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ECONOMIC DEVELOPMENT AND BIODIVERSITY

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ECONOMIC HISTORY

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ECONOMIC DEVELOPMENT AND BIODIVERSITY

Abstract

There is an urgent need for studying the development of biodiversity in the (recent) past. It is one of the biggest threats to the sustainable future of mankind, and the process is largely driven by economic and demographic changes. However, it has however not received much attention by economic historians. Several (historical) socio-economic drivers of biodiversity have been recognized, however, the extent, rate and precise causes of current decline remains unknown. A historical perspective on biodiversity and the network of socio-economic factors causing it, will lead to a more inclusive understanding of the complex human-nature relations resulting in biodiversity decline. The models currently used to simulate these processes, and theoretical notions about it, have not been sufficiently tested against the historical record. To that end, it is proposed to study biodiversity on the basis of historical records and data. Moreover, a research framework is presented that may be the starting point for the new research agenda. The framework gives a schematic overview of the interconnected natural and socio-economic systems across different temporal, spatial and biological scales. This is then applied to the case of the Netherlands in the 20th century, and the causes of the decline and recent rise of biodiversity are analyzed.

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Economic Development and Biodiversity

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Abstract

There is an urgent need for studying the development of biodiversity in the (recent) past. It is one of the biggest threats to the sustainable future of mankind, and the process is largely driven by economic and demographic changes. However, it has however not received much attention by economic historians. Several (historical) socio-economic drivers of biodiversity have been recognized, however, the extent, rate and precise causes of current decline remains unknown. A historical perspective on biodiversity and the network of socio-economic factors causing it, will lead to a more inclusive understanding of the complex human-nature relations resulting in biodiversity decline. The models currently used to simulate these processes, and theoretical notions about it, have not been sufficiently tested against the historical record. To that end, it is proposed to study biodiversity on the basis of historical records and data. Moreover, a research framework is presented that may be the starting point for the new research agenda. The framework gives a schematic overview of the interconnected natural and socio-economic systems across different temporal, spatial and biological scales. This is then applied to the case of the Netherlands in the 20th century, and the causes of the decline and recent rise of biodiversity are analyzed.

Introduction

The decline of biodiversity is one of the most urgent problems facing humanity. Biodiversity plays an important role in ecosystem functions that provide supporting, provisioning, regulating, and cultural services. These services are essential for human well-being.¹ Bees take care of a large part of the pollination of plants, and photo-synthesis produces the oxygen and the food we cannot do without. Moreover, the conservation of nature is often also seen as an ethical goal in itself. However, biologists think we are going through the sixth mass extinction in history, but this time is different: one species, homo sapiens, is largely responsible. It is the result of complex interactions between man and nature, and it is happening on an unprecedented scale.² Red List assessments show that things are getting worse, as even common and widespread species show sharp declines in occurrence and abundance, signaling wider environmental problems.³ Pollution, alteration and loss of habitats, introduction of non-native species, climate change and overexploitation of resources are recognized as the main

¹ Millennium Ecosystem Assessment 2005; Haines-Young & Potschin 2010.

² Stuart et al. 2004; Schipper et al. 2008.

³ Birdlife international 2012.

socio-economic causes of biodiversity decline.⁴ Much remains unknown, however, about the extent, rate and causes of the current decline in global biodiversity. However, it is clear that demographic and economic changes play a central role: the growth of the world's population, the increased spatial claims of economic activities (agriculture, infrastructure, build environment) and pollution related to economic activity (plastics, So2, Co2 etc.) are among the principle drivers of biodiversity decline. The decline of biodiversity is also an economic-historical problem, that has to be understood as the consequence of the dramatic expansion of human activities.

This contribution proposed to study changes in biodiversity in much the same way as economic historians study economic growth, that is by quantifying these developments and constructing large datasets that measure the various aspects of the process. This makes it possible to test hypotheses about the links between economic growth and biodiversity decline – such as the environmental Kuznets curve, which is, as the name already suggests, inspired by economic-(historical) work. This hypothesis maintains that environmental stress increases during the first stages of 'modern economic growth' as a result of which biodiversity has the tendency to decline. However, beyond a certain level, environmental policies and increased demand for nature conservation lead to a reduction in environmental stress and possibly an increase in biodiversity. In other words, the relationship between GDP per capita and biodiversity is a U-curve.

To some extent this field is covered by environmental historians. Environmental history as a discipline has emerged in response to the growing environmental problems societies were facing in the second half of the 20th century. It is, much like its twin brother historical ecology, concerned with the sustainability of societal development and with the interactions between humanity and nature in general.⁵ However, the historical process of biodiversity loss has not had a meaningful impact on the study of history or the historical profession. Environmental historians have published extensively about man-nature interactions and their consequences for individual species and eco-systems. Recent examples are the history of the rabbit in late Medieval Holland, the tiger in the Malay world, or the disappearance of the elephant from China.⁶ More general environmental histories contain much information on man nature relationships and the exploitation of eco-systems in the past, that can be integrated into the study of the development of biodiversity in recent times; for example, Roberts on the 'unnatural' history of the sea, or Richards' study of the environmental history of the early modern world.⁷ Environmental historians know a lot about the fate of certain species and about the use of natural resources, but this is only rarely studied from the perspective of biodiversity change. The concept of biodiversity is only just beginning to appear in history-published textbooks and synthetic studies. In his brilliant 'Something New Under the Sun. An Environmental History of the Twentieth Century' John McNeill spends two pages, out of a

⁴ Gaston and Fuller 2007.

⁵ Molina and Toledo 2014.

⁶ Van Dam 2010 (the rabbit in Medieval England); Boomgaard 2001 (the tiger in the Malay world); Elvin 2004 (the elephant in China).

⁷ Roberts 2007; Richards 2003.

total of 421, to discuss the topic, repeating some of the well-known facts.⁸ In the prestigious 'The Oxford Handbook of Environmental History', of close to 800 pages, the topic is mentioned four times, but mainly as something studied by ecologists – and not by historians.⁹

There is, however, no doubt that this is a vast and important subject. The biologist Edgar Wilson whose 'The Diversity of Life', a seminal study of the ebbs and flows of biodiversity in the past, helped to put the topic high on the academic agenda, argued that that he could not imagine a scientific problem of greater immediate importance for humanity.¹⁰ The historical study of biodiversity, however, has largely been left to biologists and ecologists. In the absence of historical research charting these changes, trends in the historical evolution of biodiversity have mainly been analysed by environmental scientists making use of models based on assumptions derived from contemporary research, assuming that these would also hold for the past. One of the best-known examples is the Globio3 model that simulates the decline of biodiversity since 1700 (the 'pristine' starting point before the Industrial Revolution) on the basis of changes in five 'drivers': land use, infrastructure, fragmentation, climate change and atmospheric nitrogen deposition.¹¹ A testing of these trends against the historical evidence has not been attempted – probably because biologists lack the knowledge of historical sources to do such research, and because historians have not been sufficiently interested in the problem of biodiversity loss. The implication of this is that the models on which policy decisions are based – such as the Globio3 model – are not properly tested against the actual development of biodiversity in the long run. The truth of the matter is that we do not really have a complete understanding of what drives biodiversity, and policies to redress the current dramatic decline may be based on incorrect assumptions about the long-term causes of the process.

In short, we argue that there is an urgent need for studying the development of biodiversity in the (recent) past on the basis of historical records and data – by scholars who can combine intimate knowledge of the historical sources with a deep understanding of the complex interaction between man and nature. This paper contains a number of suggestions for the development of such a research agenda, more specifically by developing one case study, the changes in biodiversity in the Netherlands during the 20th century. First, we introduce the concept and theoretical ideas about the evolution of biodiversity over time, then we discuss a framework that gives a schematic overview of the interconnected natural and socio-economic systems across spatial, temporal and biological scales. Such a framework may provide a starting point for developing the study into the causes of long-term decline in biodiversity. Finally, we propose a way forward for organizing global historical biodiversity research.

The concept

Biodiversity is a complex concept, encompassing the variety and variability of all life on Earth, ranging from the genetic level (the diversity within a certain species), to the species and to the ecosystem level (the diversity of ecosystems). Here, we limit ourselves mainly to biological diversity of species, but other forms of biodiversity can in principle be studied in the same way.

⁸ McNeill 2001.

⁹ Isenberg 2014.

¹⁰ Wilson 1992.

¹¹ Alkemade et al. 2009.

Species diversity usually refers to the number of species present in a certain territory – or in the world as a whole. It is more or less known how many species of vertebrates have, for example, become extinct globally. Current estimates suggest that since the year 1500, over 332 terrestrial vertebrates, 150 of them bird species, have been reported to become extinct.¹² It has been suggested that the current species loss is occurring over 1,000 times the natural 'background' rate of around 1-5 per year. Often, it is known when and why it happens, although, as the example of the arguably most famous case, the Dodo, illustrates, such extinctions are difficult to date precisely, and there often is debate about the exact causes.¹³ Similarly, it is for example possible to reconstruct when species appeared in the Netherlands and when they became extinct; a lot is already known about this for the recent period, but for the period before about 1900 this has to be supplemented by historical sources to get the full picture. Case studies, such as the pioneering analysis of the history of certain birds in the Netherlands between 1500 and 1900 by De Rijk, show the potential of this kind of research.¹⁴

Species extinction is however only the tip of the iceberg. It is unclear how representative vertebrates (and plants) are for biodiversity as a whole; we know for example almost nothing about the history of the 4,000 species of beetles or 700 species of spiders that occur in the Netherlands (but there is a lively debate about recent trends in the number of insects^{15,16}). Moreover, the occurrence of a species is only part of the story. Species abundance (the number of species per km2) is a more appropriate measure of biodiversity, which may change dramatically over time, even when no extinctions occur. Moreover, the spatial scope is also relevant. It is conceivable that at the global level species become extinct and biodiversity is declining, whereas at the same time, at the local level, biodiversity is stable or even rising with certain species – perhaps those adapted best to human influences - becoming more widespread. To illustrate the complexity of the concept, McGill et al. distinguished fifteen different forms of biodiversity trends in the Anthropocene, and briefly discussed the empirical evidence for these trends, concluding, however, that "even patterns that seem well established, like the global decline in biodiversity, have never been directly measured and rely on models to estimate the changes. Many trends are almost completely unstudied".¹⁷

The complexity of the concept, and the difficulties that arise when it is measured even for today, imply that historical studies can only make use of proxies that are indirect measures of biodiversity in its entirety. Historical sources – in particular when they stretch far back in time – often relate to vertebrates, especially mammals and birds, which therefore figure most prominently in historical studies. Historical studies on plants often resort to early taxonomical works, but also to herbals, agricultural statistics and historical maps. One way to overcome this problem is to select 'indicator species' that provide information on the overall status of the ecosystem and of other species in that ecosystem. Indicator species may also reflect the quality

- ¹⁴ De Rijk 2015.
- ¹⁵ Hallmann et al. 2017

¹² IUCN 2014.

