I. Title page

Title: More is Less: Net Gain in Species Richness, but Biotic Homogenization over 140 Years

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II. Abstract page

Abstract: While biodiversity loss continues globally, assessments of regional and local change over time have been equivocal. Here, we assess changes in plant species richness and beta diversity over 140 years at the level of regions within a country. Using 19th-century flora censuses for fourteen Danish regions as a baseline, we overcome previous criticisms concerning short time series and neglect of completely altered habitats. We find that species composition has changed dramatically and directionally across all regions. Substantial species losses were more than offset by large gains, resulting in a net increase in species richness in all regions. The occupancy of initially widespread species increased, while initially rare species lost terrain. These changes were accompanied by strong biotic homogenization; i.e. regions are more similar now than they were 140 years ago. Species declining in Denmark were found to be in similar decline all over Northern Europe.

III. Main text

Introduction

Through the industrial era, the human impact on the world's ecosystems has increased dramatically (Mihoub *et al.* 2017). Anthropogenic pressures, including intensification of land use for food production (Burns *et al.* 2016; Vellend *et al.* 2017a), have significantly changed living conditions for wild species. Consensus holds that, at the global scale, such changes are causing species loss (Millennium Ecosystem Assessment 2005). At smaller spatial scales however, species richness hangs on the balance between colonization and extirpation (Sax & Gaines 2003).

Recent meta-analyses of local to regional biodiversity have reported both positive and negative changes in species richness, with no net loss on average (Vellend *et al.* 2013; Dornelas *et al.* 2014; Elahi *et al.* 2015; Yoccoz *et al.* 2018). Yet, findings of no net loss remain controversial (Gonzalez *et al.* 2016; Vellend *et al.* 2017b; Cardinale *et al.* 2018; Primack *et al.* 2018), with central criticisms revolving around 1) the need for temporal baselines preceding most decisive anthropogenic changes and 2) analyses that account for land-use changes both negatively and positively affecting biodiversity. Here, we overcome central points of criticism by using high-quality landscape-scale data with a baseline well before the onset of industrialized agriculture. We further consider the separate contributions to change by native and exotic species, as suggested by Cardinale *et al.* (2018).

Biodiversity monitoring schemes (Timmermann *et al.* 2015), time-series data (Dornelas *et al.* 2014), historical collections (Hedenäs *et al.* 2002) and legacy studies (Keith *et al.* 2009) have all provided insight into changes in local and regional richness over time. All of these studies, however, have limitations. Studies that consider only a single habitat type (Alstad *et al.* 2016) or even a single site (Morueta-Holme *et al.* 2015) potentially overlook offsets of localized losses with gains elsewhere. Few studies manage to cover more than a couple of decades, and the exceptions mostly focus on unique and largely isolated environments, like islands (Sax & Gaines 2008; Chiarucci *et al.* 2017).

Historical biodiversity data can provide a baseline to measure changes against, but data can only help detecting effects of environmental changes that occurred within its timeframe. If human pressures have increased gradually over centuries, short-term data may not be able to measure biodiversity change properly (Mihoub *et al.* 2017), and may incorrectly identify the drivers of change (Beller *et al.* 2017), especially if lags in response are pronounced (Sand-Jensen *et al.* 2017). Quantifying effects of land-use change on local and regional biodiversity, in order to set informed management targets, requires relevant time scales (Mihoub *et al.* 2017).

In this study, we assess changes to regional plant species richness over c. 140 years. Our baseline data are 14 thorough regional plant censuses from Denmark published between 1857 and 1883. Change is assessed against contemporary data from the most recent national plant survey (Hartvig & Vestergaard 2015). During this period, urban area in Denmark tripled in extent, plantation area more than doubled, areal percentage rotational fields increased from 35 to 60 %, while natural and semi-natural habitats declined to less than half of their former area (Normander & Levin 2008). Although Denmark was already dominated by farmland by 1850, agricultural practice has strongly intensified since then, with more than 50 % of farmland put under drainage and nitrogen surplus increased six-fold (Normander & Levin 2008). Overall, the 14 study regions largely had a similar suite of habitat types as a point of departure, except some were almost devoid of woody plants, and they have undergone parallel land-use changes driven by economic and societal processes at the national or continental level (Fuchs *et al.* 2015). We consider both temporal changes in species richness within each region (alpha diversity) and in compositional heterogeneity between regions (beta diversity). To assess the generality of the observed biodiversity trends beyond the study area, we also compared the direction of species' change – decline or increase – to their red-list status in a range of neighbouring North European countries. We hypothesize that increased land-use intensity (farming, forestry, drainage, fertilization) has caused net losses in regional plant species richness, while the parallel increase in intentional and unintentional introduction of plant species has led to gains in regional species richness. The data enable us to obtain a fair and unbiased assessment of the net change brought about by these opposed drivers. We hypothesize the identity of winner and loser species to be similar across regions, resulting in parallel changes in the flora and greater similarity across regions.

Material and methods

Historical data: In order to identify suitable historical sources, we searched all repositories, including the botanical collections at the Natural History Museum of Denmark, for published and unpublished local to regional floras from the times of Linnaeus to year 1900 (see also Pedersen 2015). We set the upper limit in order to have a baseline well before the industrialization of agriculture, air-borne pollution and climate change characterizing the 20th century. We discovered an upsurge of interest in floristic surveys in the decades after the publication of the first widely accessible Danish field flora books (Lange 1851; Rostrup 1860), resulting in a number of comprehensive landscape floras, as well as many presence-only accounts of noteworthy species. We carefully selected 14 comprehensive floras, of which the authors explicitly stated an aim to include all wild species. As a quality check, we assessed if common and widespread species (Rostrup 1904) were included or noted as absent, and similarly for rarer species mentioned as occurring in the particular region in other sources (e.g. national floras, reports mentioning stray finds of noteworthy species, etc.). We also assessed if the total species number reported deviated from the expected based on the surveyed land area (Fig. S1).

The 14 study regions – all situated in Denmark – vary in spatial extent between 22 and 1800 km^2 and include five smaller islands, four larger islands and five tracts of mainland areas (Fig. 1; Table S1). In total, the study regions cover 6245 km^2, corresponding to c. 15 % of the country's land area. Study areas are termed 'regions' throughout the text in accordance with the terminology of Sax and Gaines (2003). The historical floras comprised between 237 and 1222 species of higher plants (Table S1);

11 out of 14 had regional abundance data on an ordinal scale, while three included presence/absence data only.

Present data: Present data were gathered from the most recent national plant-survey, Atlas Flora Danica (AFD), carried out between 1992 and 2012 by the Danish Botanical Society in 5 × 5 km grid cells (Hartvig & Vestergaard 2015). To spatially match historical with present data, AFD data were compiled from the grid cells best corresponding to the historical region (see supporting information, Appendix 2). Present regional data had between 535 and 1643 species of higher plants (Table S1). No botanical surveys exist for the focal regions from intervening times.

Data preparation: Plant taxonomy and nomenclature were thoroughly standardized, using broad species concepts in order to avoid false appearances/disappearances. Hybrids were omitted and most infraspecific taxa lumped at the species level, unless we were certain that names had been used consistently through time. Some critical taxa were pooled at the genus or section level. Only records of species from outside gardens and other cultivation were included (details in Appendix 2). Species were assigned status as either native (Buchwald *et al.* 2013, appendix 1-3) or exotic (Buchwald *et al.* 2013; NOBANIS 2017), with a few species noted as "NA", if information on origin was equivocal or if combined taxa had different status. All data are available at the Global Biodiversity Information Facility (GBIF).

After standardization of names and taxonomy between time slices and exclusion of dubious taxa, historical and present data collectively comprise 1958 taxa of terrestrial and aquatic plants (23,791 records of occurrence and abundance, 10,433 in historical and 13,358 in present data). Across all regions, 1367 taxa were recorded in the historical data (999 native, 344 exotic and 24 taxa of equivocal status) and 1822 in the present data (969 native, 823 exotic and 30 of equivocal status). These entities are hereinafter referred to as "species".

Abundance: In 11 of 14 historical floras (all except regions 2, 7, 8; Table S1), regional abundance was recorded on an ordinal scale from "rare" to "very common", or – for rare species – as a short list of named localities. We transformed this information, for each historical flora separately, into a semi-quantitative scale (0 to 1), by dividing the ordinal abundance category with the total number of categories used in the particular flora. In the present data, species' regional abundance was estimated as the number of occupied reference grid cells divided by the total number of reference cells in the region (details in Appendix 2). Henceforth, we term the resulting metric 'regional abundance', while the number of regions, in which a species is present, is termed 'occupancy'.

Analysis: All analyses were performed with R ver. 3.3.2.

Based on species presence/absence data from all 14 regions, the total species turnover, as well as relative appearances and disappearances over 140 years within each region, were computed using the "codyn" package (Hallett *et al.* 2016). Species turnover between time periods was estimated as the proportion of species either gained or lost, relative to the total number of species observed through time.

As only 11 out of 14 regions had information of regional abundance, and because abundance measures are generally more uncertain than presence/absence data, we calculated six turnover metrics with varying emphasis on presence/absence and abundance (Anderson *et al.* 2011). Specifically we calculated two purely compositional metrics: Sørensen and Jaccard binary dissimilarity (Chao *et al.* 2005), as well as four abundance metrics: Bray-Curtis, altGower, Manhattan and Euclidian distances (Anderson *et al.* 2006). All metrics were calculated using the function "vegdist" in the Vegan package (Oksanen *et al.* 2016). To visualize the changes in composition, we used Principal Coordinates Analyses (PCoA). In the PCoA, difference between the two time periods was visualized as polygons enveloping all regions at each time slice. Comparing species' regional abundance through time is probably the most critical step in our data analyses. In order to test the sensitivity of the results obtained, we reran the above analyses of beta diversity with historical and present abundance merged into three broad categories (with approximately the same number of original categories in each) as a more conservative assessment (Appendix 2, example in Table S7).

To statistically evaluate significant differences in composition across time, the permutational manova (PERMANOVA) function "adonis2" was run with 999 permutations for all distance metrics (McArdle & Anderson 2001). To evaluate whether significant homogenization of the biota has occurred over time, the difference in distance from all regions to the spatial median was calculated for the two times separately using the function "betadisper" (Oksanen *et al.* 2016) following (Anderson *et al.* 2006). Significance was tested with ANOVA analysis of variance using the function "anova" from the "vegan"-package (Oksanen *et al.* 2016). Binary indices, Sørensen and Jaccard dissimilarity, were calculated for all 14 regions and the remaining four dissimilarity-metrics based on abundance calculated for the 11 regions with regional abundance data.

Dissimilarity between regions over time may in principle arise either due to species disappearing and new species arriving, i.e. replacement, or due to the shear addition or loss of species, i.e. change in richness (Baselga, 2010). In order to approach the causes of an observed change in beta diversity, such as human introduction or eradication of species and anthropogenically driven environmental change, we decomposed Jaccard dissimilarity within each region over time into replacement and richness change following Podani & Schmera (2011). Analyses were done using the "adespatial" package (Dray *et al.* 2017; Legendre 2014).

To assess individual species' tendency to gain or lose terrain over 140 years, we used Indicator Species Analysis (Dufrêne & Legendre 1997), as implemented in the "indicspecies" R package (De Cáceres & Legendre 2016). This approach was originally developed to associate species with groups of observational units such as sites, but may be used for any *a priory* classification. We used 'time slice' (historical or present) as cluster partitioning and region as observational unit. When assigning species to time slices, their relative abundance, distribution between time slices and occupancy in number of regions were considered (Dufrêne & Legendre 1997). Three groups of species were identified: significant indicators of historical data ('losers'), significant indicators of present data ('winners') and species not significant indicators of either period, with p-values obtained by permutation test (10,000 randomizations; $\alpha < 0.05$). To compare historically 'losing' species in the 14 Danish regions with the trend in countries with similar abiotic conditions, biota and land-use history, red-list status for all relevant species was compiled for nine North European countries or regions: Norway, Sweden, Germany, United Kingdom, the Netherlands, Flanders and Brussels regions (Belgium), Wallonia (Belgium), the Czech Republic and the Wielkopolska region (Poland). We tested for association between the three groups of temporal response and the six IUCN red-list categories (transformed to a semi-quantitative scale (0 = Least concern (LC), 1 = Near threatened (NT), 2 = Vulnerable (VU), 3= Endangered (EN), 4 = Critically endangered (CR), 5 = Regionally extinct (RE)), and these figures were summed per species over countries to give a "species conservation index"). This index was then used as a predictor in a cumulative logit model (in the R package "ordinal", Christensen 2015) of species' status as significant loser, winner or stable species. This model treats data appropriately as categorical without assuming the distance between categories to be equal (Agresti 2012).

Results

Plant species composition in all 14 regions showed dramatic changes over the past 140 years. At the regional level, colonization by far exceeded extinction (Fig. 1B). Historically there were 1367 species in total across these regions, and now there are 1822 species. On average, 327 new species were added, while 125 species were lost, resulting in an average net increase of 202 species per region (Fig. 1, Table S2). All regions harboured more species in the 21st Century than they did in the 19th. Appearance rate for exotic species was 0.66 (±0.03), much higher than the disappearance rate of 0.11 (±0.01) (Fig. 1C & D; for number of species see Table S3). For natives in contrast, mean appearance rate was only 0.17 (±0.04), while a disappearance rate of 0.12 (±0.01) was similar to that for exotic species (Fig. 1C & D; Table S3). Overall, the proportion of exotic species increased from making up 25% of the reported species in historical data to 45% in present data. Changes in composition were significant for all turnover metrics, based on incidence or abundance data alike (Fig. 2; Fig. S2 and S3). On average, regions had an overlap in plant species composition of only 44% between the two time periods (Jaccard dissimilarity: 36-67%; Table S4). For most regions, the large dissimilarity was primarily caused by replacement of species, with the main exception being the historically species poor islands of Læsø and Anholt (regions 7 and 8), on which changes were rather caused by increased richness (Mean proportion for all regions, replacement: 0.228, richness: 0.208; Fig. S4).

The change to biotas was highly systematic: species composition in all regions changed largely in the same direction (Fig. 2). This shift is consistent despite differences between regions in soils, climate and land use (Hartvig & Vestergaard 2015; Statistics Denmark 2018). The directional shift was equally apparent for native and exotic species (Fig. 2; Fig. S3). In general, native species that historically had relatively high occupancy expanded to inhabit all or most regions, while many natives with historically low occupancy in number of regions (Fig. 3A) and low historical abundance within regions (Fig. S8) plummeted or were lost. Similarly, a common pool of exotic species escaped cultivation and became naturalized across regions (Fig. 3B, Fig. S8).

The flora across regions experienced strong biotic homogenization, i.e. beta diversity between the 14 regions declined (Fig. 2, Fig. S2 and S3). The median of the distance to the spatial median was always lower for present than historical data (Fig. S5, S6 and S7). However, the difference between present and historical homogeneity was only significant when abundance data was considered (Fig. S6 and S7 B-D). The fact that loss of beta diversity was significant for quantitative measures only indicates that homogenization was driven particularly by increased abundance of species already relatively common. Our conservative control analysis, using only three abundance categories, yielded very similar results: Significant directional change over time (Fig. S9) as well as biotic homogenization (Fig. S10). Despite large variation in area between regions, we found areal extent to have no detectable effect on turnover metrics (Fig. S11).

Fifty species were found to be significant losers in terms of regional abundance and occupancy across regions, while 236 species were significant winners. A total of 1672 species had no significant association to any of the time slices (Table 1, Table S5). Of the losing species, 90% are listed as threatened in nine neighbouring North European countries (Table 1). Conversely, among the winning species, 20 % were listed as threatened in neighbouring countries, which is a significantly lower percentage ($z = -12.3$, $p << 0.001$, Table S6).

Discussion

While the unfolding of a global 'extinction crisis' is widely accepted, there is controversy over the direction of recent local to regional biodiversity change (Thomas 2013; Dornelas *et al.* 2014; Gonzalez *et al.* 2016; Vellend *et al.* 2017b; Cardinale *et al.* 2018). We used 14 regional floras from Denmark to assess net change in plant species richness and composition over 140 years, during which land use has been radically transformed. For all study regions, we find great losses but even greater gains, resulting in a ubiquitous net increase in regional plant species richness. All study regions include approximately the same suite of land-use types, some of which have increased in areal coverage over the 140 year study period, e.g. plantation forest, while others have decreased, e.g. natural grasslands. Thus, the criticism of a bias towards extant pristine area and away from areas converted to arable land or concrete (Cardinale *et al.* 2018) does not apply to our study. Our analysis has a balanced representation of species, habitat and land-use change types, and includes natural areas that have been completely altered. Despite this improved ability to detect and correctly estimate losses, we find a net gain in species richness, because losses are more than outbalanced by gains. This positive balance applies non-native species in all regions as well as native species in six of 14 regions.

