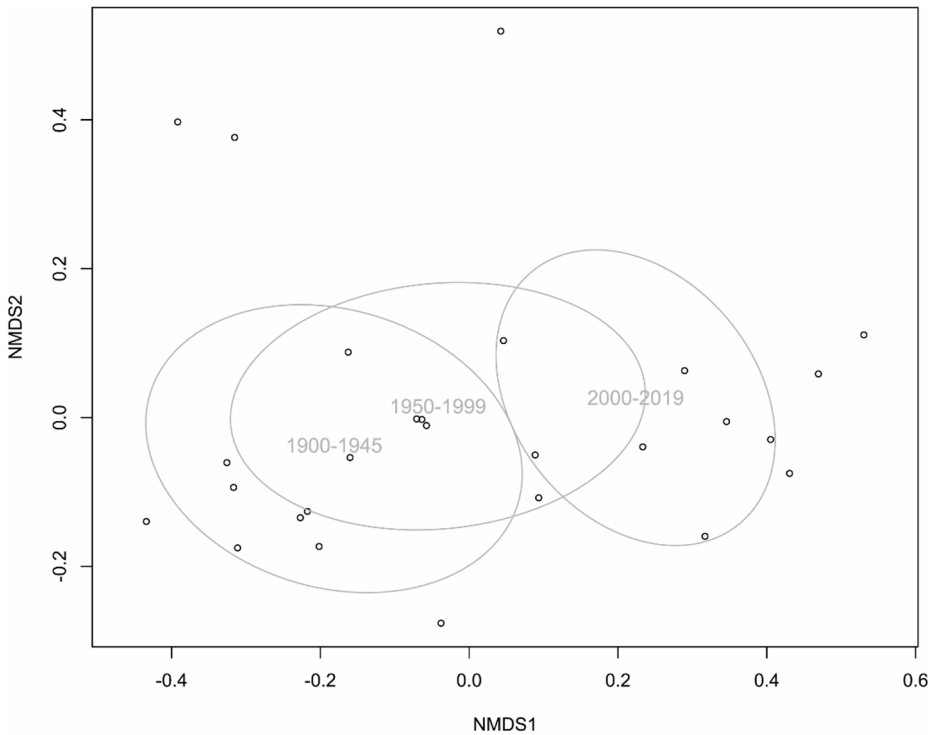


Fig. 4 Nonmetric multidimensional scaling (NMDS) ordination for butterflies. Ellipses extend to $0.4 \times$ confidence intervals for time periods (1900–1945; 1950–1999; 2000–2019)

mean difference: 8.33 species; $t=3.536$, $df=8$, $p\text{-value}=0.004$) and 1900–1949 to 2000–2019 (one-tailed t -test: mean difference: 11.67 species; $t=6.047$, $df=8$, $p\text{-value}<0.001$).

The NMDS ordination on butterfly communities (4-dimensional, final stress=0.047) explained 93.8% of the variation in species composition. Butterfly community composition overlapped along axes 1 and 2, but with distinct ellipses for 1900–1945 and 2000–2019 (Fig. 4).

Mantel tests showed significant correlations between butterfly species composition, Ellenberg N and Grime's S (Table 1).

Of the 72 butterfly species, 14 were losers and two were winners (unadjusted $p<0.2$), while eight were losers and one was winner using an unadjusted significance level of $p<0.05$ (Supplementary Information S13 lists only those classified as winners or losers at $p<0.05$ and $p<0.2$ levels). However, after Bonferroni correction for multiple testing, no species-level trends remained statistically significant (Supplementary Information S13).

Fisher's exact test showed significant differences between winners and losers (unadjusted $p<0.2$ level) suggested differences in host plant distribution ($p=0.042$, losers had host plants with more restricted distributions) and habitat openness ($p=0.008$, i.e., losers were associated with open habitats or forest-grassland ecotones).

Birds

Avian trends from 1800 to 2018 showed 60 winners and 45 loser species (numbers of winners and losers refer to national trends, not local richness), Supplementary Information S13). Species preferring forests, woodlands and human-modified landscapes increased, while those associated with grasslands, coastal habitats and freshwater wetlands declined ($p < 0.001$, Supplementary Information S14). Likewise, vegetation structure was significantly associated with species' trend ($p < 0.001$), i.e., species preferring dense habitats were mostly increasing, while species preferring open habitats were generally declining. A significant association between trophic level and species trend ($p = 0.002$) indicated that carnivorous (mainly insectivorous) species were most often declining, while omnivorous species were mostly increasing. With respect to migration, there was a significant association between migration and species trend ($p = 0.02$), indicating that migratory species were declining more often than sedentary species. Maximum latitude did not significantly differ between winners and losers ($W = 1611$, $p = 0.092$).