¹³ Fuller 2003.

¹⁶ Hallmann et al. 2018

¹⁷ McGill et al. 2015.

and changes in environmental conditions and various aspects of community composition.¹⁸ By making a careful selection of 'indicator species' representing the various biological characteristics of ecosystems in a region of country, one can get a deeper understanding of the evolution of biodiversity. Moreover, the impact of anthropogenic disturbances can be studied by selecting 'indicator species' that are sensitive to environmental change. Indicator species are in contemporary indices of the evolution of biodiversity (such as WWF Living Planet Index), which are based on what is known about trends in a limited range of species, most of them birds and mammals.¹⁹ Applying such an approach in historical biodiversity research may be more complex as availability of historical sources could be a limiting factor in selecting the appropriate indicator species. Several studies, however, have successfully used indicator species in historical research (see 'Measuring historical biodiversity').

Theoretical ideas

Biodiversity change is driven by a large number of economic, demographic, and socio-political developments, which are usually studied by economic and environmental historians. Two preindustrial events have been recognized as the beginning of human activity adversely affecting the biosphere, leading to (global) biodiversity decline.²⁰ The first was the extinction of the Pleistocene megafauna after *Homo sapiens* migrated from Africa to other continents.²¹ The second was the emergence of agriculture with the Neolithic revolution, resulting in habitat destruction and fragmentation and other human-mediated disturbances.²² The Industrial revolution, the third major event, caused a significant increase in the human impact on the global environment.²³ In the last 200 years, the global population has grown from approximately one billion to 7,6 billion, leading to a major increase in energy use (forty-fold) and economic production (fifty-fold).²⁴ Moreover, the percentage of land area impacted on by intensive human activity increased from about ten to thirty per cent.²⁵

Analyzing the exact impact of these historical socio-economic developments on biodiversity is however difficult. Although the categories of drivers – i.e. pollution, alteration and loss of habitats, introduction of non-native species, climate change and overexploitation of resources – seem to hold for the historical perspective, much remains unknown about the relative importance of each driver along the temporal-spatial gradient. Currently, most (global) historical biodiversity analyses are performed by modelling social-ecological systems. Such approaches are often based on hypothetical (linear, univariate) relationships between biodiversity loss and certain socio-economic drives, for instance, increased energy use, land-use change, forestry, and climate change.²⁶ For example, the GLOBIO3 model builds on the

¹⁸ Lindenmayer et al 2000; Siddig et al. 2016.

¹⁹ Loh et al. 2005; McRae et al. 2016.

²⁰ Steffen et al. 2011.

²¹ Alroy 2001; Roberts et al. 2001.

²² Dupouey et al. 2002; McLaughlin and Mineau 1995.

²³ Alkemade et al. 2009.

²⁴ McNeill 2000.

²⁵ Lambin and Geist 2006.

²⁶ Brink 2000.

IMAGE-NCI model and uses (empirical) cause-effect relationships to link environmental drivers with biodiversity impact.²⁷ The model describes biodiversity as the remaining mean species abundance (MSA), relative to their abundance in a pristine or primary situation, which is assumed not to be fundamentally disturbed by human activities. Individual species responses are not modelled in GLOBIO3 as MSA relates to response of a set of species.²⁸ Another model is the HYDE model, which provides spatially explicit land-use maps and cover the period 10,000 BC to AD 2000 by combining historical population, cropland and pasture statistics with satellite information and specific allocation algorithms.²⁹ Hypotheses on the size and magnitude of historical land-use changes can be tested using the model.³⁰ Different globalscale policy options have been evaluated using these models, for instance, studying the effect on biodiversity of an increase in protected areas.³¹ A common feature of these models is that they are based on assumptions derived from contemporary research, assuming that these will hold for the past.³² However, they are not sufficiently tested against the empirical historical development of biodiversity. There are several theoretical ideas with regards to the interaction between the socio-economic and natural systems to that are not included in, or reflected by, these 'simplified' models.

The occurrence of species is determined by a complex web of interrelated drivers that have an impact through different direct and indirect pathways, which may also change over time. Direct pathways include biodiversity loss due to destruction of habitats and overexploitation of species. Indirect pathways include impacting biogeochemical cycles, such as the water cycle; and even natural drivers, such as autonomous climate fluctuations, also have a significant impact on the natural system. Moreover, biodiversity decline does not simply mean losing a species or two – it can have far-reaching consequences for the stability of natural systems. Biodiverse systems are more likely to include species that can compensate for the function of species that are lost due to natural or human-induced environmental fluctuations. Moreover, losing one species from an ecological community can have cascading effects, for instance due to alteration in the food-web structure and energy flows, that lead to the extinction of other species³³. This is especially the case when keystone or foundation species are among those lost. Adding to the complexity is that the interaction between the socio-economic and natural system is multidirectional. Changes to the natural system also impact on the socio-economic system, potentially leading to positive or negative feedback loops. For example, loss of biodiversity can lead to resource scarcity, which in turn leads to the exploitation of other, alternative, natural resources. Analyzing the different socio-economic and natural drivers of biodiversity in conjunction with each other, and based on empirical data, will lead to a more inclusive understanding of biodiversity decline.

²⁷ Alkemade et al. 2009.

²⁸ Tucker and McConville 2009.

²⁹ Klein Goldewijk 2011.

³⁰ Klein Goldewijk and Drecht 2006.

³¹ Alkemade et al. 2009.

³² Brink 2000.

³³ Pearse and Altermatt 2013

The concepts and approaches (as described above) generally relate to parts of the network of drivers, pathways and effects related to historical changes in biodiversity. However, there are also theories that entail the integral socio-economic and natural system. For example, a lively scientific debate has developed revolving around the question whether economic development can benefit the environment or if it typically leads to an escalation of environmental problems.³⁴ The Ecological Modernization Theory (EMT) in sociology and the Environmental Kuznets Curve (EKC) in economics, hypothesize that economic development and modernization not necessary increase environmental problems and even suggest that the most (economically) developed countries will eventually propagate environmental reform.³⁵ The EKC hypothesis assumes that the relationship between indicators of economic development, often quantified with per capita income, and environmental quality has an inverted U-shape.³⁶ While, the EMT hypothesis suggests it is not economic development in itself that leads to environmental reform, but that modernization causes institutional changes such as the development of nature conservation organizations and the rationalization of bureaucracies.³⁷ Critical opponents of these theories, however, argue that the modernization process and economic growth in particular, almost always lead to increasing environmental degradation. They hypothesize that a tipping point is never reached and suggest that environmental impact continues due to profit maximization and the relentless drive for growth.³⁸ The empirical studies addressing this debate have mixed findings, depending on the environmental issues studied and the type of data and methodological approach used in the analysis.³⁹ Evidence for the EKC is typically found only for a few local environmental impacts, such as air and water pollution, but not for sources of global environmental problems, such as greenhouse gas emissions and resource consumption.⁴⁰ The opposing hypothesis that increased economic growth only leads to increased levels of environmental degradation, on the other hand, has received considerable empirical support.⁴¹ These national-level studies, however, focused on the emissions of greenhouse gases and air pollution, instead of biodiversity decline as environmental impact.

The framework we propose here, by disaggregating the national biodiversity series in terms of habitats, feeding type and threats, makes it possible to empirically identify the main drivers of biodiversity change in the past (see the discussion below).

A case study: reconstructing biodiversity change in the Netherlands (1900-2015)

Historically, biologists have been documenting the 'state of nature' in the Netherlands by primarily focusing on the occurrence of species. The oldest, and most basic, form is simply

³⁹ Siddig et al. 2016; Clausen & York 2008.

³⁴ Buttel 2000; Claussen & York 2008.

³⁵ Buttel 2000; Dina 2004.

³⁶ Loh et al. 2005.

³⁷ Ehrhardt-Martinez et al. 2002.

³⁸ Foster 1992; O'Connor 1998.

⁴⁰ Loh et al. 2005; Cavlovic et al. 2000; York et al. 2003.

⁴¹ Ehrhardt-Martinez et al. 2002; Cole and Neumayer 2004.

identifying and describing the different species occurring in the Netherlands. For the 19th century there are already some sources that provide such information, for example, the famous overview of Dutch birds by Nozeman⁴² or various natural history works of Temminck and Schlegel. A second measure of the 'state of nature' is the distribution of species across the Netherlands. During the middle decades of the 19th century regional natural history works on flora and fauna become available which present a wealth of information on species distribution. The third measure, and maybe the most insightful, is counting the number of individuals per species. For the period after 1900 the sources become much richer, including censuses of the population of some (fauna) species. However, for many species detailed population data has only been collected systematically from the 1970s onwards, and for some even only from the 1990s. The lack of systematically collected population data before the 1970s is reflected in more comprehensive reports and assessments on the development of Dutch nature in the twentieth century. For example, the 'Toestand van de Natuur' reports^{43,44} provide only a limited assessment of the first half of the twentieth century and Red list assessments generally work with a reference situation of 1950.

However, human pressures on the environment such as population growth, intensification of agriculture, the vast expansion of infrastructure and pollution, started long before the 1950s. A long-term perspective is thus much needed to understand the full impact of the human enterprise on nature. Such long-term analyses are scarce because of limited data availability (for many species) and the uncertainty that comes with using historical data. In this case study an approach is presented that deals with such limitations. The aim is to develop a national biodiversity index from 1900 to 2015 which provides a more precise picture of the development of biodiversity in the Netherlands during the twentieth century. Moreover, by analyzing specific assemblages of species the different drivers of biodiversity will be identified and studied.