Using 19th-century legacy data allows us to set an earlier baseline than most other studies (e.g. Keith *et al.* 2009; Vellend *et al.* 2013; Dornelas *et al.* 2014), and thereby enables a reliable assessment of biodiversity change beyond short-term fluctuations. On average, only a little more than half of the species in regional floras were constant over time, evidencing both substantial species losses and dramatic compositional change. Replacement of species, rather than richness changes, played the largest role for compositional change in most regions, with the remote and previously species poor island of Læsø and Anholt as exceptions (region 7 and 8). The observed compositional turnover was considerably larger than levels found in studies over shorter time spans (Smart et al. 2006; Alstad et al. 2016). Our data did not allow estimation of changing turnover rates, but our results nevertheless indicate a cumulative effect on species turnover as time progresses.

The compositional changes found were markedly unidirectional (Fig. 2), despite some initial between-region variation in dominant soil type and local climate. These parallel changes in species composition suggests a strong effect of similar land-use change across regions. The most likely drivers are 1) intensification of agriculture, 2) use of a common pool of woody species for afforestation and landscaping, and 3) escape of numerous exotic ornamental plant species commonly grown in gardens across Denmark, in fact across much of Europe (van Kleunen *et al.* 2015). An additional effect of climate change seems likely, with the winner species that are listed as threatened in neighbouring countries as potential examples of climate-driven changes.

The direction of change was clear: from regionally unique species towards ubiquitous species. The group of winners consists of plant species, exotic and native alike, that were relatively widespread and abundant by the mid-19th century, along with more recently introduced species, in particular garden-escapes (occupancy change Fig. 3A & B, abundance change Fig. S8). In contrast, loser species were mainly historically rare and range-restricted native species. The features common to winner species probably lie in their habitat requirements and evolutionary strategies, rather than their biogeographic origin. This is aligned with studies documenting certain plant traits, such as nitrophily and weedy lifestyle, to be associated with success in human-altered landscapes (McCune & Vellend 2013; Timmermann *et al.* 2015). Along this line of evidence, numerous stress-tolerant plant species (with traits similar to loosing native species) have been introduced as rock garden ornamentals, but almost none of these exotics have spread into the wild (Weidema 2000). This observation indicates that anthropogenic land-use change, rather than competitive effects of invasive plant species, is the main driver of the compositional changes. In other words, the exotic species are passengers rather than drivers of the observed biotic change at the regional scale (Didham *et al*. 2005, Thomas & Palmer 2015). In present data, we found a high proportion of species being exotic (45%), much higher than the figure reported for Great Britain (20%; Thomas & Palmer 2015). However, our historical and present surveys cover all types of habitat, including urban brownfields, railway yards and greenspace near gardens, not just natural habitat types, in which only about 5 % of the plant species are exotic (Danish national nature surveillance programme, unpublished data).

Vascular plants proved well suited to assessments of biotic change, not the least because of a bulk of accurate and reliable legacy data. However, plants are – in contrast to most other taxa – heavily traded and planted for ornament, and many escape into the wild (Dehnen-Schmutz *et al.* 2007). Thus, among other taxa, the contribution of naturalized escapes to outbalancing the losses of native species is probably much smaller than we have observed for plants.

On the background of global biodiversity loss, the consistent net gain in regional richness may be perceived as unambiguously positive. However, gains do not necessarily compensate losses, as we do not see replacement of like with like. For example, replacing species that represent distinct evolutionary lineages with novel species is effectively habitat loss for many specialist phytophagous and pollinating insects (Eskildsen *et al.* 2015). Moreover, the species that have lost ground in Denmark are similar across Northern Europe at large, making the long-term systematic changes relevant to biodiversity conservation at larger scales.

We found strong homogenization of species composition between regions to have taken place over time, driven by increased occupancy of a mixture of native and exotic species. Biotic homogenization can be rapid (Magurran *et al.* 2015), is a global phenomenon across time and space (Baiser *et al.* 2012) and, for plants, often driven by the spread of ubiquitous native species (Keith *et al.* 2009; McCune & Vellend 2013). Homogenization of species composition between regions leads to impoverishment of larger-scale biotas (Smart *et al.* 2006), linking the regional increase in species richness to global loss of species (Sax & Gaines 2003) and thereby posing a serious concern for global biodiversity (Gossner *et al.* 2016; Groffman *et al.* 2017).

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IV. Figure legends and table

Figure 1. *The 14 study regions in Denmark and change in number of species from 1857-1883 to 2012.* A) Study region 1–14 (details in Table S1); B) Net change in total species number per region over 140 years (PERMANOVA, $F = 6.23$, $r^2 = 0.63$, $p < 0.001$); C) Number of species appearing per region; D) Number of species disappearing per region. Colours and region numbers in panel B follow panel A. In panel C and D, native species (dark grey), exotic species (intermediate grey), and species of unknown status (light grey) are indicated.

Figure 2. *Species compositional change from historical (1857-1883) to present data (2012) in 14 Danish regions for: A) All species, B) Only exotic species, C) Only native species.* Principal Coordinates Analysis based on Jaccard dissimilarity. Blue squares are historical data, red triangles present data. Dotted lines are drawn between identical regions in historical and present data and numbers refer to regions in Fig. 1 and Table S1. Polygons are drawn around each time slice (historical = blue, present = red), with centroids marked with asterisks. Full grey lines mark the distance from each region to the centroid of each time-period. Historical species composition is significantly different from the contemporary species composition (PERMANOVAs: A) $p<0.001$; B) $p<0.001$; C) $p<0.01$. Relative eigenvalues of PCoA axis 1 (1) and PCoA axis 2 (2): A) 1=0.29, 2=0.17; B) 1=0.3, 2=14; C) 1=0.36, 2=0.12). For a comparison of distance to spatial median for all panels, see Fig. S5.

Figure 3. *Change in species' occupancy in 14 study regions over 140 years.* A. Native species, B. Exotic species. The upper panels compare present occupancy to historical. Historically common and newly introduced species have spread (position above the dotted 1:1 lines in A and B), while occupancy of many rare native species has decreased (position below the dotted 1:1 line in A). The

lower panels show the proportion of species in each historical category of occupancy that has increased (light green), decreased (dark red) or remained stable (grey) in occupancy over c. 140 years.

Table 1. *The proportion of species losing and winning in Denmark recorded as threatened in nine neighbouring NW European countries.* Significantly more species associated with the historical Danish flora are red-listed and significantly fewer associated with the contemporary Danish flora are red-listed (cumulative logit model; $p < 0.001$).

Species' trend	No. of species	Proportion of species red-listed in NW Europe
Loosing species	50	0.90
Stable species	1670	0.50
Winning species	236	0.20

Figure 1

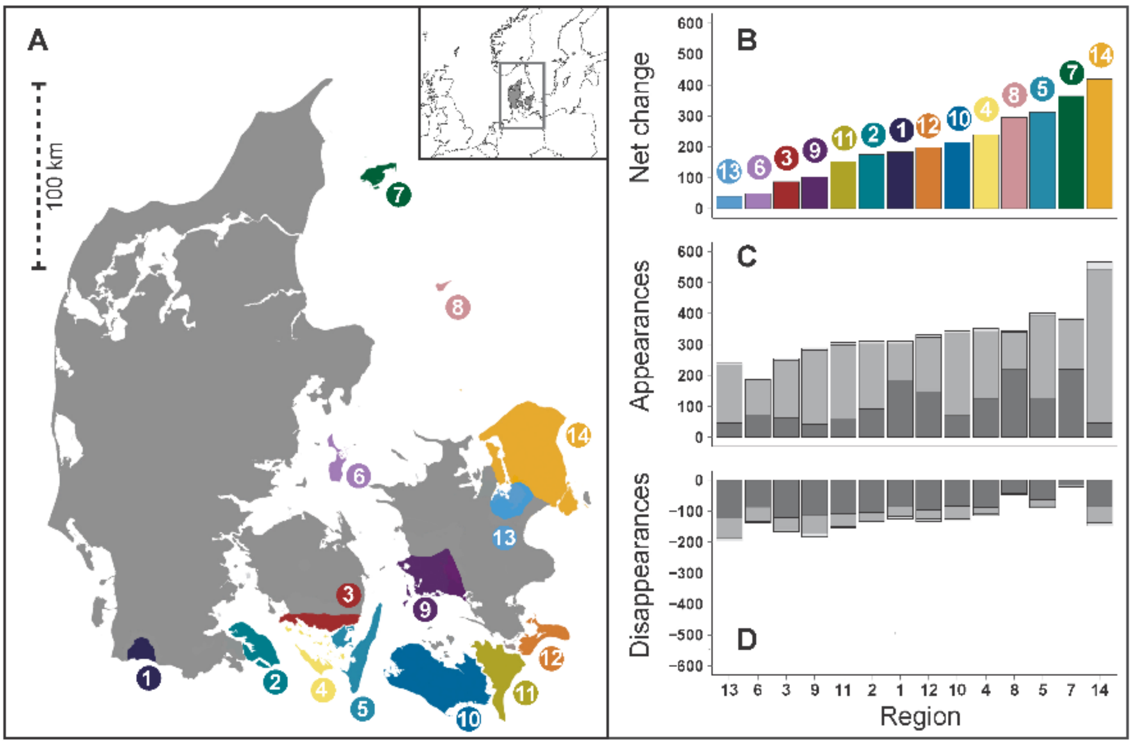
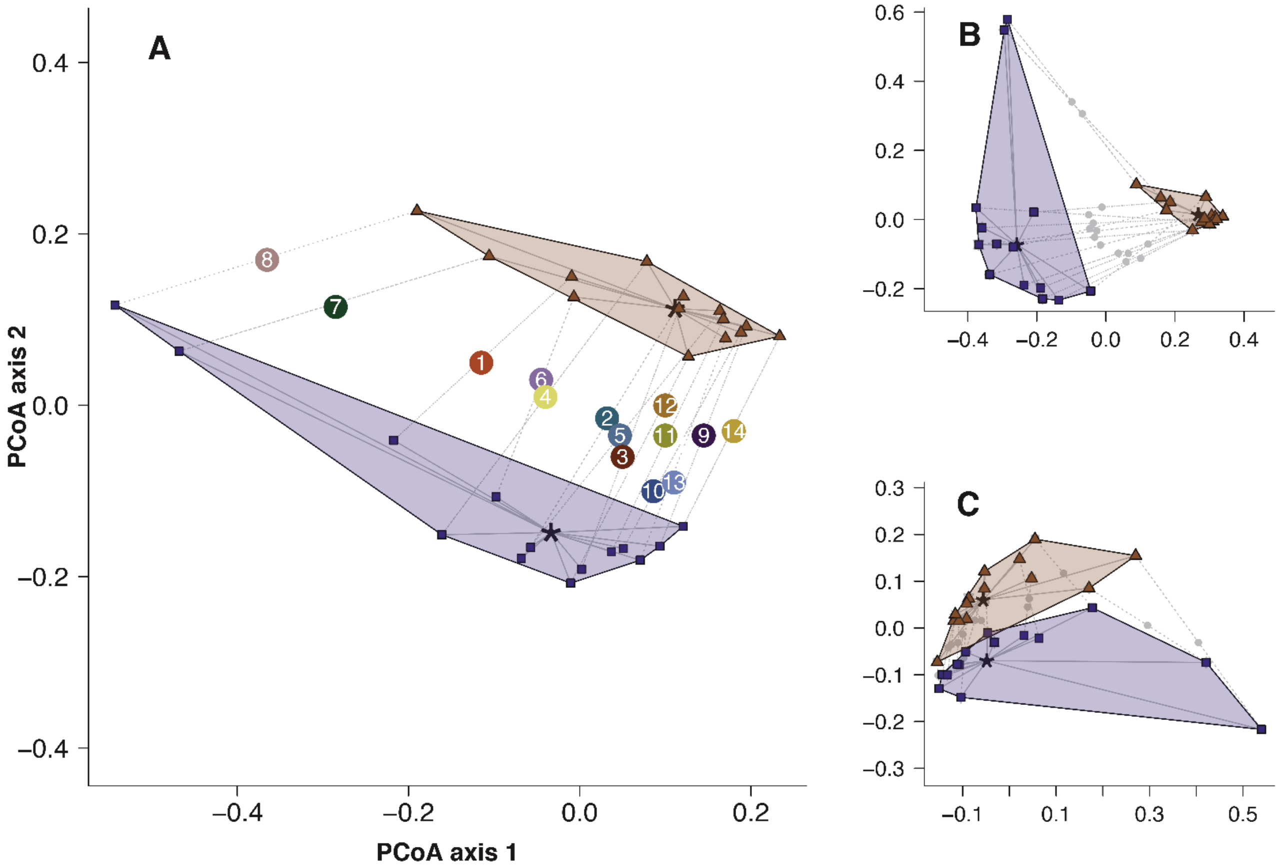


Figure 2


A
B
C
PCoA axis 1
PCoA axis 2
0.4
0.2
0.0
−0.2
−0.4
−0.4
−0.2
0.0
0.2
0.6
0.4
0.2
0.0
−0.2
−0.4
−0.2
0.0
0.2
0.4
0.3
0.2
0.1
0.0
−0.1
−0.2
−0.3
−0.1
0.1
0.3
0.5
1
2
3
4
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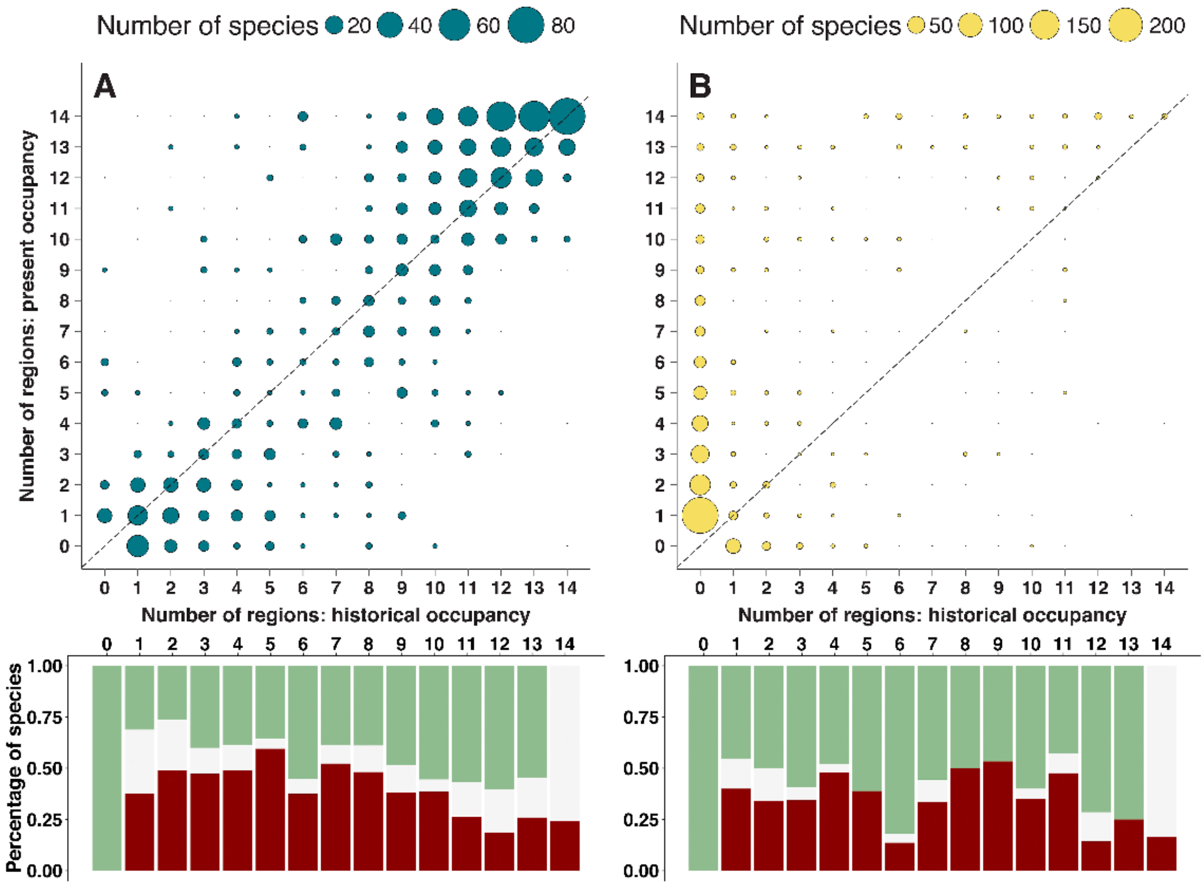
14

Figure 3


Number of species 20 40 60 80
Number of species 50 100 150 200
A
B
Number of regions: present occupancy
Number of regions: historical occupancy
Percentage of species
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14
0.00 0.25 0.50 0.75 1.00

Electronic Supplementary Material – Appendix 1

For the paper: More is Less: Net Gain in Species Richness, but Biotic Homogenization over 140 Years

By: Tora Finderup Nielsen, Kaj Sand-Jensen, Maria Dornelas & Hans Henrik Bruun

This file includes:

Supplementary Tables S1 to S6

Supplementary Figures S1 to S11

Supplementary tables

Table S1. *Historical landscape floras analyzed.* Details on author, area and year published as well as number of reference grid cells in present data and the number of species in historical and present data. Numbers refer to Fig. 1.