Land-use changes

Mean nutrient status (Ellenberg N, mean difference = 0.729, $p < 0.001$, Supplementary Information S15, D) and pH (Ellenberg R, mean difference = 0.221, $p < 0.01$, Supplementary Information S15, B) were significantly higher in current communities. The standard deviation of Ellenberg values within localities, indicating ecological heterogeneity, was lower in current than in historical localities for nutrient availability (mean difference = 0.109, $p = 0.011$, Supplementary Information S15, C) and soil pH (mean difference = 0.263, $p < 0.001$, Supplementary Information S15, A). There was no significant change in light conditions (Ellenberg L) and soil moisture (Ellenberg F) (Supplementary Information S16).

Habitat diversity and grazing/mowing affinity were significantly lower in current data than historical (mean difference habitat diversity = 0.555, $p < 0.005$; mean difference grazing/mowing affinity = 0.243, $p < 0.005$, Supplementary Information S12, D).

The cover of rotational and fallow fields was significantly higher within localities in 1881 than in 2021. Rotational fields decreased from about 39% to 4% (mean difference = 34.633, $p < 0.001$, Supplementary Information S17, A), and fallow fields from about 20% to about 4% (mean difference = 15.886, $p < 0.01$, Supplementary Information S17, D). Forest plantation cover increased significantly from about 24% to 49% (mean difference = 23.113, $p < 0.01$, Supplementary Information S17, C). There was no significant change in built-up areas within our localities (Supplementary Information S17, B).

Mire cover increased from about 1% to 10% (mean difference = 9.059, $p < 0.05$, Supplementary Information S18, C), while the density of large grazing herbivores decreased from about 173 kg/ha to 20 kg/ha in 2020 (mean difference = 152.975, $p < 0.001$, Supplementary Information S18, A). This increase in mire cover can be attributed to the abandonment of grazing or neglected drains, leading to overgrowth of wet-moist meadows and subsequently a change in land-cover from meadow to mire.

There was no significant change in meadow and grassland cover (Supplementary Information S18, B and D).

Discussion

This study exemplifies the potential of utilizing historical data to assess changes in biodiversity and landscape structure, aiming to inform restoration targets for biodiversity conservation. Significant disparities were found between historical and contemporary landscapes in habitat heterogeneity, plant and butterfly communities, and bird fauna. Historically, landscapes featured heterogeneous mosaics of grasslands and open woodlands with grazing, supporting many rare species. Since then, landscapes have been homogenized, eutrophicated, and non-arable areas have become dominated by closed-canopy vegetation, due to the cessation of extensive practices that previously induced ecosystem disturbances (Fig. 1). These processes have driven substantial losses of species now considered rare. Our findings highlight the importance of historical records in guiding ambitious and effective conservation and restoration strategies. Several species of EU-wide conservation concern, but now extinct from Denmark have vanished from the investigated sites (e.g. *Hamearis lucina* (L., 1758) and *Parnassius mnemosyne* (L., 1758)). Similarly, many endangered or regionally extinct plant species have disappeared from one or more of our sites (e.g. *Thesium ebracteatum* Hayne, RE, lost from two sites, *Anacamptis pyramidalis* L., VU, *Neotinea ustulata* L., CR, lost from three sites, *Crepis praemorsa* L., EN, lost from three sites, Supplementary Information S10). This illustrates that ignoring historical data will lead to lowered ambition levels of conservation efforts in countries, where industrialization of land-use took place relatively early.

Centennial changes in landscape, plant, butterfly and bird diversity

Since the industrial revolution, Denmark has undergone significant land-use changes, including intensified agriculture and plantation forestry, causing eutrophication and drainage (Lohrum et al. 2024). These changes have negatively impacted natural areas (www.NOVANA.dk, Fig. 1), aligning with the EU Habitats Directive report that shows 81% of habitats have poor or bad conservation status, with 36% deteriorating (EEA 2020). The extensive 19th-century drainage to boost agriculture and forestry, was revealed by significant differences in red-listed and sensitive plant species, indicating that species lost during the study period preferred higher soil moisture and lighter conditions than those still found.