A national biodiversity index – 1900-2015

The international standard for biodiversity indices is the Living Planet Index (LPI)^{45,46}. It is based on a large number of estimates of the historical evolution of population sizes of species in the (recent) past. The global and national LPI indices generally only go back to 1970. In this case study we apply a similar approach to go back to 1900. The basis for the national biodiversity index and other analyses are population trends of individual mammal, bird and fish species. The population data was collected from journal articles and reports. Data was only suitable when related to the abundance of a species (or a proxy) for the Netherlands as a whole. These include census data (e.g. White Stork, Grey Seal), fish landings (e.g. Atlantic Salmon, Atlantic Cod) and hunting records (e.g. Wild Boar), which can be translated into estimates of

⁴² Nozeman & Sepp, 1770 -1828

⁴³ Weinreich & Musters, 1989

⁴⁴ Bink et al., 1994

⁴⁵ Loh et al., 2015

⁴⁶ McRae et al., 2016

population sizes^{47,48}. No modelled population data was included. The aim was to collect population estimates of each individual species for every 5-year interval starting in 1900 until 2015. However, only for a handful of species data was available at every interval. Interpolation and extrapolation (making use of qualitative information) was therefore used to have complete population trends. No minimum number of data points cut-off was applied as opportunities for inter- and extrapolation were case dependent. The details and procedures for selecting species and inter- and extrapolation are explained in appendix I (tables A1 and A3). In total, 58 species were selected to be included in the study; 14 mammals, 14 fish and 30 birds (see table 1). Of these 58 species, 55 were breeding in the Netherlands and its territorial waters in 1900, of which 4 became extinct (Lesser horseshoe bat, Atlantic sturgeon, Allis shad and Twait shad) and 2 are almost extinct (Atlantic salmon and Spotted ray); 54 were breeding here in 2015, of which 3 resettled (Eurasian beaver, Grey seal and Wild boar) and 2 (Great crested grebe and Roe deer) vastly expanded since 1900.

These 58 species are spread more or less evenly over the respective species groups in terms of number of species occurring and listed as red list species. For mammals 19% of the species occurring in the Netherlands have been selected, for (breeding) birds 13% and for (freshwater) fish 11%. Also, 57% of the selected mammals are red list species compared to 35% for all mammals in the Netherlands (implying that our estimates may tend to be biased downward). For birds this is 40% of selected species compared to 44% all species. Furthermore, all major habitat types in the Netherlands (17) are represented by at least 4 typical species, and most (13) by 8 or more species (table 2). A general picture of the number of species that have disappeared (locally extinct) and appeared (exotic species and resettlement) in the twentieth century may also provide a sense of how representative the dataset is. In total, 240 (breeding) bird, 71 mammal and 124 fish species are currently living in the Netherlands. Since 1900, 9 bird, 3 mammal and 8 fish species have disappeared from the Netherlands⁴⁹. On the other hand, 35 bird, 8 mammal and 16 fish species have settled since 1900 as exotic species. Also, as mentioned above, three mammal species have resettled. An even broader context to be considered, as here only mammals, fish and bird species, are the total number of species occurring in the Netherlands. In total 25.200 multicellular species have been described for the Netherlands, of which approximately 24.400 species are native⁵⁰. About 600 species are known to have disappeared from the Netherlands, but it is expected to be much more. The decline is especially large for a few groups of water insects, but also for bees, groups of butterflies, beetles and fish. The knowledge of the fauna is disproportionately distributed: there are mainly many specialists for groups such as birds and mammals and only very few for the species-rich groups of invertebrates. Hence, it is paramount to remember that this paper provides a partial picture of the 'state of nature', as only the best known groups are covered because of limited data availability.

⁴⁷ Lenders et al., 2016

⁴⁸ De Groot, 2002

⁴⁹ Nederlands Soortenregister, www.nederlandsesoorten.nl. Consulted on May 15 2018.

⁵⁰ Koomen et al.,1995

Table 1. Overview the 58 selected species. **Unit** is the measure (or proxy) of species abundance, **# data points** is the number of 5-year intervals between 1900-2015 (max=24) for which data is available, **Ref** are the references to quantitative and qualitative information on species abundance.

	Species	Scientific name and subscience and state	Tin D	t # data points	first data point	Ref
nal	European rabbit	Castor fiber	number of individuals	12	1943	1, 2, 3 1
umn	Eurasian beaver	Lutro lutro	number of individuals	24 12	1900	4
Ma	Eurasian otter	Lutra lutra Rhinolombus hinnosidoros	number of individuals	15	1900	2, 5, 6, 7,
	Coeffroy's hot	Mustis amaginatus	number of individuals	15	1945	2,9
	Geoffroy's bat	Myous emarginatus	number of individuals	13	1945	2, 10, 11
	Unther and	Phone withline	number of individuals	24	1900	12
	Furge and had and	Malaa malaa	number of individuals	24	1900	12
	European badger	Correctus correctus	number of individuals	11	1900	2,15
	European roe deer	Microtus occonomus	number of 5x5 km squares	15	1900	2, 13, 10
	Ped fox	Vulpes vulpes	number of 5x5 km squares	6	1945	17, 18, 19
	Furopean hare	Vulpes vulpes	number of individuals per bectare	12	1940	2,20
	Wild boar	Sus scrofa	number of individuals (summer)	12	1900	2, 21, 22 2, 23, 24
	Harbour porpoise	Dhocoana phocoana	number of individuals (summer)	16	1030	2, 23, 24
	Atlantic salmon	Salmo salar	number of individuals in landings	18	1930	29, 20, 27,
ish	Atlantic sturgeon	A cipenser sturio	number of individuals in landings	24	1900	29, 50
ц	Furopean eel	Anguilla anguilla	number of glass eels per sample	16	1900	32
	Burbot	L ota lota	fraction of locations	24	1940	32
	Atlantic herring	Clupes harengus	million kg in landings	15	1900	33
	Atlantic cod	Gadus morbua	million kg in landings	11	1965	35
	Common sole	Solea solea	million kg in landings	13	1955	36
	European plaice	Pleuronectes platessa	million kg in landings	13	1955	30
	Allis shad	Alosa alosa	number of individuals in landings	13 24	1900	38 39
	Twait shad	Alosa fallax	number of individuals in landings	24	1900	40 41
	Sea trout	Salmo trutta	number of individuals in landings	24	1900	30 42
	Small-spotted catshark	Scyliorhinus canicula	number of egg capsules	15	1945	43
	Spotted ray	Raja montagui	number of egg capsules	15	1945	43
	Thornback ray	Rajaclavata	number of egg capsules	15	1945	43
_	Western marsh harrier	Circus aeruginosus	number of individuals	13	1940	44, 45
3 irc	Kentish plover	Charadrius alexandrinus	number of breeding pairs	24	1900	46
Н	Eurasian bittern	Botaurus stellaris	number of breeding pairs	11	1950	47, 48, 49
	Common kingfisher	Alcedo atthis	number of breeding pairs	12	1960	50, 51
	Eurasian spoonbill	Platalea leucorodia	number of breeding pairs	16	1900	52, 53
	White stork	Ciconia ciconia	number of breeding pairs	10	1910	54, 55, 56
	Red-backed shrike	Lanius collurio	number of breeding pairs	13	1900	57, 58
	Eurasian oystercatcher	Haematopus ostralegus	number of breeding pairs	9	1960	59, 60, 61,
	Grey heron	Ardea cinerea	number of breeding pairs	11	1925	63, 64
	Great crested grebe	Podiceps cristatus	number of breeding pairs	10	1930	65, 66
	Grey partridge	Perdix perdix	number of breeding pairs	9	1970	67, 68
	Sandwich tern	Thalasseus sandvicensis	number of breeding pairs	24	1900	69
	Eurasian curlew	Numenius arquata	number of breeding pairs	11	1950	70, 71
	Little grebe	Tachybaptus ruficollis	number of breeding pairs	11	1960	72, 73
	European stonechat	Saxicola rubicola	number of breeding pairs	12	1960	74, 75, 76
	Woodlark	Lullula arborea	number of breeding pairs	11	1950	77, 78
	Northern goshawk	Accipiter gentilis	number of breeding pairs	20	1900	79
	Common buzzard	Buteo buteo	number of breeding pairs	16	1940	72, 73
	Eurasian sparrowhawk	Accipiter nisus	number of breeding pairs	16	1940	72, 80
	European herring gull	Larus argentatus	number of breeding pairs	24	1900	81
	Black-tailed godwit	Limosa limosa	number of breeding pairs	12	1900	73, 82, 83
	Black grouse	Tetrao tetrix	number of cocks	11	1940	72, 84, 85,
	Ruff	Calidris pugnax	number of hens	11	1950	72, 87
	Common tern	Sterna hirundo	number of individuals	24	1900	88
	Greylag goose	Anser anser	number of individuals	11	1900	89
	Black Tern	Chlidonias niger	number of breeding pairs	18	1930	90
	Great Cormorant	Phalaocorax carbo	number of individuals	14	1950	91
	Bluethroat	Luscinia svecica	number of individuals	11	1965	91
	Rook	Corvus frugilegus	number of breeding pairs	16	1925	92
	Black-crowned Heron	Nycticorax nycticorax	number of breeding pairs	16	1940	93

The national index was calculated based on the development in the 58 species, including those species which either disappeared or resettled there. These species were included as they are integral to the story on the development of Dutch nature in the twentieth century (especially with regards to mammals and fish). Non-native, or invasive exotic, species have not been included in the dataset; we focused on 'native' species which have a long history of breeding here (including exotic species would bias the results in an upward direction). For each species the relative abundance was calculated based on the maximum abundance found for that species. The national biodiversity index was then calculated by taking the mean per 5-year interval of the series involved, the index was presented with 1900 as a base year (figure 1). The details for calculating national biodiversity index are explained in appendix I and the relative abundance series are given in appendix table A2.