Number – Region name	Author, profession	Area	Published	Regional abundance	Year issued	Area km^2	#reference grid-cells, ref. 27	#species historical data	#species present data
2 – Als[1]	Petit, E., counselor	Island of Als	Yes	No	1881	312	12	713	887
8 – Anholt[2]	Jacobsen, J. P., novelist	Island of Anholt	Yes	No	1880	22	3	237	535
11 – Falster[3]	Koch, H. P. G.; provost	Island of Falster	Yes	Yes	1862	450	19	906	1058
7 – Læsø[2]	Jacobsen, J. P., novelist	Island of Læsø	Yes	No	1880	118	7	353	787
10 – Lolland[4]	Rostrup, E., professor	Island of Lolland	Yes	Yes	1864	1250	47	928	1143
12 – Møn[5]	Petit, E., counselor	Island of Møn	No	Yes	1883	218	14	758	954
14 – NE Zealand[6]	Mortensen, H., college teacher	Peninsulas between the Sound and Isefjord	Yes	Yes	1872	1816	95	1222	1643
13 – Roskilde[7]	Thomsen, C., lecturer	Area around the city of Roskilde	Yes	Yes	1874	312	10	949	995
6 – Samsø[8]	Thomsen, C., lecturer	Island of Samsø	Yes	Yes	1876	113	6	693	746

9 – SW Zealand[9]	Nielsen, P.	South western part of Sealand	Yes	Yes	1873	794	23	1024	1134
3 – South Funen Mainland[10]	Lange, M. T.; priest	Southern part of Funen	Yes	Yes	1857	210	10	834	925
5 – South Funen, forest islands[10]	Lange, M. T.; priest	Islands south of Funen: Langeland, Thurø, Tåsinge	Yes	Yes	1857	350	18	704	1019
4 – South Funen, non-forest islands[10]	Lange, M. T.; priest	Islands south of Funen: Ærø, Lyø, Avernakø, Drejø, Strynø, Skarø, Bjørnø, Birkholm	Yes	Yes	1857	110	15	587	825
1 – Tønder[11]	Stoltenberg, N., college teacher	Area around the town of Tønder	Yes	Yes	1877	170	6	525	707

[1]Udkast til en floristisk Beskrivelse af Als, E. Petit, 1881, Botanisk Tidsskrift 12: 13-41.

[2]Fortegnelse over de på Læsø og Anholt i 1870 fundne planter, J. C. Jacobsen, 1880, Botanisk Tidsskrift 11: 88-113.

[3]Om Falsters Vegetation, H. P. G. Koch, 1862, Videnskabelige Meddelelser fra den Naturhistoriske Forening i Kjøbenhavn 1862: 79-152.

[4]Lollands Vegetationsforhold, E. Rostrup, 1864, Videnskabelige Meddelelser fra den Naturhistoriske Forening i Kjøbenhavn 1864: 37-119.

[5]Fortegnelse over Møens Pfanerogamer og Kryptogamer, E. Petit, manuscript kept in the Natural History Museum of Denmark, Copenhagen.

[6]Nordostsjællands Flora, H. Mortensen, 1872, Botanisk Tidsskrift 5: 8-168.

[7]Roskilde-Egnens Flora, C. Thomsen, 1874, Indbydelsesskrift til Afgangsprøven og Aarsprøven i Roskilde Katedralskole, H.A. Müller, Roskilde

[8]Sams-Øgruppens Plantevækst, C. Thomsen, 1876, Botanisk Tidsskrift 8: 86-142.

[9]Sydvestsjællands Vegetation, Nielsen P., 1872, Botanisk Tidsskrift 6: 261-388.

[10]Den Sydfyenske Øgaards Vegetation, M. T. Lange, 1857, Videnskabelige Meddelelser fra den Naturhistoriske Forening i Kjøbenhavn 1857: 199-272.

[11]Beitrag zur Kenntniß der Flora Tonderns, N. Stoltenberg, 1877, F. Dröhse Verlag, Tondern.

Table S2. *Turnover, all species.* Appearances, disappearances and total turnover in relative and actual number of species in all 14 regions. Numbers refer to Fig. 1 and Table S1. Total number of species in historical data can be calculated per region (rows), by subtracting appearances (col. 6) from total number of species (col. 5). For present data the total number of species per region can be calculated by subtracting disappearances (col. 7) from the total number of species (col. 5).

Number - Region	Relative appearances	Relative disappearances	Relative change, total	Total number of species, both time slices	Appearances, # species	Disappearances, # species	Total changes, # species
2 - Als	0.30	0.13	0.43	1021	307	134	173
8 - Anholt	0.59	0.08	0.67	582	344	48	296
11 - Falster	0.25	0.13	0.38	1210	302	152	150
10 - Lolland	0.27	0.10	0.37	1272	342	129	213
7 - Læsø	0.52	0.03	0.55	739	385	23	362
12 - Møn	0.30	0.12	0.42	1083	324	129	195
14 - NE Zealand	0.32	0.08	0.40	1787	563	143	420
13 - Roskilde	0.20	0.16	0.36	1188	237	193	44
4 - South Funen, non-forest islands	0.37	0.12	0.49	936	349	111	238
3 - South Funen, Mainland	0.23	0.15	0.38	1088	252	163	89
5 - South Funen, forest islands	0.36	0.08	0.44	1105	400	86	314
6 - Samsø	0.21	0.15	0.37	882	187	136	51
9 - SW Zealand	0.22	0.14	0.35	1311	285	177	108
1 - Tønder	0.37	0.15	0.52	830	305	123	182
All regions as one	0.30	0.07	0.37	1958	591	136	455
Average	0.32	0.12	0.44	1074	327	125	202

Table S3. *Turnover, native and exotic species.* Appearances, disappearances and total change in number of species for native and exotic species in all 14 regions, in all regions regarded as one and as an average across regions. Numbers refer to Fig. 1 and Table S1.

Number - Region	Native Appearances, # species	Native Disappearances, # species	Native Total changes, # species	Exotic Appearances, # species	Exotic Disappearances, # species	Exotic Total changes, # species
2 - Als	92	105	-13	209	27	182
8 - Anholt	221	42	179	119	5	114
11 - Falster	58	110	-52	239	41	198
10 - Lolland	70	84	-14	264	42	222
7 - Læsø	220	16	204	161	6	155
12 - Møn	148	97	51	175	29	146
14 - NE Zealand	46	85	-39	497	52	445
13 - Roskilde	46	123	-77	189	63	126
5 - South Funen, non-forest islands	124	88	36	218	21	197
3 - South Funen Mainland	62	121	-59	187	40	147
4 - South Funen, forest islands	127	64	63	268	21	247

6 - Samsø	74	87	-13	112	47	65
9 - SW Zealand	43	112	-69	239	60	179
1 - Tønder	184	85	99	117	33	84
All regions as one	27	57	-30	547	68	479
Average	108	87	21	214	35	179

Table S4. *Distance in Jaccard dissimilarity within area across time*. Ordered by increasing distance. Numbers refer to Fig. 1 and Table S1.

Number - Area	Jaccard dissimilarity
9 - SW Zealand	0.35
13 - Roskilde	0.36
6 - Samsø	0.36
10 - Lolland	0.37
11 - Falster	0.38
3 - South Funen Mainland	0.38
14 - NE Zealand	0.4
12 - Møn	0.42
2 - Als	0.43
4 - South Funen, forest islands	0.44
5 - South Funen, non-forest islands	0.49
1 - Tønder	0.52
7 - Læsø	0.55
8 - Anholt	0.67
Average	**0.44**

Table S5. *Loser and winner species.* Species significantly associated with Historical ("losers") and Present ("winners") in Indicator Species Analyses. This analysis compares species' regional abundance and frequency of occurrence at the two time slices. Each species receives an indicator value (range: 0-1) for each time slice. The higher of the two values is tested for statistical significance of the association using a permutation test (10,000 randomizations; α < 0.05). A total of 236 species were significantly associated with present data, 50 with historical data, while 1673 not were significantly associated with any time slice. Only the higher indicator value is shown and only species significantly associated to either historical or present.

The number of North European countries/regions, in which the species is redlisted, Species Conservation Index and the native status (nat = native; ex = exotic; NA = ambiguous) are given.

Species – consensus name	Indicator value	P-value	Sign.	Association	# countries redlisted	Species Conservation Index	Native status
Epilobium adenocaulon	1	1.00E-04	***	Present	0	0	ex
Galinsoga quadriradiata	1	1.00E-04	***	Present	0	0	ex
Lupinus polyphyllus	1	1.00E-04	***	Present	0	0	ex
Phedimus spurius	1	1.00E-04	***	Present	0	0	ex
Picea sitchensis	1	1.00E-04	***	Present	0	0	ex
Prunus cerasifera	1	1.00E-04	***	Present	0	0	ex
Rosa rugosa	1	1.00E-04	***	Present	0	0	ex
Solanum lycopersicum	1	1.00E-04	***	Present	0	0	ex
Chamomilla suaveolens	0.966	1.00E-04	***	Present	1	1	ex
Festuca trachyphylla	0.966	1.00E-04	***	Present	0	0	nat
Heracleum mantegazzianum coll.	0.966	1.00E-04	***	Present	0	0	ex
Prunus serotina	0.966	1.00E-04	***	Present	0	0	ex
Symphoricarpus albus	0.966	1.00E-04	***	Present	0	0	ex
Berberis thunbergii	0.964	1.00E-04	***	Present	0	0	ex
Cerastium biebersteinii_tormentisum	0.964	1.00E-04	***	Present	0	0	ex
Othocallis siberica	0.964	1.00E-04	***	Present	0	0	ex
Quercus rubra	0.964	1.00E-04	***	Present	0	0	ex
Reynoutria sachalinensis	0.964	1.00E-04	***	Present	0	0	ex
Reynoutria japonica	0.964	1.00E-04	***	Present	0	0	ex
Rosa glauca	0.964	1.00E-04	***	Present	1	3	ex
Symphytum xuplandicum	0.964	1.00E-04	***	Present	0	0	ex
Lactuca serriola	0.935	1.00E-04	***	Present	0	0	ex
Lunaria annua	0.935	1.00E-04	***	Present	0	0	ex
Senecio vernalis	0.935	1.00E-04	***	Present	0	0	ex
Alcea rosea	0.929	1.00E-04	***	Present	0	0	ex
Fragaria grandiflora_ananassa	0.929	1.00E-04	***	Present	0	0	ex
Galinsoga parviflora	0.929	1.00E-04	***	Present	0	0	ex
Helianthus annuus	0.929	1.00E-04	***	Present	0	0	ex
Lathyrus latifolius	0.929	0.0002	***	Present	1	2	ex
Ribes sanguineum	0.929	1.00E-04	***	Present	0	0	ex
Vicia sativa segetalis	0.929	1.00E-04	***	Present	0	0	ex

Brunnera macrophylla	0.926	1.00E-04	***	Present	0	0	ex
Clematis vitalba	0.926	1.00E-04	***	Present	0	0	ex
Epilobium lamyi	0.926	1.00E-04	***	Present	0	0	nat
Hedera hibernica	0.926	1.00E-04	***	Present	0	0	ex
Larix xmarschlinsii	0.926	1.00E-04	***	Present	0	0	ex
Oenothera glazioviana	0.926	1.00E-04	***	Present	0	0	ex
Phacelia tanacetifolia	0.926	0.0002	***	Present	0	0	ex
Rheum rhabarbarum	0.926	1.00E-04	***	Present	0	0	ex
Solidago gigantea	0.926	1.00E-04	***	Present	0	0	ex
Tulipa gesneriana	0.926	1.00E-04	***	Present	0	0	ex
Sorbus intermedia	0.907	1.00E-04	***	Present	0	0	nat
Muscari botryoides	0.897	1.00E-04	***	Present	0	0	int
Poa palustris	0.897	1.00E-04	***	Present	2	3	nat
Solidago canadensis	0.897	1.00E-04	***	Present	0	0	ex
Viola riviniana	0.897	0.0003	***	Present	1	2	nat
Impatiens parviflora	0.889	0.0004	***	Present	0	0	ex
Lysimachia punctata	0.889	0.0002	***	Present	0	0	ex
Melissa officinalis	0.889	1.00E-04	***	Present	0	0	ex
Buddleja davidii	0.886	1.00E-04	***	Present	0	0	ex
Cornus alba s.l.	0.886	1.00E-04	***	Present	0	0	ex
Hyacinthoides italica	0.886	1.00E-04	***	Present	0	0	ex
Impatiens glandulifera	0.886	1.00E-04	***	Present	0	0	ex
Leucanthemum x*superbum*	0.886	1.00E-04	***	Present	0	0	ex
Mahonia aquifolium	0.886	0.0002	***	Present	0	0	ex
Muscari armeniacum	0.886	1.00E-04	***	Present	0	0	ex
Populus x*berolinensis*	0.886	1.00E-04	***	Present	0	0	ex
Pseudofumaria lutea	0.886	1.00E-04	***	Present	0	0	ex
Rhus typhina	0.886	1.00E-04	***	Present	0	0	ex
Rosa multiflora	0.886	1.00E-04	***	Present	1	5	ex
Scilla luciliae coll.	0.886	1.00E-04	***	Present	0	0	ex
Taxus x*media*	0.886	1.00E-04	***	Present	0	0	ex
Vulpia myurus	0.886	0.0002	***	Present	0	0	ex
Rumex thyrsiflorus	0.882	0.0002	***	Present	0	0	nat
Stellaria pallida	0.882	0.0002	***	Present	1	4	nat
Hyacinthoides non-scripta	0.869	0.0005	***	Present	0	0	ex
Nicandra physalodes	0.869	0.0002	***	Present	0	0	ex
Pinus mugo s.l.	0.869	0.0004	***	Present	0	0	ex
Oxalis stricta	0.858	0.0007	***	Present	0	0	ex
Picea abies	0.858	0.0003	***	Present	0	0	nat
Senecio viscosus	0.858	0.0008	***	Present	1	2	nat
Solanum tuberosum	0.858	0.0004	***	Present	0	0	ex

Vinca minor	0.858	0.0004	***	Present	0	0	ex
Allium schoenoprasum	0.857	0.0005	***	Present	0	0	nat
Physalis alkekengi	0.857	0.0004	***	Present	0	0	ex
Chenopodium ficifolium	0.849	0.0005	***	Present	0	0	ex
Oxalis corniculata	0.849	0.0004	***	Present	0	0	nat
Rosa virginiana	0.849	1.00E-04	***	Present	0	0	ex
Ambrosia artemisiifolia	0.845	0.0002	***	Present	0	0	ex
Arum italicum	0.845	1.00E-04	***	Present	1	1	ex
Calystegia pulchra	0.845	0.0002	***	Present	0	0	ex
Cotoneaster bullatus	0.845	0.0002	***	Present	0	0	ex
Cotoneaster divaricatus	0.845	0.0002	***	Present	0	0	ex
Diplotaxis muralis	0.845	0.0004	***	Present	1	1	nat
Doronicum xexcelsum	0.845	1.00E-04	***	Present	0	0	ex
Forsythia xintermedia	0.845	0.0002	***	Present	0	0	ex
Phytolacca acinosa	0.845	0.0002	***	Present	0	0	ex
Picea glauca	0.845	0.0003	***	Present	0	0	ex
Ulmus xhollandica	0.845	1.00E-04	***	Present	0	0	ex
Zea mays	0.845	0.0003	***	Present	0	0	ex
Digitalis purpurea	0.843	0.0011	**	Present	0	0	nat
Echinochloa crus-galli	0.843	0.0013	**	Present	0	0	ex
Narcissus poeticus	0.843	0.0014	**	Present	0	0	ex
Rosa dumalis	0.843	0.0016	**	Present	2	4	nat
Sedum album	0.843	0.0018	**	Present	0	0	nat
Helianthus tuberosus	0.828	0.0014	**	Present	0	0	ex
Hippophae rhamnoides	0.828	0.0016	**	Present	0	0	nat
Salix daphnoides s.l.	0.828	0.0021	**	Present	3	9	ex
Galium xpomeranicum	0.819	0.0043	**	Present	0	0	nat
Geranium pyrenaicum	0.819	0.0047	**	Present	0	0	ex
Lychnis coronaria	0.815	0.0018	**	Present	0	0	ex
Matteuccia struthiopteris	0.815	0.0024	**	Present	4	12	nat
Pilosella aurantiaca	0.815	0.0018	**	Present	1	2	ex
Taxus baccata	0.815	0.0016	**	Present	4	10	nat
Telekia speciosa	0.815	0.0015	**	Present	0	0	ex
Rorippa microphylla	0.806	0.002	**	Present	3	10	nat
Amelanchier spicata	0.802	0.0007	***	Present	0	0	ex
Bromopsis inermis	0.802	0.0006	***	Present	0	0	ex
Centaurea dealbata	0.802	0.0005	***	Present	0	0	ex
Dipsacus strigosus	0.802	0.0005	***	Present	0	0	ex
Elodea canadensis	0.802	0.0007	***	Present	1	3	ex
Epilobium ciliatum	0.802	0.0008	***	Present	0	0	ex
Euphorbia cyparissias	0.802	0.0002	***	Present	0	0	nat