The shift from rotational field to forest within localities was accompanied by contrasting biodiversity responses among taxa. Total vascular plant richness is higher in the current dataset, but this increase does not translate into improved conservation status: the richness of red-listed plant species declined across localities, and butterfly species richness declined markedly over the study period. By contrast, the national trend analysis for breeding birds indicates increases in several forest and dense-vegetation species (e.g., *Erithacus rubecula* (L. 1758), *Turdus philomelos* (C.L.Brehm 1831), *Coccothraustes coccothraustes* (L., 1758), *Dendrocopos major* (L., 1758) and *Poecile montanus* (Conrad von Baldenstein, 1827), consistent with expanded forest cover and canopy closure. Similarly, a shift in plant communities towards medium-dry, nutrient rich and shaded conditions has been documented, corresponding to intensified agriculture (eutrophication and drainage) and silviculture (dark, homogenous plantations) (Finderup Nielsen et al. 2021) in line with our findings of species associated with low-growing grassland (*Helianthemum nummularium* L.) and fens (*Carex dioica* L., *Eriophorum latifolium* Hoppe) as well as open woodland (*Lathyrus vernus*

L.) disappearing from several localities. Overall, these patterns suggest that afforestation and canopy densification have contributed to biotic change and habitat restructuring, but not to a recovery of specialist or conservation-relevant taxa. Historically, wood pastures supported a range of species affiliated with forest ecotones. Modern forestry and nature management have sharpened habitat boundaries, reducing ecotones (Habel et al. 2023). Plantation forests, especially those with exotic conifers, negatively impact bird diversity and abundance due to low structural heterogeneity, lack of native species, and short rotation times (Castaño-Villa et al. 2019).

Butterfly richness declined by about 11 species from 1900 to 2019, with species linked to open habitats and host plants with limited distribution being the most affected (e.g., *Fabriciana adippe* (Denis and Schiffermüller 1775) (forest glades), using violets such as *Viola hirta* L. as larval host plants). Our results align with early 20th -century declines and regional extinctions of butterfly species associated with forest-grassland ecotones and open woodlands in Denmark and Europe (Streitberger et al. 2012; Bubová et al. 2015; Eskildsen et al. 2015). Habel et al. (2019), found the most significant decline in butterfly abundance in Germany since 1950. This aligns with our finding of a substantial species loss since 1950, despite limitations in our data size and temporal analysis precision. Nevertheless, species sensitive to increased nutrients, intensive grazing, and bog drainage are among the losers, consistent with the effect of unfavorable management practices on red-listed butterflies in Europe (Bubová et al. 2015).

Grazing practices have dramatically changed over the last 150 years, from extensive grazing across habitat types to paddocks of intensive summer grazing and large landscapes ungrazed, leading to litter accumulation, encroachment, and homogenization. 19th -century grazing areas supported greater biodiversity (more red listed and sensitive plant species, more butterflies etc.) due to their heterogeneity, low nutrient status, and near-natural levels of large herbivores often roaming the land year-round creating open habitats and forest-grassland ecotones. Regional floras are more similar today than 140 years ago (Finderup Nielsen et al. 2019), indicating homogenization due to intensive land use. Regional richness increases in Denmark largely reflect neophyte additions, while rare species became rarer (Finderup Nielsen et al. 2019) corresponding to our finding that red-listed plant species are declining and increase in regional richness may reflect neophyte additions and sampling completeness. This should be considered conservative given the better and more systematic coverage of the current data. For butterflies, the shift in community composition was more pronounced than community homogenization (Fig. 4). Species sensitive to intensive grazing, bog drainage or high nutrient levels also declined (e.g., intensive grazing: *Lycaena hippothoe* (L., 1761), *Polyommatus amandus* (Schneider, 1792), bog drainage: *Melitaea diamina* (Lang, 1789), *Boloria aquilonaris* (Stichel, 1908), Supplementary Information S13). Generalist species with nitrophilous host plants such as *Vanessa cardui* (L., 1758) increased, while *Apatura iris* (L., 1758) may have increased as part of a northward range expansion documented in northern Europe over recent decades. Such range expansions are consistent with climate-associated shifts in butterfly distributions, but they are also mediated by land use and species-specific traits rather than being driven by temperature alone (Sunde et al. 2023).

Long-term shift and homogenization of communities and their links to landscape and habitat homogenization have been documented previously (e.g., Eskildsen et al. 2015; Warren et al. 2021), and habitat and landscape homogenization negatively affect special-