The index shows an interesting pattern. As may be expected, there is a long-term decline in biodiversity between 1900 and 1970. The decline starts slowly with the industrialization that gains speed in the Netherlands between the 1900s and the 1930s. Around the war period the decline of biodiversity seems to slow down, only to speed up again in the after-war period. The economic recovery after 1945 seems to result in a strong decline in biodiversity, leading to a low point in the 1970s. At the lowest point, the biodiversity may have been at less than half the level of 1900. This low point didn't go unnoticed as awareness of the environmental crisis has grown since the 1960s, partly triggered by the publication of 'silent spring' in 1962⁵¹. Since the 1970s various protective measures and nature conservation programs have gained prominence^{52,53}. After 1975 there was a turning point and the biodiversity index continued to increase during the rest of the period, but not yet reaching the same levels as in 1900. Part of the increase since 1970 might be attributed to improved knowledge and census methods, but the recovery of biodiversity is beyond doubt and well known from other studies (see below)



Figure 1. National diversity index, 1900-2015, based on species abundance of 58 species (mammals, birds, fish) (1900 = 1).

⁵¹ Carson, 1962

⁵² Cramer, 1988

⁵³ LeRoy, 1994

The assumption on which Figure 1 is based is that these 58 species are a random, representative sample of all Dutch species, and that they together therefore reflect trends in overall biodiversity. However, this is a strong assumption; the fact that historical data are available for these species, already casts doubts on it. Another way to process the same information is to select those species that can be seen as indicator species representing the various ecosystems of the Netherlands. The population of grey seals, for example, is indicative of the health of the Waddenzee area, and the lapwing and the black-tailed godwit represent the peat and meadow areas of the country. By weighting the population series by the size of these various ecosystems (in 1900 or 2000 – the choice of weights may also be important), we get another set of estimates of the average relative abundance (figure 2). See appendix II and table A4 for calculation details of the weighted index. The unweighted index in figure 2 is based on a slightly different set of species as compared to figure 1, i.e. indicators species of salt marches, grassland, arable land, raised bogs, forest and heathland. Resulting in a relatively higher low point in the 1970s and better recovery in the 2000s (almost even with 1900 values). This may be explained by the fact that estuaries and river habitats were not included in the index. The weighted indices showed a similar pattern, however, the recovery phase since the 1970s was much higher, especially for the index weighted with ecosystem size in 2000. This can be explained the relative weight of forests in both 1900 and 2000, and the fact that the unweighted trend for forest shows a relatively large increase in the 20th century.



Figure 2. Weighted indices based on indicators species of salt marches, grassland, arable land, raised bogs, forest and heathland. Species population series weighted by the size of the respective ecosystems in 1900 and 2000.

Validating the results of the national biodiversity index is complicated as there are no other indices for the Netherlands describing biodiversity on such a long time scale. However, one way to do it is to compare the contemporary part of the index to other recent indices of biodiversity. In figure 3 the results of the national biodiversity index are compared to the Living Planet Index (LPI) for vertebrates in the Netherland from 1990 to 2015⁵⁴. The national biodiversity index has a 39% increase since 1990 compared to 22% of the LPI. The indices can

⁵⁴ Strien et al. 2016

also be aggregated based on taxonomic class. The biodiversity index for mammals showed a 70% increase while the vertebrate LPI had a 123% increase, for birds this was 29% versus 14% and for fish this was 33% versus 14%. The recovery that we find in recent period is consistent with the LPI, and with much of the recent research on the evolution of biodiversity in the Netherlands⁵⁵



Figure 3. Comparison National Biodiversity Index and Living Planet Index for all vertebrate species (top left panel) and separate species groups from 1990 to 2015.

Disaggregation of the national index

The value of the national index is to chart the long term evolution of biodiversity of the country as a whole. The underlying data also make it possible to analyze changes in abundance of certain groups of species, allowing for a more detailed analysis of the causes of the changes. Separate indices based on taxonomic class (mammals, fish and birds), red list listing (red list species versus not threatened species) and feeding type (herbivore, omnivore, carnivore, insectivore, piscivore) were derived based on the 58 selected species. The different indices have been calculated based on the same procedures as for calculating the national biodiversity index, but only including those species relevant for the respective categories. The details for calculation and species categorization can be found in appendix I and table A3, respectively. For each separate index the similarity in species composition between 1900 and 2015 was

⁵⁵ Strien et al., 2016

calculated to assess the level of species turnover (see table 2 for the results). Species turnover is hard to distil from a biodiversity index, for example, it might occur that species disappear between two time periods, while the biodiversity index stays stable. The similarity index provides a number between 0 and 1, with 0 representing no change in species composition and 1 representing maximum change (see appendix III for calculation details).

Figure 4 presents the disaggregated indices based on taxonomic class, red list listing and feeding type. It is reassuring that the indices based on taxonomic class show a similar pattern compared to the national biodiversity index, at least, for mammals and birds. Here it has to be noted that mammals show a high similarity index, indicating that while the biodiversity levels for mammals between 1900 and 2015 seem comparable, the species composition has changed significantly. This can, in part, be explained by the resettlement of several species (e.g. beaver and grey seal) in the twentieth century. Fish species, on the other hand, show a similar pattern of decline, while not showing a recovery after 1970. This can mainly be explained by the especially poor performance of migratory fishes in the second half of the 20th century. The red list indices are somewhat of a litmus test. As expected, the red list species did not show a significant increase since 1950, the reference year for red list assessments, while the index of not-threatened species showed a strong increase.

The distinction in different feeding types makes it possible to get a first impression of the underlying causes of the evolution of biodiversity. The feeding type indices show a similar pattern of biodiversity decrease and recovery since 1970, with less recovery for carnivores. Looking at carnivores in more detail shows that piscivore species (fish eating) had a low-point at 1965, slightly earlier than carnivores overall. Maybe unexpected based on the fish species index, but piscivores have recovered since 1965. This may be explained by the fact that many of the species in the piscivore index feed on true freshwater fish, which are largely absent from the fish species index. Insectivore species showed no recovery since the low-point of the 70s, which is consistent with the recent literature of the decline of insects⁵⁶. Also, the index for insectivore had a low similarity index, indicating that all insectivore species showed a similar decline in abundance. The use to this day of insecticides may explain why insectivores are still on a low point^{57,58}.

⁵⁶ Hallmann et al. 2018

⁵⁷ Hallmann et al., 2017

⁵⁸ Hallmann et al., 2014

Table 2. Species indexes for a selection of years aggregated by various categories (1900 = 1). # species refers to the number of species in each category, Similarity index (1900-2015) measures whether the species composition is similar between 1900 and 2015.

		# species	1900	1925	1950	1975	2000	2015	Similarity index (1900-2015)
	All species	58	1	0.89	0.71	0.45	0.69	0.85	0.46
Taxonomic	Mammals	14	1	0.84	0.54	0.38	0.67	1.06	0.61
class	Fish	14	1	0.80	0.66	0.32	0.26	0.35	0.10
	Birds	30	1	0.96	0.82	0.56	0.96	1.06	0.46
Red list	Red list species	30	1	0.90	0.64	0.39	0.32	0.43	0.15
	Not threatened	28	1	0.85	0.74	0.57	1.30	1.57	0.24
Feeding	Carnivore	46	1	0.87	0.67	0.43	0.64	0.75	0.36
type	Insectivore	13	1	0.97	0.74	0.42	0.54	0.53	0.15
	Piscivore	12	1	0.75	0.49	0.41	0.62	0.86	0.40
	Herbivore	8	1	1.03	0.91	0.57	0.73	1.23	0.56
	Omnivore	6	1	0.92	0.93	0.68	1.24	1.24	0.50
Habitat	Salt marches	11	1	0.97	1.06	0.70	0.81	0.99	0.52
	Open water, marches	18	1	0.90	0.66	0.57	0.86	1.16	0.38
	Streams and rivers	11	1	0.80	0.46	0.26	0.24	0.45	0.23
	Estuaries	16	1	0.80	0.56	0.29	0.24	0.45	0.21
	Wet open dunes	15	1	0.95	0.82	0.61	0.86	0.90	0.41
	Raised bogs	9	1	0.97	0.71	0.43	0.51	0.54	0.07
	Wet heathlands	14	1	0.93	0.74	0.47	0.63	0.71	0.31
	Dry heath, inland dunes	10	1	0.93	0.81	0.48	0.75	0.88	0.41
	Urban areas	4	1	0.81	0.88	1.11	1.53	2.03	0.00
	Open grasslands	13	1	0.94	0.87	0.60	0.68	0.70	0.21
	Open arable land	5	1	0.94	0.88	0.81	1.10	0.88	0.38
	Cultural landscapes	12	1	0.90	0.80	0.57	1.02	1.03	0.51
	Scrublands	7	1	0.83	0.55	0.43	0.78	1.09	0.49
	Deciduous forests	9	1	0.82	0.96	1.14	2.53	2.47	0.15
	Mixed forests	8	1	0.82	0.93	1.00	2.37	2.57	0.15
	Coniferous forests	6	1	0.79	0.79	0.63	1.80	2.03	0.19
Threats	Hunting, persecution	22	1	0.73	0.56	0.64	0.92	1.28	0.49
	Pollution	19	1	0.70	0.41	0.26	0.57	0.74	0.45
	Eutrophication	6	1	0.91	0.71	0.48	0.45	0.52	0.30
	Weather extremes	5	1	0.84	0.65	0.55	0.83	0.86	0.13
	Disturbance	12	1	0.90	0.65	0.43	0.39	0.68	0.48
	Habitat loss	28	1	0.79	0.57	0.36	0.45	0.59	0.26
	Habitat fragmentation	9	1	0.57	0.35	0.43	0.38	0.68	0.64
	Desiccation	4	1	1.02	1.02	0.93	0.54	0.49	0.00
	Diseases	4	1	0.96	1.00	1.92	1.91	2.24	0.16



Figure 4. The aggregate indices from 1900 to 2015 based on taxonomic class, red list listing and feeding type. The y-axis runs from 0.2 to 1.6 at 0.2 intervals, the red dotted line =1.