Laburnum alpinum	0.802	0.0005	***	Present	0	0	ex
Lepidium draba	0.802	0.0005	***	Present	1	1	ex
Mahonia x*decumbens*	0.802	0.0006	***	Present	0	0	ex
Narcissus tazetta	0.802	0.0004	***	Present	0	0	ex
Symphoricarpos x*chenaultii*	0.802	0.0005	***	Present	0	0	ex
Beta vulgaris maritima	0.786	0.0073	**	Present	1	2	nat
Bromopsis erecta	0.786	0.0071	**	Present	1	1	nat
Antirrhinum majus	0.772	0.0061	**	Present	0	0	ex
Beta vulgaris	0.772	0.0064	**	Present	2	3	ex
Erigeron annuus	0.772	0.0045	**	Present	0	0	ex
Pinus nigra	0.772	0.0062	**	Present	0	0	ex
Robinia pseudoacacia	0.761	0.0039	**	Present	0	0	ex
Setaria pumila	0.761	0.0047	**	Present	0	0	ex
Viola xwittrockiana	0.761	0.0038	**	Present	1	1	ex
Cymbalaria muralis	0.759	0.0215	*	Present	0	0	ex
Juglans regia	0.759	0.0212	*	Present	0	0	ex
Silene noctiflora	0.759	0.0194	*	Present	6	15	nat
Abies procera	0.756	0.0024	**	Present	0	0	ex
Asarum europaeum	0.756	0.0012	**	Present	1	2	ex
Barbarea intermedia	0.756	0.0025	**	Present	0	0	nat
Centranthus ruber	0.756	0.0022	**	Present	1	1	ex
Chamaecyparis lawsoniana	0.756	0.0023	**	Present	0	0	ex
Fallopia baldschuanica	0.756	0.0015	**	Present	0	0	ex
Helianthus x*laetiflorus*	0.756	0.0018	**	Present	0	0	ex
Hyacinthus orientalis	0.756	0.0012	**	Present	0	0	ex
Iberis umbellata	0.756	0.0023	**	Present	0	0	ex
Miscanthus sinensis	0.756	0.0021	**	Present	0	0	ex
Petasites japonicus	0.756	0.0026	**	Present	0	0	ex
Phalaris arundinacea cult.	0.756	0.0016	**	Present	0	0	ex
Populus x*wettsteinii*	0.756	0.0014	**	Present	0	0	ex
Pseudotsuga menziesii	0.756	0.002	**	Present	0	0	ex
Sisymbrium altissimum	0.756	0.002	**	Present	1	2	ex
Sorbaria sorbifolia	0.756	0.0017	**	Present	0	0	ex
Vinca major	0.756	0.0012	**	Present	0	0	ex
Atriplex longipes	0.741	0.0205	*	Present	1	3	nat
Centaurea montana	0.741	0.0185	*	Present	1	2	ex
Leucojum vernum	0.741	0.0225	*	Present	3	9	ex
Rhamnus catharticus	0.741	0.0216	*	Present	0	0	nat
Rorippa sylvestris	0.741	0.0203	*	Present	0	0	nat
Veronica longifolia	0.741	0.0215	*	Present	3	6	ex
Amaranthus hybridus	0.725	0.0173	*	Present	0	0	ex

Crocus vernus	0.725	0.0171	*	Present	0	0	ex
Panicum miliaceum	0.725	0.0187	*	Present	0	0	ex
Poterium sanguisorba	0.725	0.0176	*	Present	0	0	NA
Fritillaria imperialis	0.713	0.0123	*	Present	0	0	ex
Abies grandis	0.707	0.0048	**	Present	0	0	ex
Abies nordmanniana	0.707	0.0058	**	Present	0	0	ex
Aconitum xstoerkianum	0.707	0.0048	**	Present	0	0	ex
Amaranthus retroflexus	0.707	0.0052	**	Present	0	0	ex
Claytonia perfoliata	0.707	0.0055	**	Present	0	0	ex
Cotoneaster dielsianus	0.707	0.0055	**	Present	0	0	ex
Echinops bannaticus	0.707	0.0065	**	Present	0	0	ex
Hemerocallis fulva	0.707	0.0059	**	Present	0	0	ex
Lonicera pileata	0.707	0.0057	**	Present	0	0	ex
Malus toringo sargentii	0.707	0.0053	**	Present	0	0	ex
Othocallis amoena	0.707	0.0056	**	Present	0	0	ex
Poa bulbosa	0.707	0.0065	**	Present	4	9	nat
Prunus laurocerasus	0.707	0.0052	**	Present	0	0	ex
Rosa rubiginosa cult.	0.707	0.0052	**	Present	0	0	ex
Symphyotrichum novi-belgii	0.707	0.0055	**	Present	0	0	ex
Symphytum caucasicum	0.707	0.0059	**	Present	0	0	ex
Tropaeolum majus	0.707	0.0055	**	Present	0	0	ex
Stellaria neglecta	0.694	0.0499	*	Present	2	3	nat
Cerastium glutinosum	0.676	0.0444	*	Present	2	5	nat
Lilium martagon	0.676	0.0434	*	Present	1	1	ex
Abutilon theophrasti	0.655	0.0171	*	Present	0	0	ex
Anemone blanda	0.655	0.0144	*	Present	0	0	ex
Arenaria leptoclados	0.655	0.0157	*	Present	1	4	nat
Aubrieta xcultorum	0.655	0.0155	*	Present	0	0	ex
Caragana arborescens	0.655	0.0158	*	Present	0	0	ex
Cosmos bipinnatus	0.655	0.0158	*	Present	0	0	ex
Crataegus rhipidophylla	0.655	0.0159	*	Present	1	5	nat
Cucurbita pepo	0.655	0.0158	*	Present	0	0	ex
Diplotaxis tenuifolia	0.655	0.0145	*	Present	0	0	ex
Echinops exaltatus	0.655	0.0161	*	Present	0	0	ex
Eschscholzia californica	0.655	0.0146	*	Present	0	0	ex
Fragaria vesca cult.	0.655	0.0145	*	Present	0	0	ex
Helleborus foetidus	0.655	0.0152	*	Present	1	2	ex
Lavandula angustifolia	0.655	0.0141	*	Present	0	0	ex
Lychnis chalcedonica	0.655	0.0143	*	Present	0	0	ex
Malus prunifolia	0.655	0.0144	*	Present	0	0	ex
Parthenocissus inserta	0.655	0.0166	*	Present	0	0	ex

Pinus contorta	0.655	0.016	*	Present	0	0	ex
Polypodium interjectum	0.655	0.0147	*	Present	5	10	nat
Puschkinia scilloides	0.655	0.0152	*	Present	0	0	ex
Rubus spectabilis	0.655	0.0182	*	Present	0	0	ex
Rudbeckia laciniata	0.655	0.0147	*	Present	0	0	ex
Sorghum halepense	0.655	0.0158	*	Present	0	0	ex
Thuja plicata	0.655	0.0161	*	Present	0	0	ex
Tsuga heterophylla	0.655	0.0159	*	Present	0	0	ex
Viburnum lantana	0.655	0.0144	*	Present	2	2	ex
Allium hollandicum	0.598	0.0375	*	Present	0	0	ex
Anaphalis margaritacea	0.598	0.0402	*	Present	0	0	ex
Aruncus dioicus	0.598	0.0419	*	Present	1	1	ex
Aster xversicolor	0.598	0.0412	*	Present	0	0	ex
Bergenia cordifolia coll.	0.598	0.0389	*	Present	0	0	ex
Carex pendula	0.598	0.0402	*	Present	2	6	nat
Chaenomeles japonica	0.598	0.0392	*	Present	0	0	ex
Cotoneaster horizontalis	0.598	0.0447	*	Present	0	0	ex
Cotoneaster lucidus	0.598	0.0366	*	Present	0	0	ex
Crocus xstellaris	0.598	0.0406	*	Present	0	0	ex
Dicentra formosa	0.598	0.0412	*	Present	0	0	ex
Echium plantagineum	0.598	0.039	*	Present	0	0	ex
Eruca vesicaria sativa	0.598	0.0362	*	Present	0	0	ex
Eryngium planum	0.598	0.0402	*	Present	1	4	ex
Helleborus orientalis	0.598	0.0383	*	Present	0	0	ex
Lonicera tatarica	0.598	0.0415	*	Present	0	0	ex
Luzula sylvatica	0.598	0.0416	*	Present	1	2	nat
Papaver setiferum	0.598	0.0413	*	Present	0	0	ex
Parietaria judaica	0.598	0.0399	*	Present	1	3	ex
Pentaglottis sempervirens	0.598	0.0429	*	Present	0	0	ex
Populus deltoides	0.598	0.0375	*	Present	0	0	ex
Potentilla indica	0.598	0.0384	*	Present	0	0	ex
Prunus mahaleb	0.598	0.0403	*	Present	1	3	ex
Pulmonaria rubra	0.598	0.0412	*	Present	0	0	ex
Rosa spinosissima cult.	0.598	0.0406	*	Present	0	0	ex
Sedum forsterianum	0.598	0.0377	*	Present	1	3	ex
Setaria italica	0.598	0.0399	*	Present	0	0	ex
Spinacia oleracea	0.598	0.0429	*	Present	0	0	ex
Stachys byzantina	0.598	0.0396	*	Present	0	0	ex
Symphytum grandiflorum	0.598	0.0415	*	Present	0	0	ex
Tagetes patula	0.598	0.0399	*	Present	0	0	ex
Verbascum speciosum	0.598	0.0402	*	Present	0	0	ex

Veronica scutellata	0.935	1.00E-04	***	Historical	2	2	nat
Camelina sativa	0.929	1.00E-04	***	Historical	2	7	nat
Lolium temulentum	0.886	1.00E-04	***	Historical	6	24	nat
Agrostemma githago	0.882	0.0002	***	Historical	5	19	nat
Pedicularis palustris	0.882	0.0002	***	Historical	5	18	nat
Camelina alyssum	0.845	0.0003	***	Historical	5	25	ex
Lolium remotum	0.845	0.0003	***	Historical	6	30	ex
Marrubium vulgare	0.845	0.0002	***	Historical	6	21	nat
Parnassia palustris	0.828	0.0017	**	Historical	5	15	nat
Fagopyrum tataricum	0.806	0.0016	**	Historical	1	5	ex
Bromus secalinus	0.802	0.0075	**	Historical	5	15	nat
Cuscuta epithymum trifolii	0.802	0.0007	***	Historical	0	0	ex
Lythrum portula	0.802	0.0061	**	Historical	2	3	nat
Anacamptis morio	0.786	0.0077	**	Historical	5	16	nat
Dianthus armeria	0.786	0.008	**	Historical	7	15	nat
Galeopsis ladanum	0.786	0.0094	**	Historical	4	8	nat
Chenopodium murale	0.761	0.0045	**	Historical	6	15	nat
Chenopodium urbicum	0.761	0.0048	**	Historical	4	15	nat
Cystopteris fragilis	0.761	0.0053	**	Historical	2	3	nat
Gentianella campestris	0.761	0.0052	**	Historical	8	27	nat
Veronica opaca	0.761	0.0039	**	Historical	5	19	nat
Antennaria dioica	0.759	0.0229	*	Historical	6	20	nat
Rorippa nasturtium-aquaticum	0.759	0.0201	*	Historical	3	7	nat
Cuscuta epilinum	0.756	0.0024	**	Historical	5	25	ex
Neslia paniculata	0.756	0.002	**	Historical	2	6	nat
Pulicaria vulgaris	0.756	0.0018	**	Historical	6	24	nat
Rhamnus cathartica	0.756	0.0021	**	Historical	0	0	nat
Verbena officinalis	0.741	0.0219	*	Historical	1	2	ex
Veronica triphyllos	0.741	0.0225	*	Historical	5	14	nat
Eriophorum latifolium	0.725	0.0194	*	Historical	6	19	nat
Ranunculus circinatus	0.713	0.0147	*	Historical	2	7	nat
Avena strigosa	0.707	0.0056	**	Historical	2	10	ex
Medicago lupulina willdenowii	0.707	0.0061	**	Historical	0	0	nat
Larix decidua	0.676	0.0465	*	Historical	0	0	ex
Limosella aquatica	0.676	0.0465	*	Historical	4	7	nat
Nepeta cataria	0.676	0.049	*	Historical	4	9	nat
Potamogeton alpinus	0.676	0.0449	*	Historical	6	17	nat
Eleocharis acicularis	0.661	0.0318	*	Historical	2	7	nat
Herminium monorchis	0.661	0.0338	*	Historical	8	29	nat
Arnoseris minima	0.655	0.0139	*	Historical	7	27	nat
Campanula rapunculus	0.655	0.0142	*	Historical	2	5	nat

Ranunculus arvensis	0.655	0.0167	*	Historical	7	21	nat
Carduus nutans	0.598	0.0401	*	Historical	2	2	nat
Crepis setosa	0.598	0.0411	*	Historical	1	4	ex
Elsholtzia cristata	0.598	0.0419	*	Historical	0	0	ex
Filago lutescens	0.598	0.0399	*	Historical	7	27	nat
Neotinea ustulata	0.598	0.0409	*	Historical	6	26	nat
Persicaria mitis	0.598	0.0382	*	Historical	2	4	nat
Scandix pecten-veneris	0.598	0.0405	*	Historical	8	30	nat
Spergula arvensis maxima	0.598	0.0445	*	Historical	3	15	ex

Table S6. *Summary statistics loser and winner species.* Numbers and proportion of species being winners, stable and losers (identified by Indicator Species Analyses) in categories of a "species conservation index", which is based on red-list threat category in nine neighboring North European countries and provinces.

	0		**1-10**		**11-20**		**21-30**		**Total Red Listed (NT-RE)**		**Median Species Conservation Index**
	No. Sp.	Prop. of species in association	No. Sp.	Prop.	No. Sp.	Prop.	No. Sp.	Prop.	**No. Sp.**	**Prop.**	
Sign_Present	190	0.81	44	0.19	2	0.01	0	0.00	**46**	**0.20**	**0**
No_Assoc	831	0.50	640	0.38	170	0.10	29	0.02	**839**	**0.50**	**1**
Sign_Historical	50	0.10	18	0.36	14	0.28	13	0.26	**45**	**0.90**	**15**