ist butterflies more than generalists (Habel et al. 2023), with specialist species preferring nutrient-poor habitats being particularly vulnerable (Habel et al. 2016). For birds, landscape homogenization and agricultural dominance leads to absence of expected bird species (i.e., avian dark diversity) (Andersen et al. 2023). For clarity, counts of ‘winners’ versus ‘losers’ reflect national population trends rather than net changes in local richness. Birds rely on a mosaic of habitats for breeding (Dolman 2012), and agricultural intensification and landscape homogenization have led to declines in open land bird populations across Europe, especially in countries with intensive agriculture like Denmark (Donald et al. 2001; Heldbjerg et al. 2018). In our study, declining bird species were often associated with grasslands, coastal areas and freshwater wetlands (e.g., *Perdix perdix* (L., 1758), *Ciconia ciconia* (L., 1758), *Vanellus vanellus* (L., 1758), *Tringa totanus* (L., 1758), *Chlidonias niger* (L., 1758) and *Falco subbuteo* (L., 1758)) and were typically carnivorous/insectivorous and migratory. Our findings correspond with documented declines (1990–2015) in insectivorous birds in Denmark and Europe (Bowler et al. 2019), with insect declines proposed as a contributing factor (Tallamy and Shriver 2021). Most carnivorous/insectivorous breeding birds in northern Europe are also migrants, making it hard to separate the effects of a migration from diet on population change. Like us, Bowler et al. (2019) also found a link between long-distance migrants and insectivores, hampering conclusions about whether migration habit or diet may be the ultimate driver of declines.

Our results show some congruence in plant, butterfly, and bird diversity changes despite differences in mobility and resource needs. Similar patterns have been observed in other studies linking farmland configuration to species richness across taxonomic groups (birds, spiders, butterflies, hares) (e.g., Šálek et al. 2018). The loss of plant, butterfly and bird species over the last 100–180 years is not unique to Denmark. Recent analyses indicate 19% of red-listed species in Europe are threatened with extinction, with plants and invertebrates at higher risk due to agricultural land-use changes (Hochkirch et al. 2023). Specialist species are lost more often than generalists, leading to both taxonomic and functional biodiversity homogenization (Clavel et al. 2011). The loss of large-scale natural processes supporting landscape and habitat heterogeneity e.g., hydrology, coastal dynamics, and grazing has had devastating effects on biodiversity (Perino et al. 2019; Svenning 2020). Restoring these processes (rewilding) can enhance ecological variation and biodiversity (Vera 2010).

Informed targets for conservation and ecological restoration

High-quality data series rarely extend back more than a few decades, so historical data from diary notes and collections were used to illustrate biodiversity loss over the last 180 years. The early 19th -century starting point and focus on plants, butterflies, and birds were dictated by data availability, not lack of relevance of earlier time periods or other taxonomic groups. We consider it certain that our study period is suboptimal, as many species were also vanishing prior to our starting point, leading to an underestimation of biodiversity loss (Mihoub et al. 2017). Some species may have benefited from human intervention in historical landscapes, occurring in densities exceeding pre-agricultural levels (Szabo 2014). Linking species data with environmental changes is further complicated by extinction debt, or species’ lag in response to changes, potentially extending beyond 100 years (Bulman et al. 2007; Sand-Jensen et al. 2017). For example, butterfly loss associated with forest glades is visible in our data, but the cause dates back to changed forestry practices in 1805 or shortly

thereafter. Likewise, there is a discrepancy between lost species and current habitat protection. For example, *Carterocephalus palaemon* (Pallas, 1771) and *Parnassius mnemosyne* (L., 1758) are listed in the Habitat Directive, but they were already eradicated from Denmark when the Habitat Directive was adopted. Hence, it is up to other countries to ensure their populations and create suitable habitats for them. However, we should use historical data to ensure habitats for species that historically lived here. While historical baselines have limitations (Douda et al. 2023), evolutionary baselines of pre-human conditions may be more relevant for restoring self-sustaining ecosystems, though challenged by data-deficiencies. Paleoeological evidence suggests that pre-agricultural Holocene (around 11,700–10,000 years ago) landscapes in Europe were mostly forested with significant glades and pasture-woodlands, indicating high forest heterogeneity. Disturbance by large herbivores played a crucial role in maintaining habitats for a wide range of species (Svenning 2002), although perhaps at reduced levels compared to the Pleistocene where pre-human landscapes had open and semi-open areas throughout as an effect of megafauna impacts (Pearce et al. 2023). Our historical reference indicates that some of these ecosystem features, such as grazing, habitat mosaic and openness may have been somewhat preserved in 18th century landscapes, supporting biodiversity.

Implications

The advent of the EU Restoration Law highlights the importance of international biodiversity references. Using a historical or evolutionary reference help setting targets for biotic integrity (Vačkář et al. 2012; Plumptre et al. 2021) and for habitat-generating ecosystem processes (Rouget et al. 2006), respectively, and provide relevant targets for evaluating restoration success. The process of compiling empirical evidence on biodiversity responses to reestablishing natural processes is ongoing, but we still have much to learn, e.g. species' true habitat requirements.

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Data availability Data will be made available on request.

Declarations

Competing interests The authors declare no competing interests.

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