Besides species type, the 58 selected species can also be grouped based on habitat preference (see table A3 for categorization per species), linking them to the changing spatial structures of the Netherlands. Aggregate indices for 17 major habitat types in the Netherlands have been constructed based on these categorizations. See table 2 for the results of all habitat types for a selection of years. The recent recovery of biodiversity is almost entirely due to the urban areas and the forests; both have increased in size and in their contribution to national biodiversity. Figure 5 presents the aggregate indices based on species habitat preference for open vegetation, water, high human impact and forest habitats. Open vegetation habitats show the familiar pattern of decreasing biodiversity until the 1970s and a recovery phase since that period. However, for raised bogs, and to a lesser extent, wet heathland the recovery is minimal, not reaching the biodiversity levels of 1900. The similarity index for raised bogs is low, indicating that the decrease in abundance is carried by all species. This can be explained by the fact that the hectares of raised bogs and wet heathland have decreased with 85% in 2015 compared to 1900⁵⁹. The indices for estuaries and streams and rivers of the water habitats show a steady decline since 1900, with only a minor recovery since the 1970s low point. The 2015 biodiversity levels for these habitats are only at half compared to 1900. This can again be explained by the poor status of migratory fishes. The different habitats of high human impact show a somewhat disparate picture. Habitat of urban areas show a strong increase in biodiversity since 1900, although this is based on only 4 species, while open cultural landscapes show a more familiar pattern with a low point in the 1970s. The similarity index is very low for urban areas and high for open cultural landscapes. Open grasslands show no recovery since 1970 and open arable lands show a peak in the 90s, although based on only 5 species. In part, this can be explained by developments in the landscape. Urban areas, for example, saw a 6fold increase compared to 1900, while arable land also saw large increases. However, surface area alone cannot explain everything, as habitat quality also needs to be considered. Forest habitats show sharp increases in biodiversity since the second half of the 1970s, except for shrubland which remains at 1900 levels after recovering from a low point in the 1970s. The similarity index for mixed, coniferous and deciduous forest is low, indicating abundance increase across all species. The increase in biodiversity for forest, based on abundance, can be again explained by changes in the landscape (there was a 30% increase in forest surface area).

⁵⁹ Knol et al., 2009



Figure 5. The aggregate indices from 1900 to 2015 based on species habitat preference for open vegetation, water, high human impact and forest habitats. The y-axis runs from 0.2 to 2.6 at 0.2 intervals, the red dotted line =1.

Another, and maybe more experimental, approach is to group species based on reported causes of decline in the twentieth century. Qualitative statements on the causes of decline in abundance have been collected for each species (if applicable), and subsequently aggregate indices have been derived for several categories of 'species threats'. See table 2 for the results of all species threats for a selection of years. Figure 6 presents the aggregate indices based on species threats for hunting and persecution, eutrophication, pollution and weather extremes. Species that have endured hunting and persecution show a decreasing trend from 1900 onwards, with a low point in the 1950s. It is striking that the level in 2015 is almost 40% higher compared to 1900. This may again be explained by the fact that several species (e.g. beaver and grey seal) were extinct in 1900 due to hunting and persecution but resettled successfully in the twentieth century. This is also confirmed by the relative high similarity index, suggesting high species turnover. Moreover, the biodiversity levels in 1900 may have been low in general for the species included because of intensive hunting and persecution in the nineteenth century and even before that time. The index of eutrophication (the oversupply of minerals and nutrients due to artificial fertilizers) shows a steady decrease, with a steady level reached since the 1970s well below the 1900 level. This suggests that eutrophication is still a problem for these species, although the index remains steady since 1970s. The pollution index has a low point around the 1960s and 1970s, with increases ever since. This is as to be expected because of the increased awareness of pollution since the beginning of the 1960s and the subsequent banning of many toxic substances. The most notable example being banning DDT in 1968/69⁶⁰. The weather extremes index related to species (5) that have suffered because of strong winters. The index shows a low point around 1965, several years after the coldest winter of the twentieth century in the Netherlands (1962-1963).



Figure 6. The aggregate indices from 1900 to 2015 for species threats based on hunting and persecution, eutrophication, pollution and weather extremes. y-axis runs from 0 to 1.4 at 0.2 intervals, the red dotted line =1.

⁶⁰ Van Zanden & Verstegen, 1993

Methodological approach

Before discussing the results in a broader context, some limitations and uncertainties regarding the methodological approach need to be addressed first. Important, of course, is the uncertainty that comes with using historical population data. For many species, historical sources are available that report abundance data. However, often it is not directly evident that the data meets the modern standards of a census. Estimates of historical species counts are notorious for being not accurate mainly by underreporting species numbers. Collecting census data in a detailed and systematic manner is a relative modern phenomenon and such data is therefore largely absent for the first half of the twentieth century. Although there are exceptions, some 'iconic species' such as the White stork and species with specific characteristics, for example, the Grey heron living in breeding colonies, have been counted systematically. For most species, however, collating population trends from historical sources is a laborious endeavour. This involves collecting the multiple historical accounts of species abundance and carefully combining and weighing them, often corroborated with qualitative information. Additionally, more creative sources of abundance data were available, such as fish landings and hunting records. This type of data is accepted and used as a proxy for species abundance⁶¹.

The approach with regard to species selection resulted in a limited number of species in the dataset, putting a strain on the representativeness of the species set. This trade-off was acceptable, however, as gaps in representativeness were identified by categorizing species based on type and habitat preferences, and subsequently filled by searching data for specific species. Another aspect related to species selection which should be acknowledged is the fact that some of the selected species are heavily influenced by humans. Populations of the Wild boar (in particular) and Roe deer (to a lesser extent) are directly managed both in terms of size and distribution. These species were nevertheless included because all species occurring in the Netherlands are affected, more or less, by humans. In fact, understanding the impact of humans on species occurrence is central in this study.

Aggregate indices can be a powerful tool to identify and explore different drivers of biodiversity based on a limited dataset. However, there are also limitations to this approach. For example, the individual aggregate indices need to be careful interpreted as they are often the result of a combination of factors. This can be done by comparing multiple aggregate indices and corroborating the results with independent data. Also, some selected species are not limited to a single category of type, habitat preference or threat. This can lead to a 'double counting effect', making it harder to interpret the patterns and introducing more uncertainty to the results, especially when only a few species are considered. Two other points of attention are (mainly) related to the species threat indices. First, there is the danger of circular reasoning. Any changes in these indices are likely to be attributed to the specific driver on which it was based. This is potentially biased as other factors may be important for explaining the trends. The species threat indices should therefore be approached as a method for testing hypotheses. Second, the drivers (of the respective indices) may have impacted the species on different moments in time, resulting in a weak or no signal in the biodiversity trends. This does however

⁶¹ Lenders et al., 2016

not mean the respective drivers didn't have an impact. Despite the limitations, however, the aggregate index approach vastly amplifies the use of historical population data and can provide important pointers for further investigations.

Finally, the development of biodiversity as measured in this way reflects trends in the territory of the Netherlands, which does not entirely coincide with the impact the economy and society of this country and its citizens has on nature of the globe. Many economic activities have strong international dimensions and repercussions. For example, the Dutch bio industry is based on imports of animal feedstuffs from all over the globe – including soy beans from Brazil or tapioca from Thailand – and therefore indirectly has an impact on biodiversity abroad. Mass tourism of Dutch citizens to foreign destinations may have similar effects. The turn in the EKC after the 1970s may therefore be linked to changes in the international position of the Dutch economy, but this topic is beyond the scope of this paper.

Correlation with GDP per capita

A lively scientific debate has developed revolving around the question whether economic development can benefit the environment or if it typically leads to an escalation of environmental problems. The Ecological Modernization Theory (EMT) in sociology and the Environmental Kuznets Curve (EKC) in economics, hypothesize that economic development and modernization not necessary increase environmental problems and even suggest that the most (economically) developed countries will eventually propagate environmental reform. The EKC hypothesis assumes that the relationship between indicators of economic development, often quantified with per capita income, and environmental quality has an inverted U-shape. While, the EMT hypothesis suggests it is not economic development in itself that leads to environmental reform, but that modernization causes institutional changes such as the development of nature conservation organizations and the rationalization of bureaucracies. Critical opponents of these theories, however, argue that the modernization process and economic growth in particular, almost always lead to increasing environmental degradation. They hypothesize that a tipping point is never reached and suggest that environmental impact continues due to profit maximization and the relentless drive for growth. The empirical studies addressing this debate have mixed findings, depending on the environmental issues studied and the type of data and methodological approach used in the analysis. Evidence for the EKC is typically found only for a few local environmental impacts, such as air and water pollution, but not for sources of global environmental problems, such as greenhouse gas emissions and resource consumption. The opposing hypothesis that increased economic growth only leads to increased levels of environmental degradation, on the other hand, has received considerable empirical support. These national-level studies, however, focused on the emissions of greenhouse gases and air pollution, instead of biodiversity decline as environmental impact.



Figure 7. Scatter plot of average relative species abundance and GDP per capita for the Netherlands from 1900 to 2010.

In figure 7 the development of GDP per capita and biodiversity in the Netherlands (1900-2010) is plotted (Bolt & Van Zanden, 2014). The Pearson correlation coefficients for four time periods are -0.81 (1900-1925), -0.22 (1925-1950), -0.88 (1950-1975) and +0.92 (1975-2010). The average relative species abundance shows a negative correlation with GDP per capita from 1900 to 1975. So earlier economic growth – early industrialisation – had a strong negative effect on the environment. From 1975 onwards, however, there is a spectacular turning point, towards a positive correlation between biodiversity and GDP per capita. This is consistent with the environmental Kuznets curve, hypothesizing that economic development not necessary increase environmental problems and even suggest that the most (economically) developed countries will eventually propagate environmental reform.

Conclusion

Society and economy are highly dependent on a large range of eco-system services. At the very basic level, we cannot breathe without the oxygen that has been produced by photosynthesis in plants. Yet, at the same time biodiversity is declining dramatically on a global scale due to economic, demographic and socio-political changes, meaning that the capacity to deliver these eco-system services is eroding. It is of fundamental importance to analyse these changes and to learn from past experiences. However, almost no historical research into the development of biodiversity is carried out, as biologists lack the knowledge of historical sources and methods of research and (economic) historians are not trained to research these environmental topics. Communication and cooperation between biologists and ecologists on the one hand and economic and environmental historians on the other hand is rare.