Supplementary figures

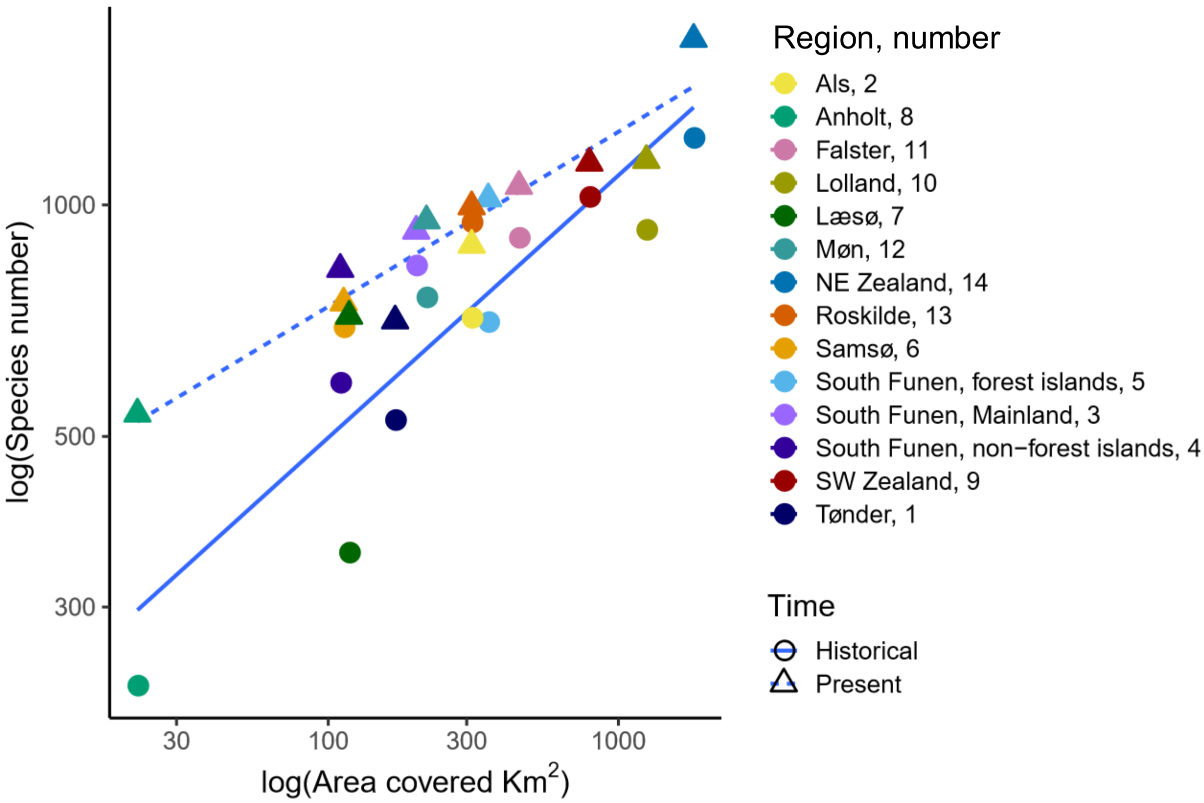
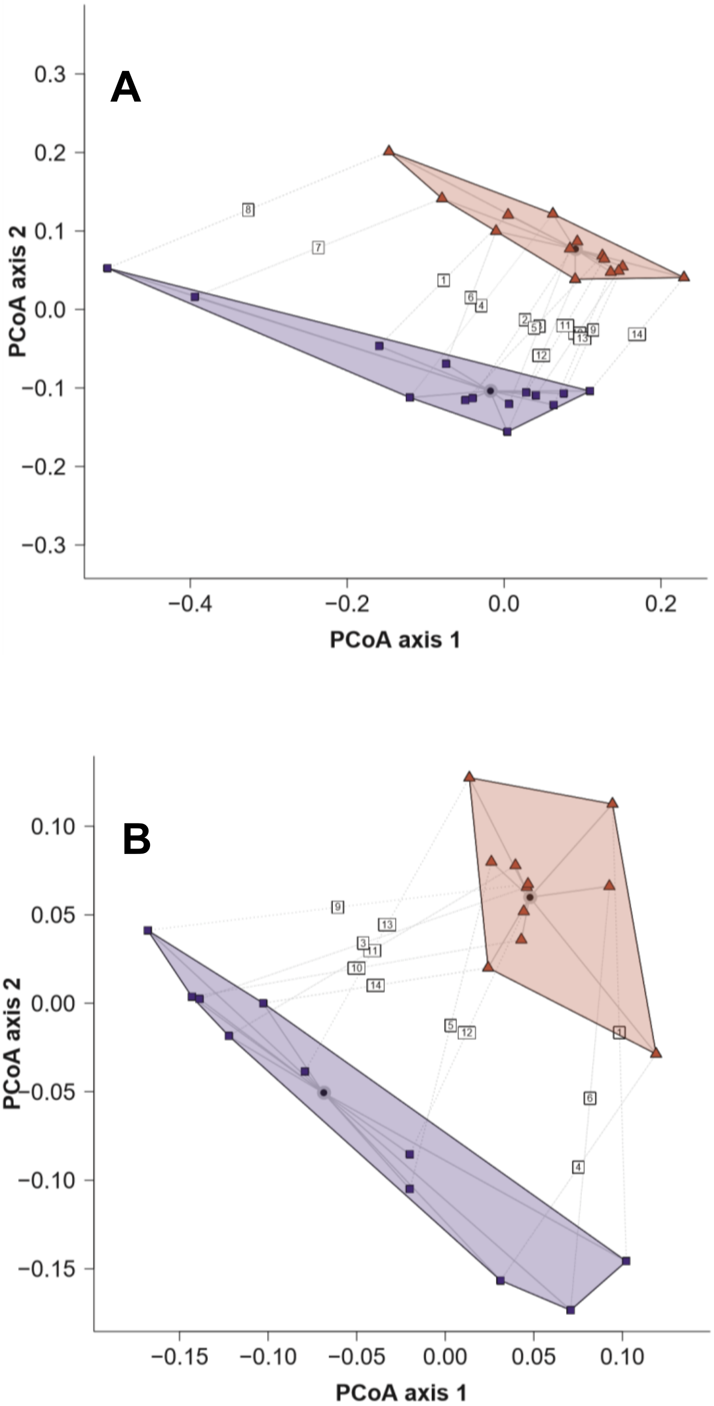
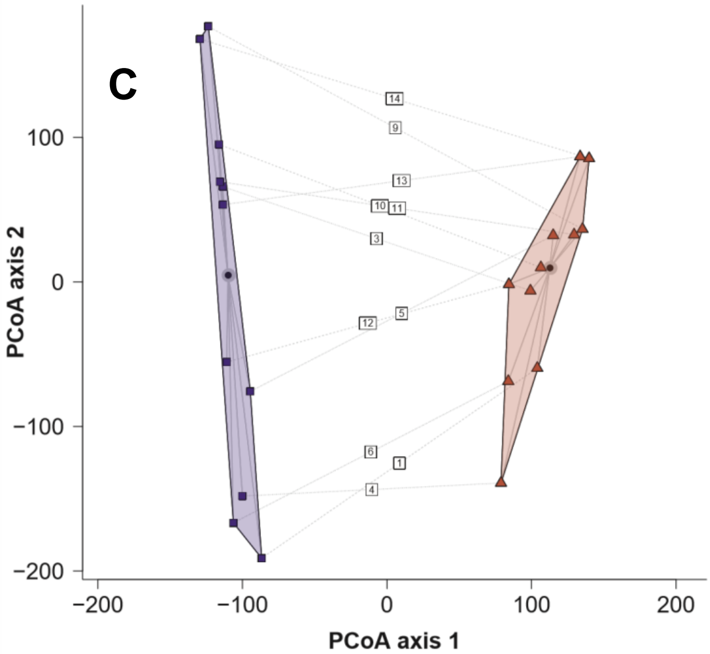


Figure S1. *Species richness as a function of area.* 14 Danish regions, historical (1857-81, circles) and present survey (2012, triangles). Axes are $\log_{10}$ transformed. Linear regressions are: y = 0.3928x + 570 (historical survey, solid line) and y = 0.4727x + 738 (contemporary survey, dashed line) (non-log-transformed equations). Colours and numbers refer to Fig. 1.


A
PCoA axis 1
PCoA axis 2
0.3
0.2
0.1
0.0
−0.1
−0.2
−0.3
−0.4
0.2
B
0.10
0.05
0.00
−0.05
−0.10
−0.15
0.00
0.05



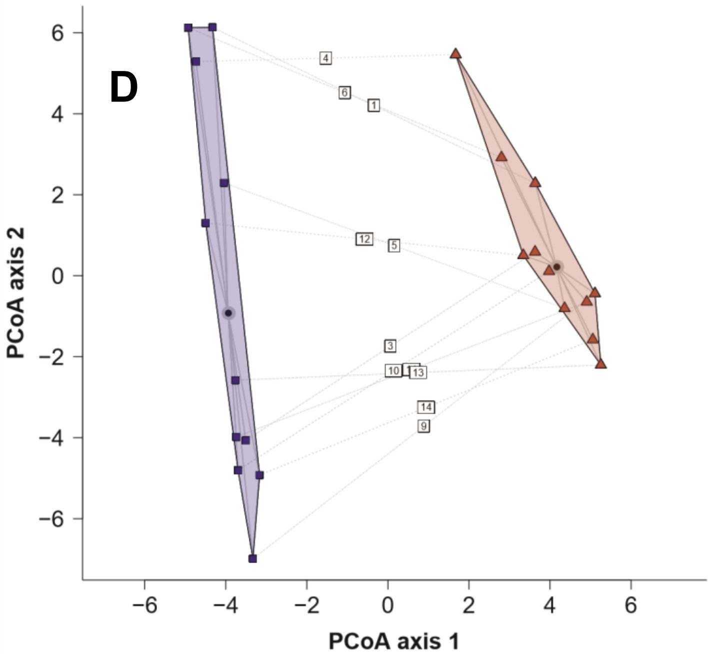


Figure S2 A-D. *PCoAs of alternative beta-diversity measures.* Measured as: A) Sørensen dissimilarity; B) AltGower dissimilarity; C) Manhattan dissimilarity; D) Euclidian dissimilarity. Sørensen dissimilarity is calculated on presence/absence data (14 regions) other measures on abundance data from 11 regions. Blue squares are historical regional data and red triangles present data. Dotted lines are drawn between identical regions in historical and present data and numbers refer to regions in Fig. 1 and Table S1. A polygon is drawn around each time-period (historical =

blue, present = red) and centroids for each time-period marked as a filled circle, full grey lines mark the distance from each region to the spatial median of each time-period. PERMANOVA, $p < 0.001$ for all measures. For a comparison of distance to spatial median, see figure S7.

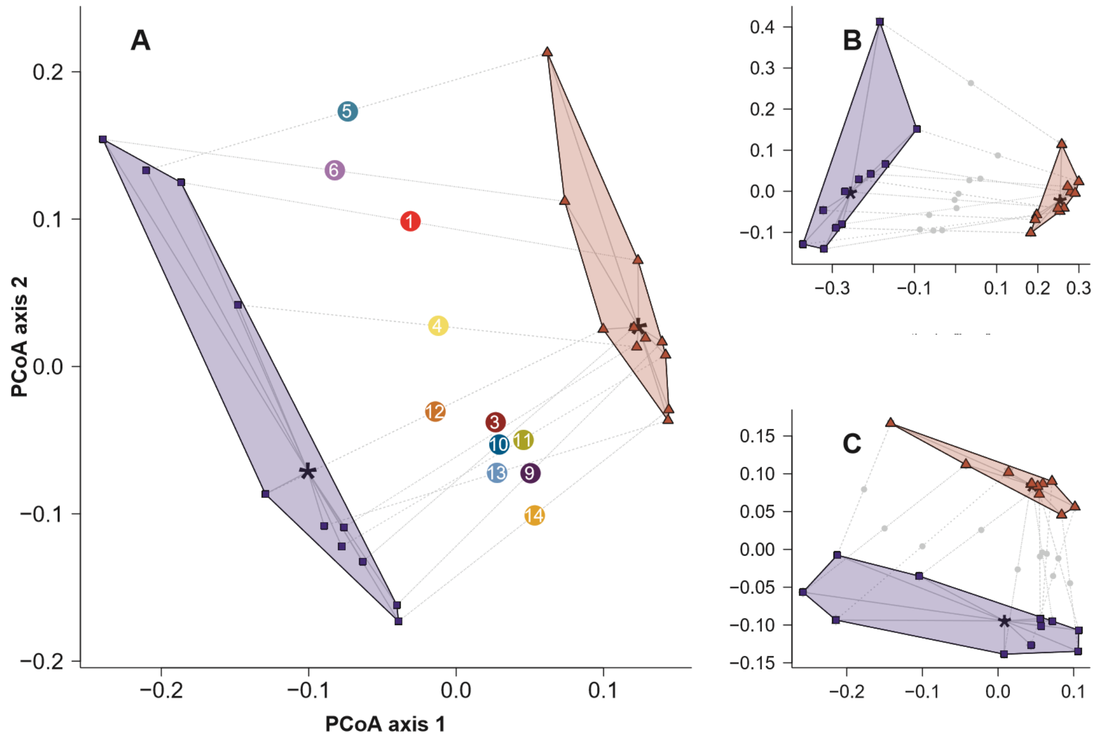


Figure S3 A-C. *Change in species composition over 140 years in 11 Danish regions measured as Bray-Curtis dissimilarity.* A) All species, B) Only exotic species, C) Only native species. Blue squares are regions in historical data and red triangles in present data. Dotted lines are drawn between identical regions in historical and present data and numbers refer to regions in Fig. 1 and Table S1 (Region number 2, 7 and 8 are not included as abundance data in historical sources were not satisfying for these regions). Polygons are drawn around each time-period (historical = blue, present = red) and centroids for each time-period marked as a asterisks, full grey lines mark the distance from each region to the centroid of each time-period. Historical species composition (1857-1883) are significantly different from the contemporary species composition (2012) in all three panels (PERMANOVAs: A) $p < 0.001$; B) $p < 0.001$; C) $p < 0.01$). Relative eigenvalues of PCoA axis 1 (1) and PCoA axis 2 (2): A) 1=0.29, 2=0.2; B) 1=0.49, 2=0.1; C) 1=0.26, 2=0.2. For a comparison of distance to spatial median in all panels, see figure S6.

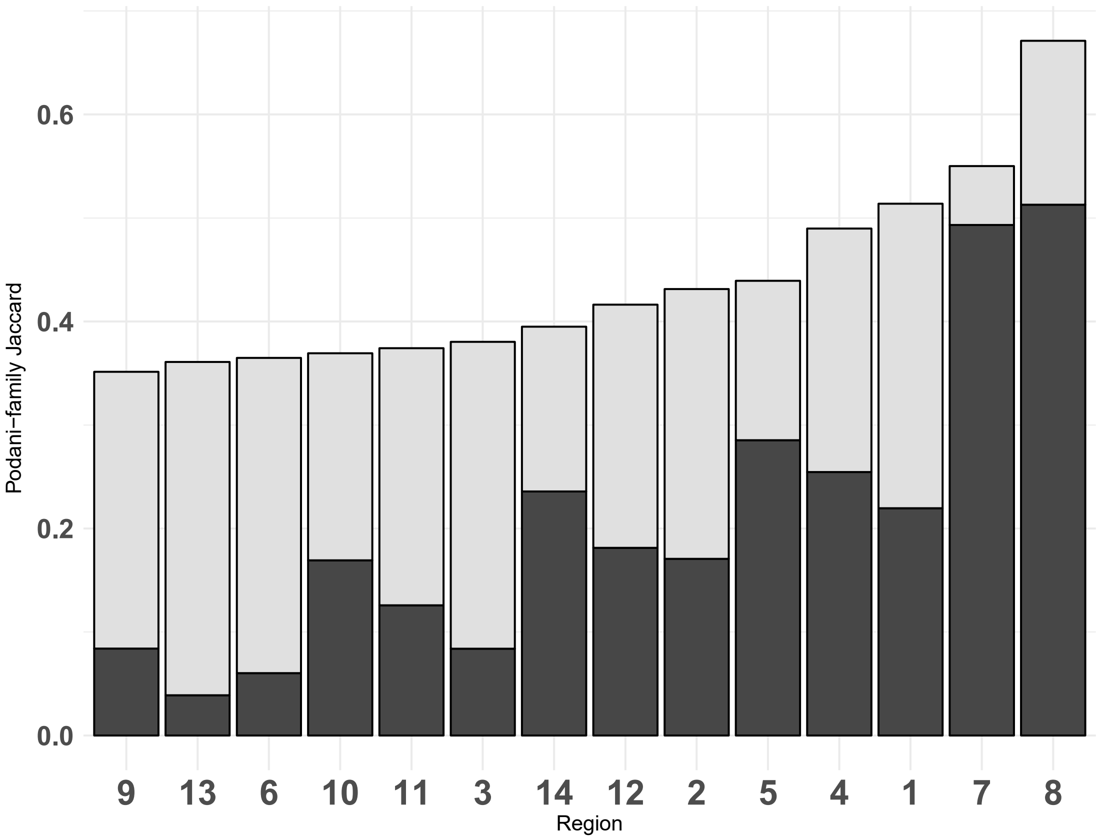


Figure S4. *Podani-family partitioning of Jaccard dissimilarity into replacement and richness.* Region numbers follow Fig. 1 and Table 1. Regions are ordered by increasing Jaccard dissimilarity. Light grey = replacement, dark grey = species richness. Mean proportion of Jaccard dissimilarity for all regions except 7 & 8: Replacement = 0.248, Richness = 0.159; for region 7 & 8: Replacement = 0.108, Richness = 0.503.

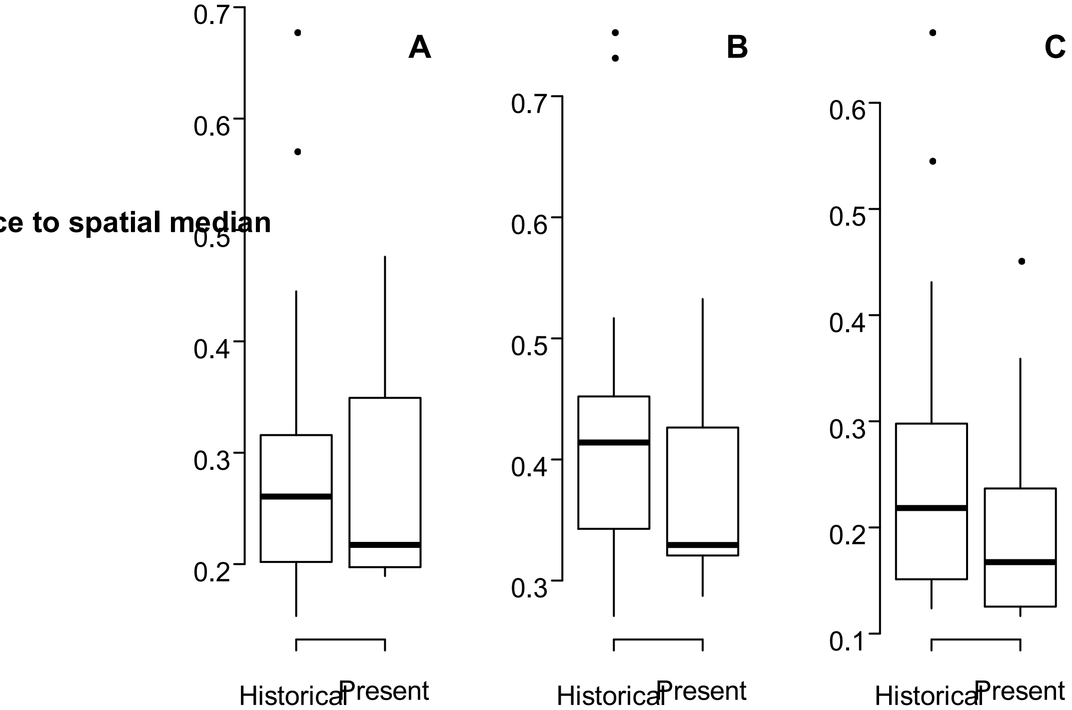


Figure S5 A-C. *Homogenization for Jaccard dissimilarity measured as distance to historical and present spatial median.* A) All species, B) Only exotic species, C) Only native species. Corresponding PCoA is Fig. 2.