This paper, written by a biologist and an economic historian, suggests an approach which makes it possible to study the evolution of biodiversity in the past, making intensive use of historical sources on the evolution of the population sizes (abundance) of species (mammals,

birds and fish) in the twentieth century. It focuses on the construction of a biodiversity index for this period – which can be presented in both an unweighted version (where all species are considered equal) and a weighted version (where species are given weights related to the size of the eco-system they are representing). Moreover, by identifying the habitats, threats, and feeding types of the species concerned, it is also possible to trace the main drivers of decline or growth of these species.

The constructed index of biodiversity shows a very strong decline during the first seven decades of the 20th century, followed by rapid recovery after about 1975. This pattern is consistent with the environmental Kuznets curve discussed in the literature. Most interesting is the turn in the curve in the 1970s, which is probably related to 1. A strong reduction of pollution after the emergence of the environmental movement in the 1960s and 1970s; 2. A strong reduction in the pressure from hunting and other forms of persecution; 3. The adaptation of certain species to intense human contact, resulting in a rise of biodiversity in urban areas (also resulting from the reduction in persecution); 4. The growth of forest area (and protected nature reserves in general) and the improved management of these forests (increasingly focused on nature preservation). However, we also find evidence that increased agricultural intensification, resulting in eutrophication, in low biodiversity in arable and grass lands and in declines of insect populations (leading to low abundances of insectivore species), is the main cause of low levels of biodiversity, in particular in the countryside. That total biodiversity has recovered from the deep crisis it was in during the 1960s and 1970s is a sign of hope, as it shows that a rich nature can probably be maintained in a society with a very dense population and a high level of real income. We add the caveats that historical data are sparse and difficult to standardize, and that changes in the international position of the Dutch economy not analysed here may also have played a large role.

These are tentative conclusions, however, as much more work is necessary to better understand the links between biodiversity and its drivers. More progress has to be made in linking these results to quantitative data on the drivers of the changes in biodiversity, such as pollution, hunting, intensification of agriculture, urban growth, and, on the positive side, environmental protection and the increase of nature reserves. The disaggregated indices presented here already point to the relative importance of some of these drivers, but it should be possible to test those links more carefully making use of independent data on changes in these fields.

More international comparative research is also required to situate the case of the Netherlands in an international context. Is the recent recovery of biodiversity a more general phenomenon, also found in other rich countries, or specific for north western Europe, where the movement for nature conservation is particularly strong and where policies are quite effective? The holy grail of this research is to estimate the evolution of biodiversity on a regional and finally on a global scale, making it possible to analyse and understand what is explaining the dramatic decline that we witness at that level.

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Appendix

Appendix I: Species selection procedure, inter- and extrapolation and calculation national biodiversity indices

Table A1. References for species population data

Table A2. Abundance index per species

Table A3. Species categorization

Appendix II: Calculation weighted terrestrial index

Table A4. Development surface area habitats 1900-2000

Appendix III: Calculation similarity index

Appendix I: Species selection procedure, inter- and extrapolation and calculation national biodiversity indices.

The national biodiversity indices are based on population data of individual mammal, bird and fish species. Population data (in this regards) refers to the abundance of a species for the Netherlands as a whole. Data was collected for each individual species from journal articles and reports. Not only census data was included in the dataset, but also proxies of species abundance trends such as fish landings and hunting records. No modelled population data was included. The minimum number of data points per species were not used as a selection criterion as opportunities for inter- and extrapolation was case dependent (see next section). In total 58 species were included in the dataset, see table A1 for an overview.

The aim was to collect population data of each individual species for every 5-year interval starting in 1900 until 2015. Some species (12 in total) had data for each year (or most years) in the studied time period. In this case the running average of the 5 years around each 5-year interval was taken. However, most species had gaps in the data, either missing data in between different 5-year intervals or missing data for the earliest time period (mostly between 1900-1950). In this case data was inter- and extrapolated, 10 species had interpolation, 24 extrapolation and 12 a combination of inter- and extrapolation. Linear interpolation was used when data for no more than three consecutive 5-year intervals was missing. When data gaps were larger additional qualitative information was consulted (see extrapolation). Population data was extrapolated when data was missing for the earliest time period. Extrapolation was based on quantitative information from journals and reports and abundance data from later periods. Estimates were made conservatively, e.g. not assuming a linear trend upfront. See table A2 for (standardized) population data, the inter- and extrapolated estimates are indicated in red.

For each species the relative abundance was calculated based on the maximum abundance found for that species. The biodiversity indices were then calculated by taking the mean per 5-year interval of the series involved, the index was presented with 1900 as a base year. The disaggregated indices (based on taxonomic class, feeding type, etc.) have been calculated based on the same procedures as for calculating the national biodiversity index, but only including those species relevant for the respective categories. The details of species categorization can be found in table A3.

Table A1. References for species population data

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 Table A2. Abundance index per species

| 1900 | 1905 | 1910 | 1915 | 1920 | 1925

 | 1930
 | 1935

 | 1940 | 1945 | 1950 | 1955 | 1960 | 1965 | 1970
 | 1975
 | 1980 | 1985 | 1990
 | 1995 | 2000
 | 2005 | 2010 | 2015 |
|------|---|--|---|--
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0.42	0.38

 | 0.42
 | 0.38

 | 0.42 | 0.50 | 0.42 | 0.25 | 0.05 | 0.21 | 0.33
 | 0.42
 | 0.54 | 0.63 | 0.75
 | 1.00 | 0.48
 | 0.50 | 0.57 | 0.65 |
| 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00

 | 0.00
 | 0.00

 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00
 | 0.00
 | 0.00 | 0.00 | 0.04
 | 0.10 | 0.19
 | 0.40 | 0.67 | 1.00 |
| 1.00 | 0.86 | 0.86 | 0.79 | 0.79 | 0.71

 | 0.57
 | 0.43

 | 0.29 | 0.05 | 0.14 | 0.29 | 0.43 | 0.32 | 0.21
 | 0.14
 | 0.09 | 0.04 | 0.00
 | 0.00 | 0.00
 | 0.02 | 0.08 | 0.16 |
| 1.00 | 0.99 | 0.99 | 0.98 | 0.97 | 0.96

 | 0.94
 | 0.92

 | 0.89 | 0.87 | 0.50 | 0.25 | 0.12 | 0.06 | 0.05
 | 0.02
 | 0.00 | 0.00 | 0.00
 | 0.00 | 0.00
 | 0.00 | 0.00 | 0.00 |
| 0.71 | 0.68 | 0.65 | 0.61 | 0.58 | 0.53

 | 0.47
 | 0.42

 | 0.37 | 0.31 | 0.26 | 0.16 | 0.11 | 0.04 | 0.04
 | 0.05
 | 0.04 | 0.05 | 0.12
 | 0.23 | 0.60
 | 1.00 | 0.56 | 0.48 |
| 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00

 | 0.00
 | 0.00

 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00
 | 0.00
 | 0.00 | 0.01 | 0.03
 | 0.08 | 0.17
 | 0.44 | 0.79 | 1.00 |
| 1.00 | 0.87 | 0.81 | 0.75 | 0.73 | 0.73

 | 0.65
 | 0.58

 | 0.48 | 0.38 | 0.33 | 0.23 | 0.06 | 0.06 | 0.03
 | 0.02
 | 0.02 | 0.03 | 0.03
 | 0.06 | 0.13
 | 0.14 | 0.26 | 0.29 |
| 1.00 | 0.83 | 0.75 | 0.67 | 0.58 | 0.50

 | 0.42
 | 0.40

 | 0.38 | 0.37 | 0.36 | 0.35 | 0.33 | 0.27 | 0.20
 | 0.17
 | 0.13 | 0.15 | 0.18
 | 0.25 | 0.28
 | 0.38 | 0.42 | 0.42 |
| 0.02 | 0.03 | 0.03 | 0.03 | 0.03 | 0.04

 | 0.04
 | 0.06

 | 0.08 | 0.09 | 0.11 | 0.15 | 0.19 | 0.21 | 0.22
 | 0.25
 | 0.31 | 0.39 | 0.48
 | 0.56 | 0.64
 | 0.71 | 0.78 | 1.00 |
| 1.00 | 1.00 | 0.99 | 0.98 | 0.98 | 0.97

 | 0.96
 | 0.96

 | 0.95 | 0.94 | 0.92 | 0.91 | 0.89 | 0.87 | 0.85
 | 0.83
 | 0.80 | 0.78 | 0.74
 | 0.70 | 0.70
 | 0.68 | 0.73 | 0.75 |
| 0.39 | 0.38 | 0.38 | 0.37 | 0.37 | 0.36

 | 0.35
 | 0.34

 | 0.32 | 0.39 | 0.49 | 0.53 | 0.58 | 0.63 | 0.68
 | 0.74
 | 0.79 | 0.84 | 0.92
 | 0.99 | 0.99
 | 0.98 | 0.99 | 1.00 |
| 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00

 | 1.00
 | 1.00

 | 1.00 | 1.00 | 0.80 | 0.60 | 0.40 | 0.30 | 0.22
 | 0.20
 | 0.60 | 0.90 | 1.00
 | 1.00 | 0.70
 | 0.70 | 0.80 | 0.70 |
| 0.00 | 0.00 | 0.02 | 0.03 | 0.03 | 0.03

 | 0.03
 | 0.04

 | 0.04 | 0.10 | 0.16 | 0.18 | 0.21 | 0.27 | 0.32
 | 0.39
 | 0.43 | 0.47 | 0.64
 | 0.71 | 0.73
 | 0.91 | 1.00 | 0.92 |
| 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00

 | 1.00
 | 0.94

 | 0.94 | 0.59 | 0.12 | 0.02 | 0.00 | 0.00 | 0.00
 | 0.00
 | 0.00 | 0.00 | 0.01
 | 0.03 | 0.12
 | 0.34 | 0.53 | 0.65 |
| 0.97 | 1.00 | 0.93 | 0.92 | 0.44 | 0.40

 | 0.21
 | 0.07

 | 0.06 | 0.04 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00
 | 0.00
 | 0.00 | 0.00 | 0.00
 | 0.00 | 0.01
 | 0.00 | 0.00 | 0.01 |
| 1.00 | 0.64 | 0.17 | 0.05 | 0.04 | 0.02