ANOVA between times: A: p > 0.05; B: p > 0.05; C: p > 0.05.

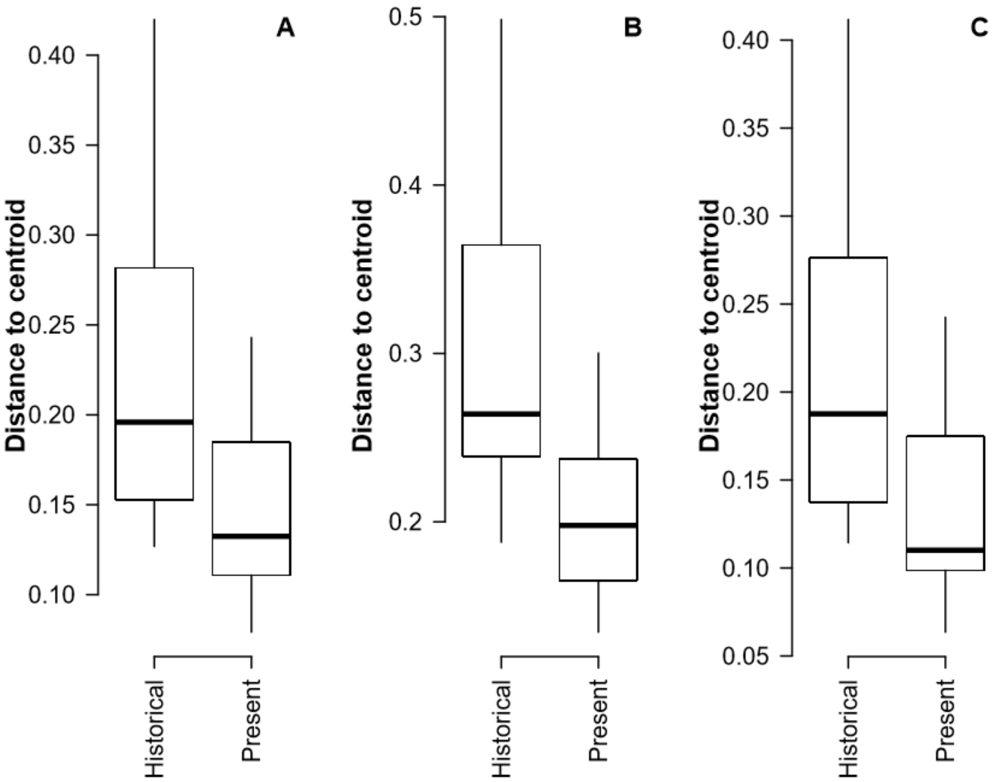


Figure S6 A-C. *Homogenization for Bray-Curtis dissimilarity measured as distance to historical and present spatial median.* A) All species, B) Only exotic species, C) Only native species. Corresponding PCoA is Fig. S3.

ANOVA between times: A: $p < 0.05$; B: $p < 0.01$; C: $p < 0.05$.

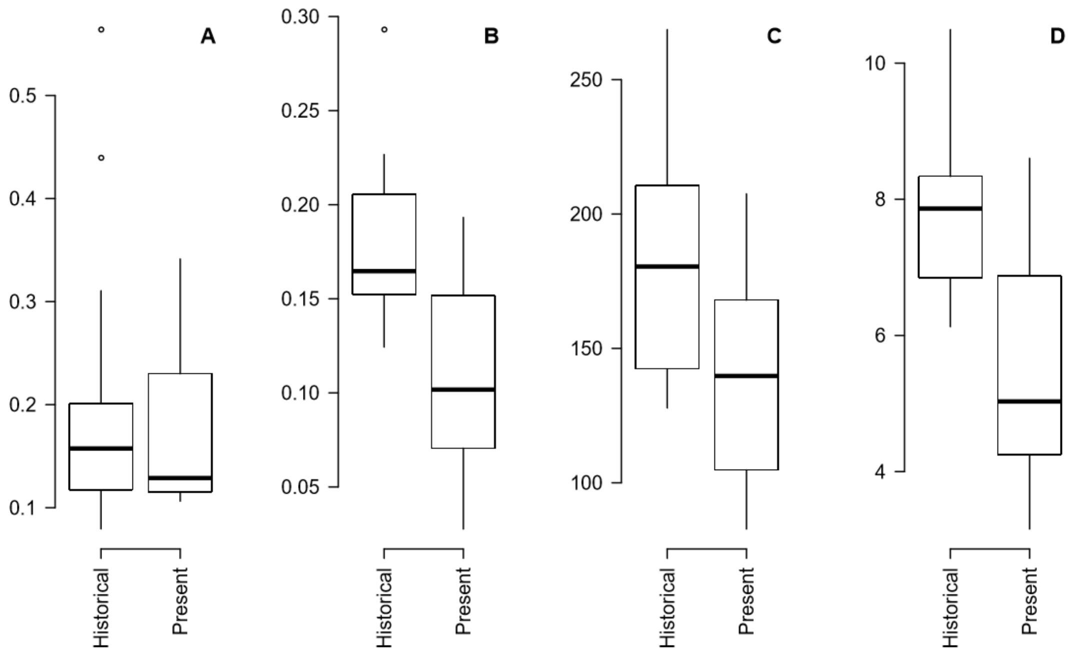


Figure S7 A-D. *Homogenization measured as distance to historical and present spatial median for four dissimilarity measures of beta-diversity.* Based on presence-absence data from 14 regions: A) Sørensen dissimilarity and abundance data from 11 regions: B) AltGower; C) Manhattan; D) Euclidian dissimilarity. Corresponding PCoA is Fig S2 A-D. ANOVA between times: A) $p > 0.05$; B) $p < 0.01$; C) $p < 0.05$; D) $p < 0.01$.

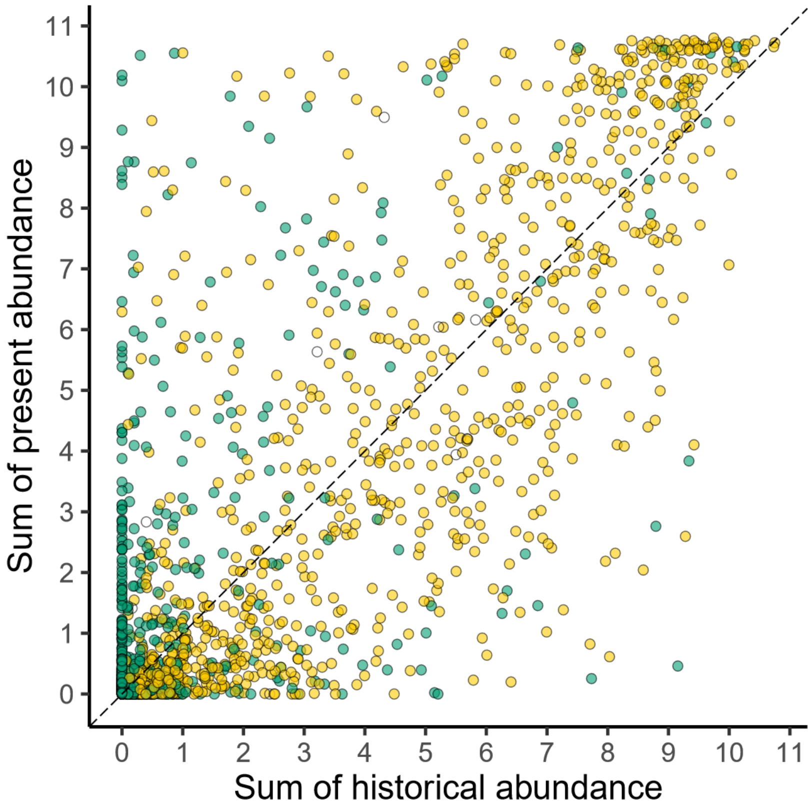
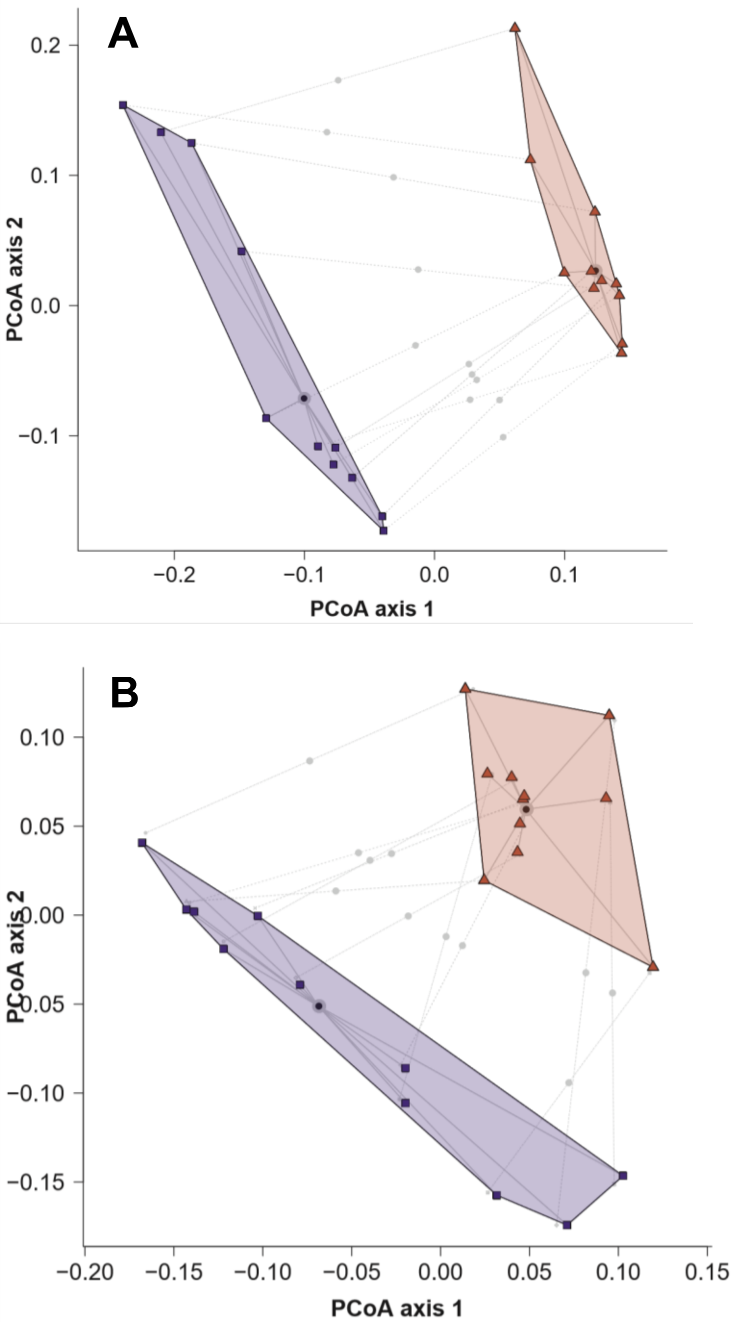


Fig. S8. *Sum of historical regional abundance (x-axis) versus present regional abundance (y-axis) for 11 regions.* Green dots indicate exotic species, yellow dots native species and white dots species with no origin assigned (NAs). Dashed black 1:1 line denotes no change. As regional abundance is between 0-1 the maximum value within a region is 1 and hence 11 on both axis indicate maximum abundance in all regions.


A
0.2
0.1
0.0
−0.1
PCoA axis 2
−0.2
−0.1
0.0
0.1
PCoA axis 1
B
0.10
0.05
0.00
−0.05
−0.10
−0.15
PCoA axis 2
−0.20
−0.15
−0.10
−0.05
0.00
0.05
0.10
0.15
PCoA axis 1

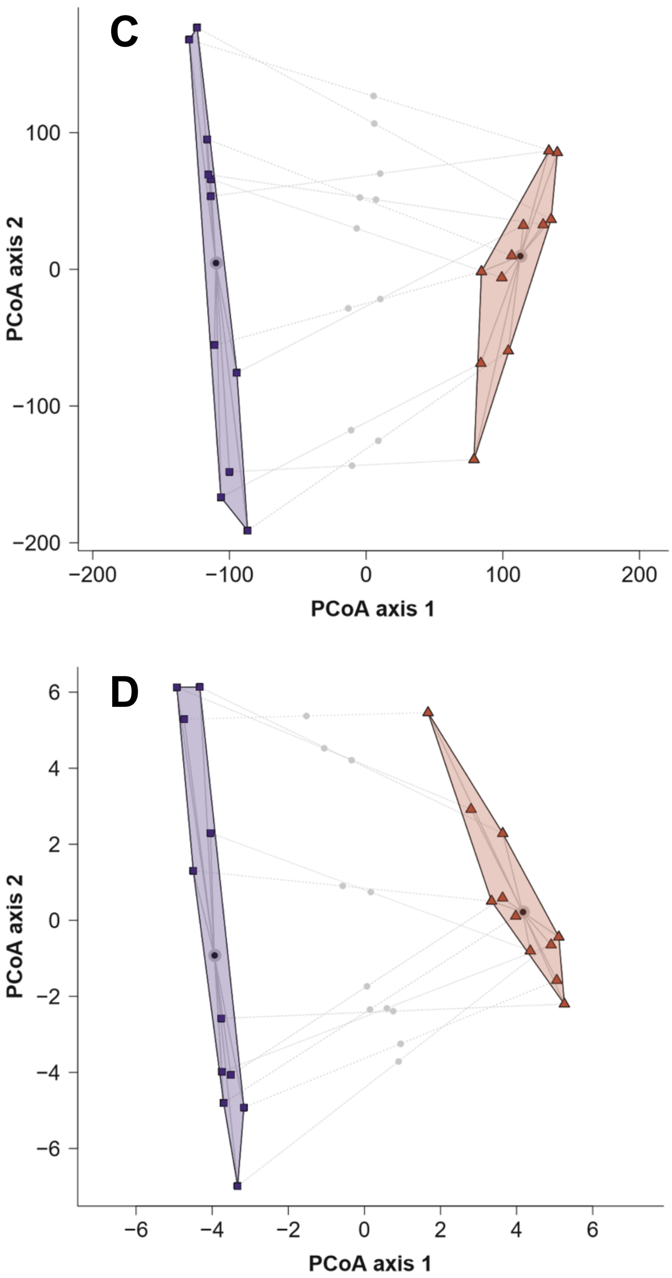


Figure S9 A-D. *Three abundance categories.* PCoAs of beta-diversity measures based on three abundance categories. Measured as: A) Bray-Curtis dissimilarity; B) AltGower dissimilarity; C) Manhattan dissimilarity; (C), D) Euclidian dissimilarity. Based on abundance data in three categories from 11 regions. Blue squares are historical regional data and red triangles present data. Dotted lines are drawn between identical regions in historical and present data. Polygons are drawn around each time-period (historical = blue, present = red) and centroids for each time-period marked as a circle, full grey lines mark the distance from each region to the spatial median of each time-period. PERMANOVA, $p < 0.05$ for B and D, A and C $p > 0.1$. For a comparison of distance to spatial median, see figure S10.

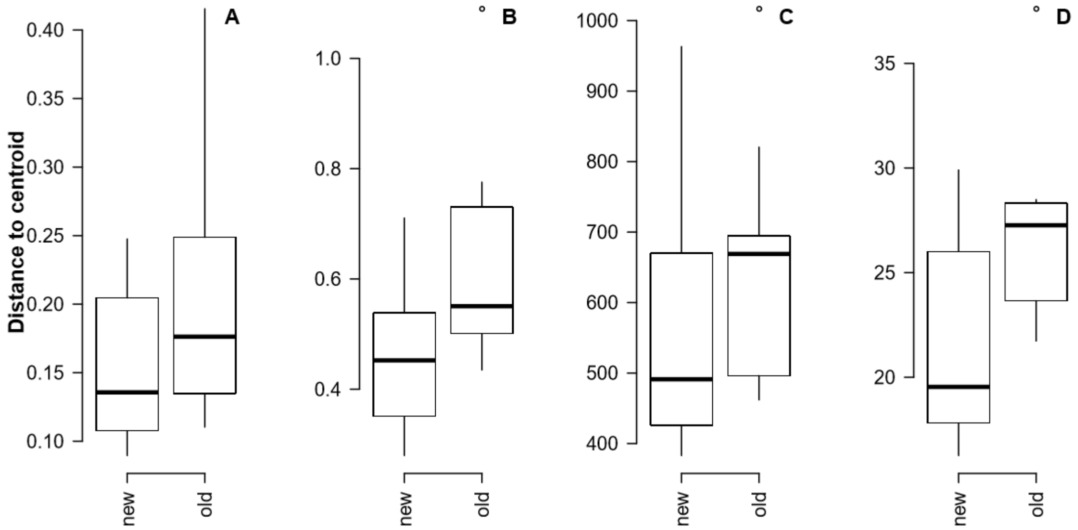


Figure S10

A-D. *Three abundance categories.* Homogenization measured as distance to historical and present spatial median for four dissimilarity measures of beta-diversity, based on three abundance categories. Abundance data in three categories from 11 regions: A) Bray-Curtis; B) AltGower; C) Manhattan; D) Euclidian.