 | 0.01
 | 0.00

 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00
 | 0.00
 | 0.00 | 0.00 | 0.00
 | 0.00 | 0.00
 | 0.00 | 0.00 | 0.00 |
| 0.35 | 0.35 | 0.35 | 0.35 | 0.35 | 0.35

 | 0.35
 | 0.35

 | 0.33 | 0.22 | 0.11 | 0.40 | 1.00 | 0.92 | 0.47
 | 0.69
 | 0.71 | 0.18 | 0.06
 | 0.11 | 0.03
 | 0.02 | 0.02 | 0.04 |
| 1.00 | 1.00 | 0.99 | 0.99 | 0.97 | 0.96

 | 0.92
 | 0.88

 | 0.81 | 0.72 | 0.62 | 0.48 | 0.35 | 0.25 | 0.17
 | 0.11
 | 0.07 | 0.04 | 0.03
 | 0.03 | 0.03
 | 0.03 | 0.04 | 0.04 |
| 0.81 | 0.81 | 0.81 | 0.81 | 0.81 | 0.81

 | 0.81
 | 0.81

 | 0.81 | 1.00 | 0.80 | 0.63 | 0.52 | 0.40 | 0.09
 | 0.03
 | 0.05 | 0.19 | 0.28
 | 0.18 | 0.33
 | 0.38 | 0.37 | 0.41 |
| 0.77 | 0.77 | 0.77 | 0.77 | 0.77 | 0.77

 | 0.77
 | 0.77

 | 0.77 | 0.77 | 0.77 | 0.77 | 0.77 | 0.75 | 1.00
 | 0.75
 | 0.65 | 0.51 | 0.40
 | 0.41 | 0.29
 | 0.20 | 0.37 | 0.47 |
| 0.76 | 0.76 | 0.76 | 0.76 | 0.76 | 0.76

 | 0.76
 | 0.76

 | 0.76 | 0.76 | 0.76 | 0.80 | 1.00 | 0.96 | 0.88
 | 0.57
 | 0.51 | 0.57 | 0.98
 | 0.71 | 0.47
 | 0.36 | 0.43 | 0.54 |
| 0.47 | 0.47 | 0.47 | 0.47 | 0.47 | 0.47

 | 0.47
 | 0.47

 | 0.47 | 0.47 | 0.47 | 0.43 | 0.49 | 0.57 | 0.54
 | 0.45
 | 0.43 | 0.60 | 0.59
 | 0.38 | 0.40
 | 0.43 | 0.75 | 1.00 |
| 1.00 | 0.77 | 0.29 | 0.03 | 0.02 | 0.02

 | 0.02
 | 0.00

 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00
 | 0.00
 | 0.00 | 0.00 | 0.00
 | 0.00 | 0.00
 | 0.00 | 0.00 | 0.00 |
| 0.21 | 0.11 | 0.14 | 0.24 | 0.10 | 0.33

 | 0.37
 | 0.71

 | 1.00 | 0.07 | 0.06 | 0.04 | 0.04 | 0.01 | 0.00
 | 0.00
 | 0.00 | 0.00 | 0.00
 | 0.00 | 0.00
 | 0.00 | 0.02 | 0.00 |
| 0.08 | 0.08 | 0.50 | 1.00 | 0.33 | 0.58

 | 0.43
 | 0.33

 | 0.23 | 0.33 | 0.33 | 0.33 | 0.67 | 1.00 | 0.50
 | 0.33
 | 0.33 | 0.43 | 0.33
 | 0.50 | 0.33
 | 0.33 | 0.23 | 0.23 |
| 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00

 | 1.00
 | 1.00

 | 1.00 | 1.00 | 0.69 | 0.60 | 0.64 | 0.28 | 0.11
 | 0.13
 | 0.12 | 0.29 | 0.21
 | 0.47 | 0.51
 | 0.52 | 0.55 | 0.54 |
| 0.86 | 0.86 | 0.86 | 0.86 | 0.86 | 0.86

 | 0.86
 | 0.86

 | 0.86 | 0.86 | 1.00 | 0.78 | 0.36 | 0.06 | 0.04
 | 0.12
 | 0.07 | 0.12 | 0.07
 | 0.11 | 0.06
 | 0.05 | 0.05 | 0.02 |
| 0.75 | 0.75 | 0.75 | 0.75 | 0.75 | 0.75

 | 0.75
 | 0.75

 | 0.75 | 0.75 | 1.00 | 0.71 | 0.43 | 0.22 | 0.16
 | 0.05
 | 0.05 | 0.13 | 0.16
 | 0.16 | 0.14
 | 0.14 | 0.16 | 0.20 |
| 0.69 | 0.69 | 0.69 | 0.69 | 0.69 | 0.69

 | 0.69
 | 0.62

 | 0.55 | 0.35 | 0.28 | 0.24 | 0.17 | 0.14 | 0.12
 | 0.31
 | 0.90 | 0.66 | 0.94
 | 0.96 | 1.00
 | 0.86 | 0.76 | 0.72 |
| 0.89 | 0.92 | 0.93 | 0.95 | 0.93 | 0.90

 | 0.92
 | 0.95

 | 0.95 | 1.00 | 0.90 | 0.69 | 0.59 | 0.69 | 0.69
 | 0.89
 | 0.77 | 0.59 | 0.40
 | 0.28 | 0.24
 | 0.24 | 0.19 | 0.14 |
| 0.93 | 0.90 | 0.87 | 0.83 | 0.80 | 0.77

 | 0.73
 | 0.70

 | 0.67 | 0.63 | 0.55 | 0.57 | 0.67 | 0.75 | 0.92
 | 1.00
 | 0.67 | 0.50 | 0.38
 | 0.45 | 0.59
 | 0.58 | 0.52 | 0.56 |
| 0.81 | 0.81 | 0.81 | 0.81 | 0.81 | 0.81

 | 0.81
 | 0.81

 | 0.81 | 0.81 | 0.72 | 0.63 | 0.54 | 0.07 | 0.11
 | 0.33
 | 0.21 | 0.20 | 0.24
 | 0.37 | 0.54
 | 1.00 | 0.77 | 0.90 |
| 0.12 | 0.12 | 0.11 | 0.11 | 0.10 | 0.12

 | 0.14
 | 0.16

 | 0.18 | 0.19 | 0.20 | 0.18 | 0.14 | 0.11 | 0.08
 | 0.09
 | 0.11 | 0.14 | 0.21
 | 0.33 | 0.49
 | 0.65 | 0.90 | 1.00 |
| 0.72 | 0.66 | 0.60 | 0.55 | 0.51 | 0.45

 | 0.42
 | 0.39

 | 0.37 | 0.30 | 0.24 | 0.12 | 0.06 | 0.04 | 0.02
 | 0.02
 | 0.02 | 0.02 | 0.02
 | 0.09 | 0.16
 | 0.33 | 0.73 | 1.00 |
| 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 0.80

 | 0.60
 | 0.50

 | 0.50 | 0.20 | 0.05 | 0.05 | 0.04 | 0.03 | 0.02
 | 0.02
 | 0.02 | 0.01 | 0.02
 | 0.02 | 0.01
 | 0.02 | 0.04 | 0.05 |
| 0.04 | 0.04 | 0.04 | 0.04 | 0.04 | 0.04

 | 0.04
 | 0.04

 | 0.05 | 0.06 | 0.07 | 0.08 | 0.09 | 0.22 | 0.38
 | 0.42
 | 0.53 | 0.71 | 1.00
 | 0.83 | 0.67
 | 0.55 | 0.43 | 0.38 |
| 0.78 | 0.73 | 0.68 | 0.63 | 0.58 | 0.52

 | 0.47
 | 0.42

 | 0.39 | 0.35 | 0.32 | 0.29 | 0.27 | 0.25 | 0.60
 | 0.70
 | 0.74 | 0.81 | 0.98
 | 0.95 | 1.00
 | 1.00 | 0.83 | 0.70 |
| 0.02 | 0.02 | 0.02 | 0.02 | 0.02 | 0.02

 | 0.02
 | 0.02

 | 0.02 | 0.02 | 0.03 | 0.05 | 0.08 | 0.17 | 0.26
 | 0.39
 | 0.57 | 0.78 | 1.00
 | 1.00 | 0.78
 | 0.79 | 0.68 | 0.69 |
| 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00