ANOVA between times: A: $p > 0.1$; B: $p < 0.05$; C: $p > 0.1$; D: $p < 0.05$.

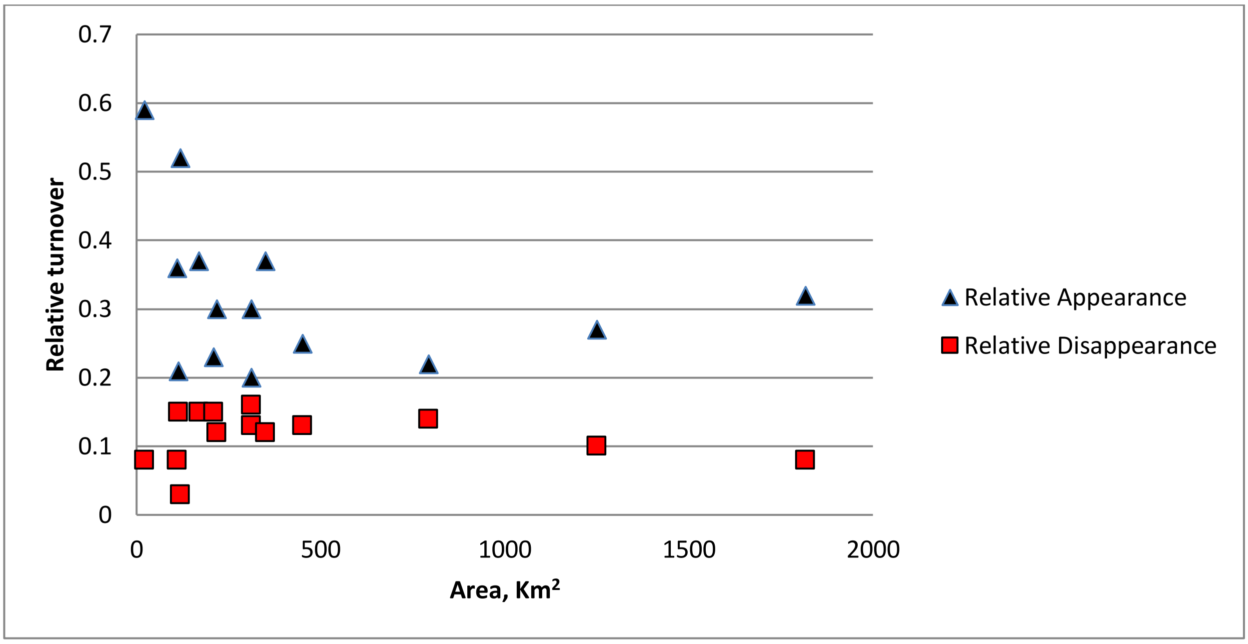


Figure S11. *Relative turnover related to area of regions.* Relative turnover in appearance and disappearance (number of species appearing or disappearing / total number of species at both time slices) related to area of regions in 14 regions over 140 years.

Electronic Supplementary Material – Appendix 2

For the paper: More is Less: Net Gain in Species Richness, but Biotic Homogenization over 140 Years

By: Tora Finderup Nielsen, Kaj Sand-Jensen, Maria Dornelas & Hans Henrik Bruun

This file includes:

Supplementary Materials and Methods

Supplementary Tables S7 and S8

Supplementary Figures S12 to S16

Method details

Data collection and preparation

Spatially matching historical and present data

Historical and present species data were obtained using methods that were fundamentally similar and which share an overarching goal, i.e. using strategic expert search to obtain an exhaustively list of species for an area. In addition, the modern survey aimed at assessing species' occurrence in each grid cell, and therefore differ from the historical survey in details of the methodology. It is important to make the distinction between a survey's ability to i) produce a presence-absence list of species for a region, and ii) to produce an accurate assessment of species' regional abundance. The methodological differences between the historical and recent surveys used for our analyses are of little or no importance to the former, but with some consideration to be made for the latter (see below).

In the historical data, species were recorded either as presence/absence only or presence/absence amended with regional abundance within an explicitly delimited area (example: yellow line in Fig. S13). In the present data, species presences were recorded in grid cells of 5 × 5 km. Grid cells were either "reference cells", in which the aim was to record all species and the resulting data therefore are presence/absence, or "non-reference cells", in which only noteworthy species were recorded and the resulting data presence-only (Fig. S13).

Regions covered by historical data were in the present data covered by between 3 and 95 reference grid cells, depending on their areal extent. When spatially aligning present data to historical regions, present grid cells were assigned to an historical region if more than half of the land area in the grid cell was part of the historical region (se example in Fig. S13). As input to calculations of species appearance, disappearance or continued presence per region, we used complete historical species lists and present species lists from reference and non-reference grid cells together (Fig. S13, red and blue cells). For comparison of regional abundance – see below.

Sampling effort and detectability

Comparable detectability is important to assure, when comparing species records from two different times, as differences can lead to pseudo turnover (Nilsson, I.N. & Nilsson, S.G. (1985). Experimental estimates of census efficiency and pseudoturnover on islands: error trend and between-observer variation when recording vascular plants. J. Ecol., 73, 65-70). Undoubtedly, considerably more person-hours were spent in each region searching for plant occurrences in the recent than in the historical surveys. However, the vast majority of the extra search effort was spent on establishing species' occupancy, i.e. their presence or absence across many grid cells, and a minor part spent on establishing the total species list of the region. Therefore, species detection probability on the level of regions was comparable between the two surveys. This may be substantiated using the accounts on species' distribution in Denmark, published 1931-1980 in a long series of papers in Danish under the title Topographical-Botanical Investigation of Denmark (for an overview, see Vestergaard, P. & Hansen, K. (1989). Distribution of Vascular Plants in Denmark. Opera Botanica, 96, 1-163). From these accounts, we may be quite sure that plant species, which we have found to have increased in occupancy across regions and/or in abundance within regions, were either absent or rare in our study regions up to a point in the 20th Century. It has, however, not been possible to use this series for quantitative comparison of changes in plant diversity, as all published distribution maps contain a level of subjective expert judgement by the authors.

Standardization of taxonomy and nomenclature

Plant taxonomy and nomenclature were meticulously standardized. Most infraspecific taxa were lumped at the species level, unless we were certain that names had been used consistently through time. Some critical taxa were pooled at genus level (e.g. *Callitriche*, *Alchemilla, Euphrasia* and *Taraxacum*) or at the level of sections (*Rubus* and *Hieracium*).

Taxa excluded

Hybrids: Primary hybrids were excluded from both historical and present data, while hybridogenous taxa forming viable populations, e.g. *Symphytum* x*uplandicum*, and complex cultivars, e.g. *Doronicum* x*excelsum*, were kept. In total for both time periods, 160 hybrid taxa were excluded from the data.

Unconfirmed historical records: From historical data, species were excluded if they were not trusted to be present in the region at the time of the completion of the historical flora. For example, some of the historical floras include older records, which the author of the flora explicitly mentions as not extant. In total, 26 species were excluded from historical data based on this information.

Uncertain nomenclature: Species with uncertain circumscription or nomenclature through time were excluded from analyses. This was done in order to minimize the effect of false appearances/disappearances due to inconsistent species delimitation through time. In total, 29 species with uncertain nomenclature were excluded.

Furthermore, in the historical data, 10 species were only recorded at the genus level. To avoid false appearances, all species of the relevant genus recorded in the present data from that region were considered as present historically, except for species known only to have been absent from Denmark entirely at the time of completion of the historical floras.

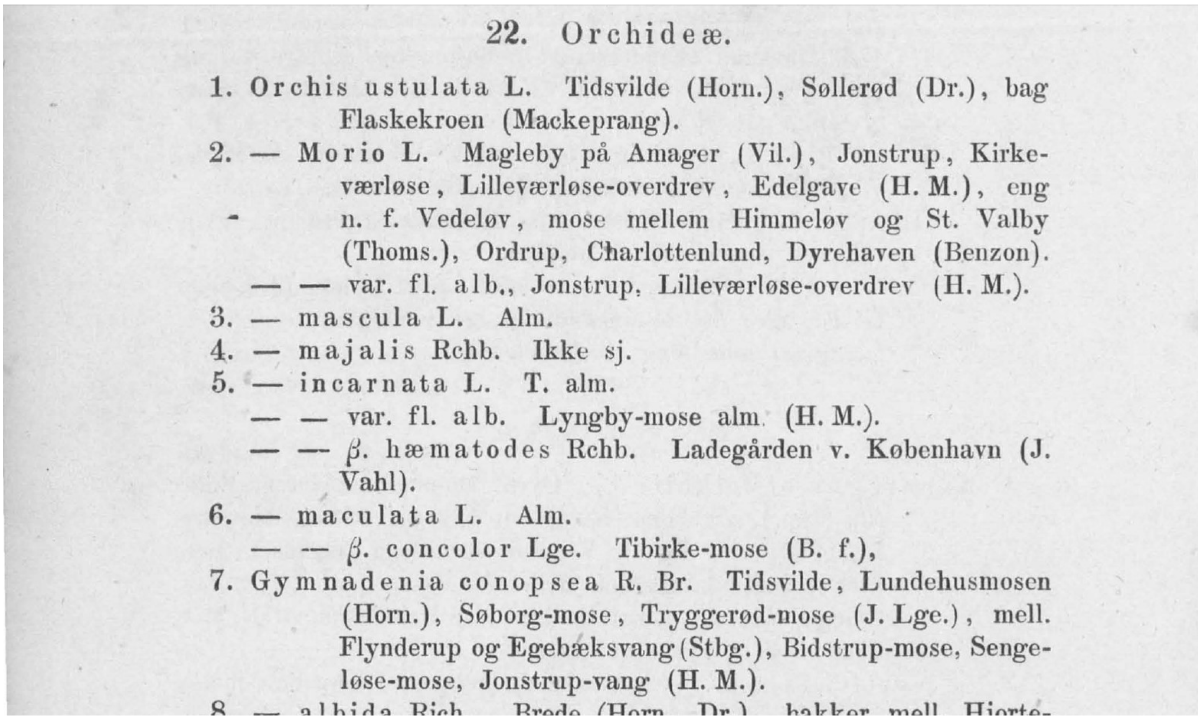
Only wild plants

In both historical and present data, only species recorded outside gardens and other cultivated settings were recorded, i.e. archaeophytes, naturalized neophytes, arable weeds and haphazard garden escapes to the wild. Thus, cultivated species were included in the dataset, but only when they are found in the wild. For present data, the explicit instruction to recorders in the Atlas Flora Danica survey was to only include wild species, meaning autochthonous populations outside cultivation. For historical data, the objective was the same, to record wild and naturalized species within a specific region. A representative example is Mortensen, 1872, pp. 60, who states that his flora is (translated from Danish):"*An inventory of the wild and naturalized species found in North East Zealand"*.

Regional abundance – calculation and standardization

Historical data

Regional abundance was specified in 11 out of the 14 historical floras. Species were in general assigned abundance scores on an ordinal scale from "very rare" to "very common" (or similar) within the survey region. For rare species, however, a list of named occurrence locations was given (example in Fig. S12). Some species had assigned both an abundance category and a list of sites. These dual species records allowed us to estimate the number of occurrence sites that would correspond to a given abundance category. It was found, invariably across historical floras, that the number of occurrences listed increased as expected from the lowest abundance category (“very rare” and “rare”) to intermediate categories (e.g. “here and there”), but leveled out or decreased for the higher abundance categories (e.g. “very common”). We interpret this as follows: the number of sites noted for the lower abundance categories corresponds well to the actual number of occurrence sites for a given species (thus, the list of sites is exhaustive), whereas for species in the higher categories, named sites are merely given as examples. For each species only listed with a number of sites, the abundance category estimated by the described relation was used (example in Fig. S14). Thus, a common ordinal abundance scale for all species within a region, common and rare species alike, was thus obtained, as shown in Table S7. Patterns of numbers of species per abundance class roughly follows the expected based on Raunkiær’s law of many rare species, fewer common and few intermediately abundant species (Papp, L. & Izsák, J. (1997). Bimodality in occurrence classes: A direct consequence of lognormal or logarithmic series distribution of abundances - a numerical experimentation. Oikos, 79, 191-194). The number of species per final abundance category per historical flora is shown in Fig. S15 (blue bars).


22. Orchideæ.

1. Orchis ustulata L. Tidsvilde (Horn.), Søllerød (Dr.), bag Flaskekroen (Mackeprang).
2. — Morio L. Magleby på Amager (Vil.), Jonstrup, Kirkeværløse, Lilleværløse-overdrev, Edelgave (H. M.), eng n. f. Vedeløv, mose mellem Himmeløv og St. Valby (Thoms.), Ordrup, Charlottenlund, Dyrehaven (Benzon).
— — var. fl. alb., Jonstrup, Lilleværløse-overdrev (H. M.).
3. — mascula L. Alm.
4. — majalis Rchb. Ikke sj.
5. — incarnata L. T. alm.
— — var. fl. alb. Lyngby-mose alm. (H. M.).
— — β. hæmatodes Rchb. Ladegården v. København (J. Vahl).
6. — maculata L. Alm.
— — β. concolor Lge. Tibirke-mose (B. f.),
7. Gymnadenia conopsea R. Br. Tidsvilde, Lundehusmosen (Horn.), Søborg-mose, Tryggerød-mose (J. Lge.), mell. Flynderup og Egebæksvang (Stbg.), Bidstrup-mose, Sengeløse-mose, Jonstrup-vang (H. M.).

Figure S12. *Example of historical regional flora: H. Mortensen, Nordostsjællands Flora, Botanisk Tidsskrift 5 (1872): p. 100.* The regional abundance is given as “Alm.” (i.e. common) or similar for relatively common species, such as *Orchis mascula*, whereas a list of named occurrence sites is given for relatively rare species, e.g. *Neottinea ustulata* (syn. *Orchis ustulata*), for which three sites are mentioned. Two of the species listed are now extinct from the region in question, whereas the remaining have become much rarer.

Present data

In order to enable comparison of abundance over time, the present data were similarly transformed to an ordinal 0-1 scale. For this, we used recent presence-absence data, i.e. based on reference grid cells only. For each species, the number of occupied reference cells was divided by the total number of reference grid cells within the relevant region (red cells, Fig. S13). To avoid false disappearances, the abundance of species only recorded in non-reference cells, was calculated as if the species was found in one reference cell. Example of calculation, see Table S8. Patterns of numbers of species per abundance class roughly follow Raunkiær's law, as expected. Number of species within each final abundance category is shown in Fig. S15 (red bars).

Abundance in three steps – historical and present

To test the sensitivity of our assessment of abundance change to the assignment of abundance classes, we tried a more conservative approach, simplifying the abundance scale to three broad classes. All species' abundance values on the 0-1 ordinal scale, historical and present, were sliced into three abundance categories with approximately the same number of original categories in each new category, without regarding the number of species. See Table S7 and S8 for examples of historical and present data, respectively.

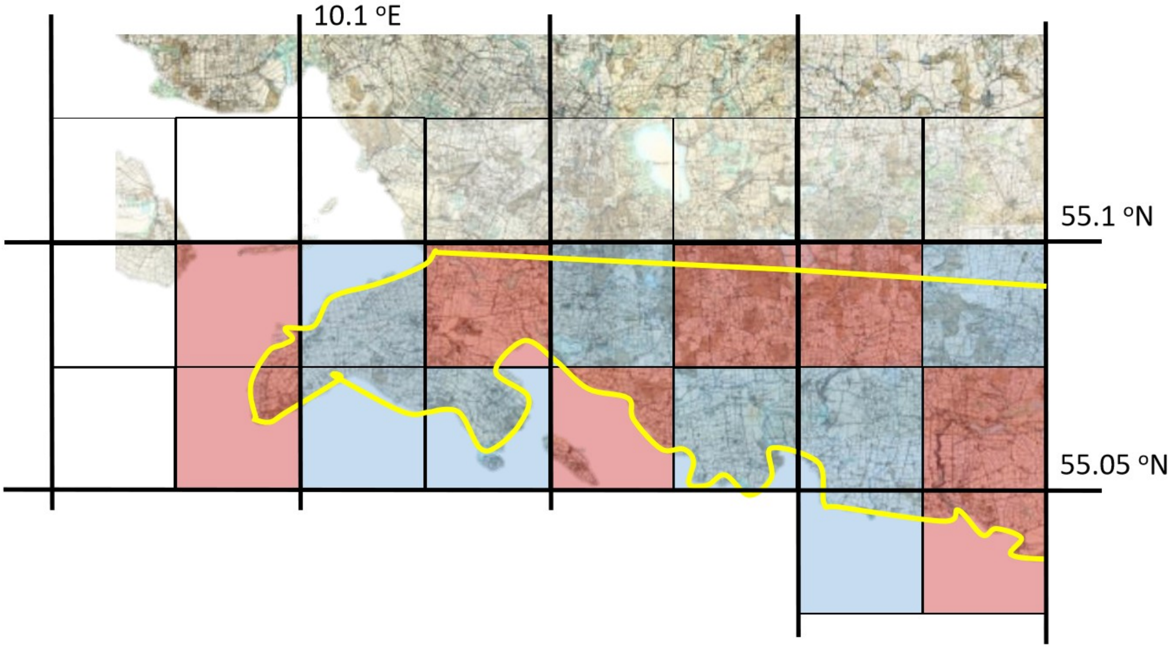


Figure S13. *Matching occurrence and abundance in historical data from polygon regions with present grid cell data.* A historical map (1:20,000 ordnance map, 1865) showing a part of the region "Southern Funen Mainland" (region #3 in Fig. 1). Approximate longitude and latitude are noted to imply spatial scale. Historical data relate to the area within the yellow line (borders indicated using place names and administrative units given in the historical flora), while present data (Atlas Flora Danica survey) were done in grid cells of 5 × 5 km (black lines). Red cells are "reference cells" and blue cells "non-reference cells", both included (as more than 50% of their land area lie within the yellow polygon), while white cells were excluded. In the recent survey, at least two grid cells per tetrad (10 × 10 km; bold black lines) were fully investigated, i.e. "reference cells".

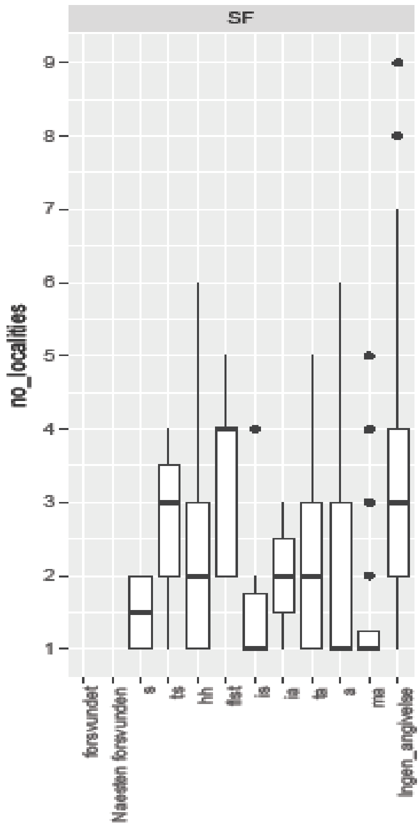


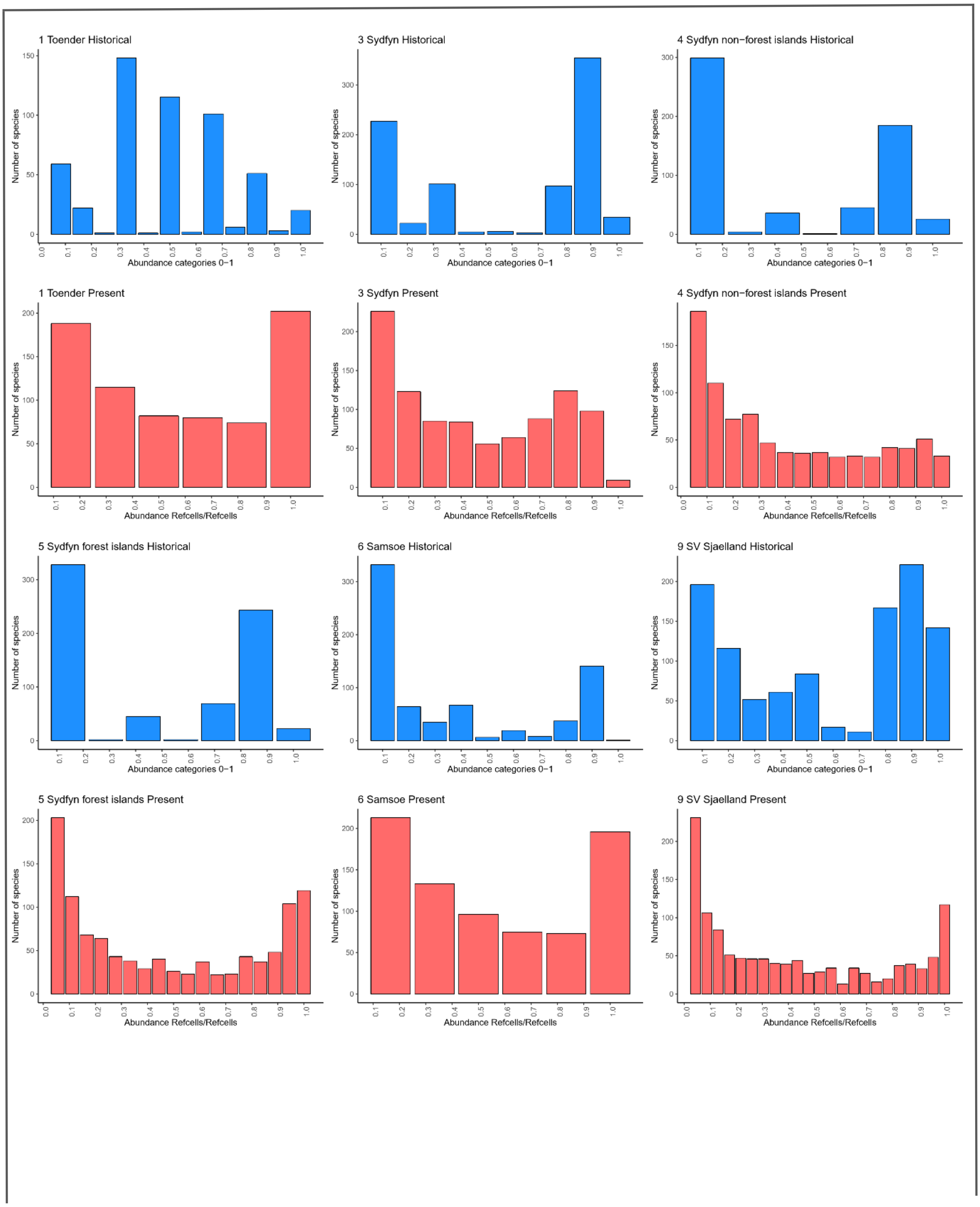
Figure S14. *Number of localities specified for each abundance-category, example from region #3 "Southern Funen Mainland" (834 species).* The abscissa indicates abundance-categories with increasing abundance from left to right. Categories are (in Danish abbreviations from left to right): forsvundet = extinct; næsten forsvundet = nearly extinct; s = rare; ts = relatively rare; hh = here and there; flst = several places; is = not rare; ia = not common; ta = relatively common; a = common; ma = very common; ingen_angivelse = number of localities not specified. For this particular regional flora, we judged that the number of localities increased through the categories 'rare' (s) and 'relatively rare' (ts) and then decreased. We therefor assigned the category 'rare' to species occurring at 1-3 localities and the category 'relatively rare' to species occurring at >3 localities, as seen in table S7.

Table S7. *Historical data. Translation of number of occurrence sites to abundance categories and to final regional abundance.* Example from region # 3, Southern Funen Mainland. Number localities are translated to abundance categories based on Fig. S9. Final regional abundance is calculated as abundance category number divided by the total number of abundance categories (=9). Abundance is sliced into three broad categories with approximately the same number of original categories in each (here = 3).

Number of localities	**Abundance category (*Danish abbreviation*)**	**Abundance category number**	**Final Regional Abundance**	**Regional Abundance in 3 categories**
1	Rare (*s*)	1	0.11	1
2	Rare (*s*)	1	0.11	1
3	Rare (*s*)	1	0.11	1
4	Relatively rare (*ts*)	2	0.22	1
5	Relatively rare (*ts*)	2	0.22	1
6	Relatively rare (*ts*)	2	0.22	1
-	Rare (*s*)	1	0.11	1
-	Relatively rare (*ts*)	2	0.22	1
-	Here & there (*hh*)	3	0.33	1
-	Several places (*flst*)	4	0.44	2
-	Not rare (*is*)	5	0.56	2
-	Not common (*ia*)	6	0.67	2
-	Relatively common (*ta*)	7	0.78	3
-	Common (*a*)	8	0.89	3
-	Very common (*ma*)	9	1.00	3

Table S8. *Recent data. Calculation of abundance on a 0-1 ordinal scale.* Example of the first six species in an alphabetical list from region #3, Southern Funen Mainland.

Scientific name	**# observations – all grid-cells**	**# observations – reference grid-cells**	**Total # reference grid-cells**	**Final Abundance (#ObsRefGrid-cells / #RefGrid-cells)**	**Abundance in 3 categories**
Abies alba	5	5	10	0.5	2
Abies grandis	1	1	10	0.1	1
Abies nordmanniana	2	2	10	0.2	1
Abies procera	1	1	10	0.1	1
Abutilon theophrasti	1	1	10	0.1	1
Acer campestre	8	8	10	0.8	3
...	…	…	…	…	…


1 Toender Historical
3 Sydfyn Historical
4 Sydfyn non−forest islands Historical
1 Toender Present
3 Sydfyn Present
4 Sydfyn non−forest islands Present
5 Sydfyn forest islands Historical
6 Samsoe Historical
9 SV Sjaelland Historical
5 Sydfyn forest islands Present
6 Samsoe Present
9 SV Sjaelland Present
Number of species
Abundance categories 0−1
Abundance Refcells/Refcells

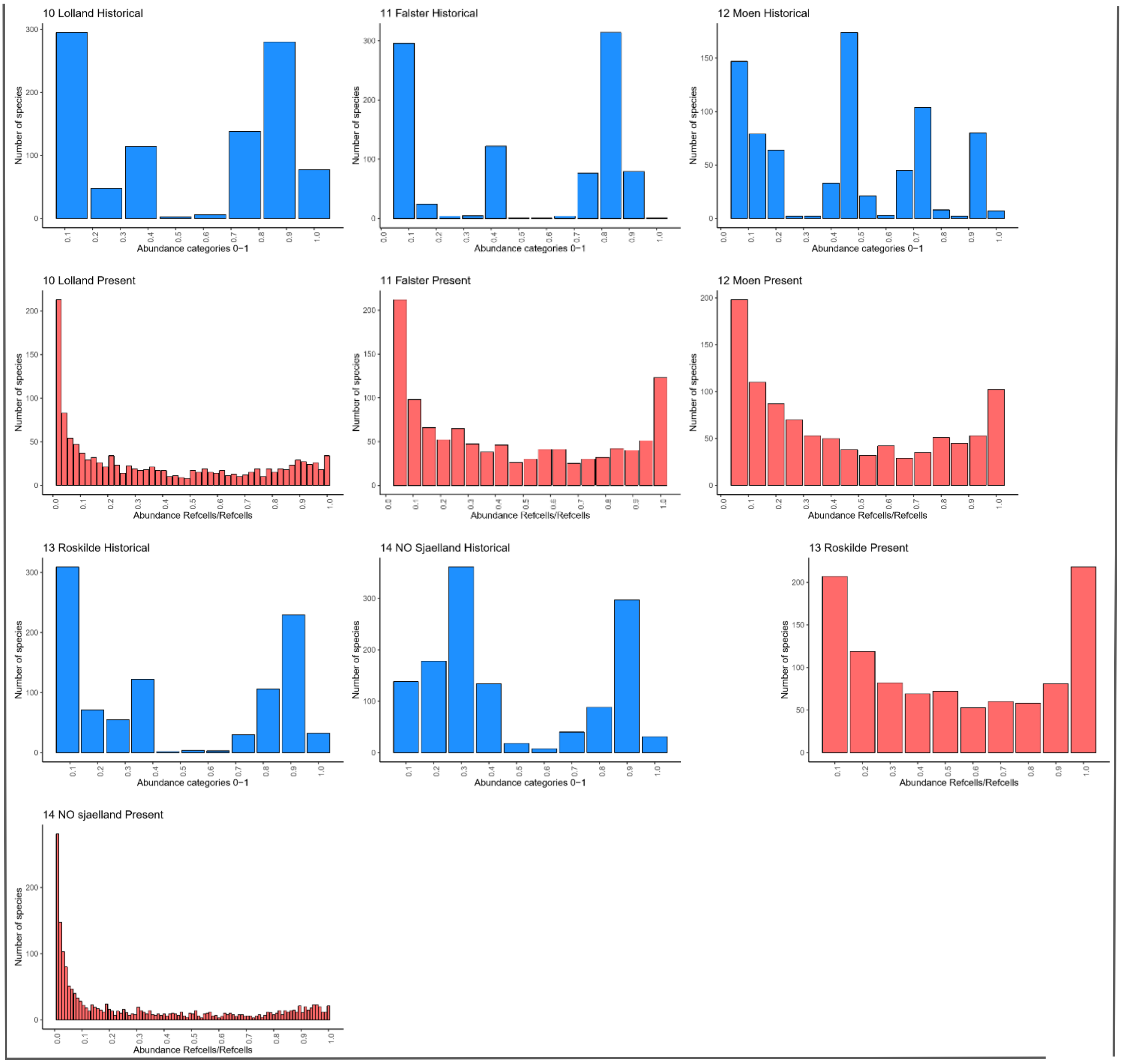


Figure S15. *Number of species within each final abundance category for 11 regions.* Historical data are blue bars and present data red bars. The number of species in each category is shown in original ordinal categories 0-1. Plots ordered by region number, following Fig. 1. 11 regions with abundance data (excluded are regions: 2, 7 and 8).

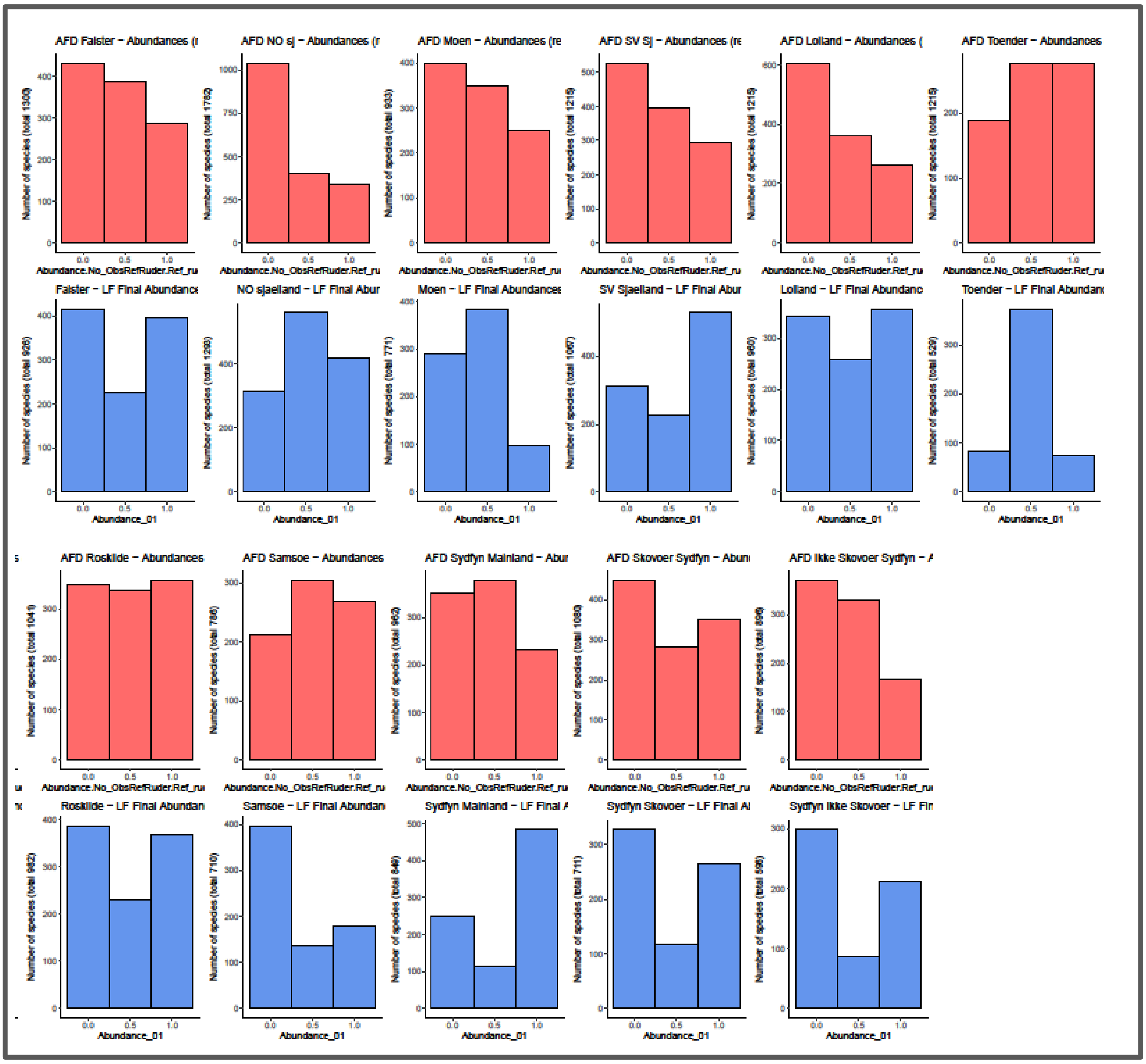


Figure S16. *Number of species within each abundance category in three categories, for 11 regions.* Present data are red bars and historical data blue bars. Y-axis is the number of species within each category and x-axis ordinal categories from 0-1. From left to right the region-numbers following Fig. 1 are: 11; 14; 12; 9; 10; 1; 13; 6; 3; 5; 4.