 | 1.00
 | 1.00

 | 1.00 | 1.00 | 1.00 | 0.93 | 0.85 | 0.78 | 0.70
 | 0.63
 | 0.52 | 0.41 | 0.43
 | 0.30 | 0.16
 | 0.17 | 0.11 | 0.07 |
| | 1900 0.42 0.00 1.00 1.00 0.71 0.00 1.00 0.71 0.00 1.00 0.22 1.00 0.39 1.00 0.39 1.00 0.39 1.00 0.97 1.00 0.77 0.76 0.47 1.00 0.21 0.76 0.47 1.00 0.86 0.75 0.69 0.81 0.12 0.72 1.00 0.47 1.00 0.88 0.93 0.81 0.12 0.72 1.00 0.04 0.78 0.02 1.00 | 190019050.420.380.000.001.000.861.000.990.710.680.000.001.000.871.000.830.020.031.001.000.390.381.001.000.071.000.080.001.000.640.350.351.001.000.810.810.770.760.760.760.470.011.000.770.210.110.860.860.750.690.890.920.930.900.810.810.120.120.720.661.001.000.440.780.750.691.001.000.240.730.020.221.001.00 | 1900 1905 1910 0.42 0.38 0.42 0.00 0.00 0.00 1.00 0.86 0.86 1.00 0.99 0.99 0.71 0.68 0.65 0.00 0.00 0.00 1.00 0.87 0.81 1.00 0.83 0.75 0.02 0.03 0.03 1.00 1.00 0.99 0.39 0.38 0.38 1.00 1.00 0.99 0.39 0.38 0.38 1.00 1.00 1.00 0.01 1.00 0.22 1.00 1.00 1.00 0.02 1.00 1.00 0.47 0.47 0.47 0.56 0.75 0.75 0.47 0.47 0.47 1.00 1.01 0.14 0.48 0.86 0.86 0.47 0.47 0.47 | 19001905191019150.420.380.420.460.000.000.000.001.000.860.860.791.000.990.990.980.710.680.650.610.000.000.001.001.000.870.810.751.000.830.750.670.020.330.031.031.001.000.990.980.390.380.380.371.001.001.001.000.000.020.331.000.000.000.020.331.001.001.001.000.011.001.001.000.971.000.930.921.000.640.170.550.350.350.350.351.001.000.990.990.810.810.810.810.770.770.770.770.760.760.760.760.470.470.470.471.000.770.290.030.210.110.140.240.860.860.860.860.750.750.750.750.690.690.690.690.810.810.810.810.820.920.930.950.830.920.930.950.840.84 | 190019051916191519200.420.380.420.460.420.000.000.000.000.001.000.860.860.790.791.000.990.990.980.970.710.680.650.610.580.000.000.000.001.001.000.870.810.750.731.000.830.750.670.580.020.030.030.030.031.001.000.990.980.980.390.380.380.370.371.001.001.001.001.000.000.020.030.331.031.001.001.001.001.000.971.000.930.920.441.000.640.170.050.440.350.350.350.350.351.001.001.001.001.010.770.770.770.770.770.760.760.760.760.760.470.470.470.470.471.000.770.750.750.750.690.690.690.690.690.890.920.930.950.930.930.900.870.830.800.840.810.810.810.810.750.750.75 </td <td>1900190519161915192019250.420.380.420.460.420.380.000.000.000.000.001.001.000.990.990.980.970.960.710.680.650.610.580.530.000.000.000.000.001.001.000.870.810.750.730.731.000.830.750.670.580.510.020.030.030.030.030.041.001.000.990.980.980.970.390.380.370.370.360.370.390.380.370.370.360.311.001.001.001.001.001.000.000.020.030.030.330.331.001.001.001.001.001.000.971.000.930.920.440.401.000.770.770.770.770.760.760.760.760.760.810.810.810.810.810.770.770.770.770.770.760.760.760.760.760.750.750.750.750.750.690.690.690.690.690.840.840.810.810.810.750.750.750.75<td>19001905191019151920192519300.420.380.420.460.420.380.420.000.000.000.000.000.000.001.000.860.860.790.790.710.571.000.990.990.980.970.960.940.710.680.650.610.580.530.470.000.000.000.000.000.001.001.000.870.810.750.730.730.651.000.830.750.670.580.500.420.020.030.030.030.030.040.041.001.000.990.980.980.970.960.390.380.370.370.360.350.351.001.001.001.001.001.001.000.000.000.020.030.030.030.031.001.001.001.001.001.001.000.700.700.750.750.750.750.751.000.740.470.470.470.470.750.750.750.750.750.750.760.760.760.760.760.760.770.770.770.770.770.770.760.750.750.750.750.75<tr< td=""><td>190019051910191519201925193019350.420.380.420.460.420.380.420.380.000.000.000.000.000.000.001.000.990.990.970.710.570.431.000.990.990.980.970.960.940.920.710.680.650.610.580.530.470.420.000.000.000.000.000.000.000.001.000.830.750.730.730.650.581.000.830.750.670.580.500.420.400.020.030.030.030.030.040.060.960.390.380.380.370.370.360.350.341.001.001.001.001.001.001.001.000.000.000.020.030.030.030.030.041.001.001.001.001.001.001.000.010.020.030.350.350.350.350.350.350.350.350.350.350.350.440.410.470.470.470.470.770.770.770.770.770.770.760.760.760.760.760.760.470.470.47</td><td>1900190519101915192019251930193519400.420.380.420.380.420.380.420.380.420.000.000.000.000.000.000.000.000.001.000.860.860.790.710.570.430.291.000.990.990.980.970.960.940.920.890.710.680.650.610.580.530.470.420.370.000.000.000.000.000.000.000.000.000.001.000.870.810.750.730.730.650.580.481.000.830.750.670.580.500.420.400.380.020.030.030.030.040.040.060.950.390.380.380.370.370.360.350.340.321.001.001.001.001.001.001.001.001.000.000.000.020.330.330.330.330.340.321.001.001.001.001.001.001.001.001.000.011.001.001.001.001.001.001.001.000.050.350.350.350.350.350.350.350.350.760.760</td><td>19001905191019151920192519301935194019450.420.380.420.380.420.380.420.380.420.380.420.500.000.000.000.000.000.000.000.000.000.000.001.000.860.860.790.710.570.430.290.551.000.990.990.980.970.960.940.920.890.870.710.680.650.610.580.530.470.420.370.310.000.000.000.000.000.000.000.000.000.001.000.870.810.750.730.730.650.580.480.381.000.330.330.030.040.400.640.380.370.200.330.330.330.040.400.640.101.001.001.001.001.001.001.001.001.001.000.010.020.030.030.030.030.040.440.410.020.030.030.030.030.040.040.040.000.000.020.030.030.030.350.350.330.220.011.001.001.001.001.001.001.001.001.00<</td><td>19001910191019101920192819201928193019401940194019500.420.380.420.380.420.380.420.380.420.500.420.000.000.000.000.000.000.000.000.000.000.001.000.860.860.790.710.570.430.290.890.570.710.680.650.610.580.530.470.420.370.310.000.030.310.730.730.730.550.580.480.380.331.000.870.810.750.730.730.730.400.400.660.940.920.390.380.370.360.350.340.320.390.490.920.390.380.370.370.360.350.340.320.390.491.001.001.001.001.001.001.001.001.001.000.390.380.370.370.360.350.340.320.390.490.491.001.001.001.001.001.001.001.001.</td><td>19001905191019151920192519301935194019451946195519560.420.380.420.380.420.380.420.580.500.520.000.000.000.000.000.000.000.000.000.000.001.000.860.860.790.710.570.430.290.890.870.500.250.710.680.650.610.580.530.470.420.370.310.260.160.00</td><td>1900 1910 1915 1920 1935 1940 1945 1946 1945 1956 1956 1956 0.42 0.38 0.42 0.38 0.42 0.38 0.42 0.50 0.00 0.</td><td>1900 1915 1920 1920 1920 1935 1940 1945 1950 1950 1966 0.42 0.38 0.42 0.38 0.42 0.38 0.42 0.50 0.42 0.25 0.42 0.25 0.42 0.25 0.42 0.25 0.41 0.30 0.00 0.</td><td>1900 1905 1910 1920 1930 1930 1930 1930
1930 <th< td=""><td>1906 1906 1915 1920 1930 1930 1940 1944 1950 1950 1956 1960 1965 1970 1975 0.00 0</td><td>1900 1905 1904 1904 1904 1904 1905 1905 1905 1970 1975 1980 0.42 0.38 0.42 0.46 0.44 0.38 0.42 0.53 0.42 0.54 0.54 0.52 0.05 0.00 0.</td><td>1900 1905 1916 1917 1928 1938 1948 1958 1950 1957 1976 1975 1976 1976 1975 1976 1975 1976 1975 1976 1975 1976 1975 1976 1975 1976 1975 1976 1975 1976 <th< td=""><td>1900 1905 1916 1915 1926 <th< td=""><td>1900 1905 1905 1960 1965 1960 1965 1960 1965 1960 1965 1960 1965 1960 1965 1960 1965 1960 1965 1960 1965 1960 1965 1960 <th< td=""><td>1900 1900 1910 1913 1920 1933 1940 1945 1950 1960 1960 1980 1980 1980 1980 1980 1980 1990 100<td>1900 1910 <th< td=""><td>1906 1910
1910 <th< td=""></th<></td></th<></td></td></th<></td></th<></td></th<></td></th<></td></tr<></td></td> | 1900190519161915192019250.420.380.420.460.420.380.000.000.000.000.001.001.000.990.990.980.970.960.710.680.650.610.580.530.000.000.000.000.001.001.000.870.810.750.730.731.000.830.750.670.580.510.020.030.030.030.030.041.001.000.990.980.980.970.390.380.370.370.360.370.390.380.370.370.360.311.001.001.001.001.001.000.000.020.030.030.330.331.001.001.001.001.001.000.971.000.930.920.440.401.000.770.770.770.770.760.760.760.760.760.810.810.810.810.810.770.770.770.770.770.760.760.760.760.760.750.750.750.750.750.690.690.690.690.690.840.840.810.810.810.750.750.750.75 <td>19001905191019151920192519300.420.380.420.460.420.380.420.000.000.000.000.000.000.001.000.860.860.790.790.710.571.000.990.990.980.970.960.940.710.680.650.610.580.530.470.000.000.000.000.000.001.001.000.870.810.750.730.730.651.000.830.750.670.580.500.420.020.030.030.030.030.040.041.001.000.990.980.980.970.960.390.380.370.370.360.350.351.001.001.001.001.001.001.000.000.000.020.030.030.030.031.001.001.001.001.001.001.000.700.700.750.750.750.750.751.000.740.470.470.470.470.750.750.750.750.750.750.760.760.760.760.760.760.770.770.770.770.770.770.760.750.750.750.750.75<tr< td=""><td>190019051910191519201925193019350.420.380.420.460.420.380.420.380.000.000.000.000.000.000.001.000.990.990.970.710.570.431.000.990.990.980.970.960.940.920.710.680.650.610.580.530.470.420.000.000.000.000.000.000.000.001.000.830.750.730.730.650.581.000.830.750.670.580.500.420.400.020.030.030.030.030.040.060.960.390.380.380.370.370.360.350.341.001.001.001.001.001.001.001.000.000.000.020.030.030.030.030.041.001.001.001.001.001.001.000.010.020.030.350.350.350.350.350.350.350.350.350.350.350.440.410.470.470.470.470.770.770.770.770.770.770.760.760.760.760.760.760.470.470.47</td><td>1900190519101915192019251930193519400.420.380.420.380.420.380.420.380.420.000.000.000.000.000.000.000.000.001.000.860.860.790.710.570.430.291.000.990.990.980.970.960.940.920.890.710.680.650.610.580.530.470.420.370.000.000.000.000.000.000.000.000.000.001.000.870.810.750.730.730.650.580.481.000.830.750.670.580.500.420.400.380.020.030.030.030.040.040.060.950.390.380.380.370.370.360.350.340.321.001.001.001.001.001.001.001.001.000.000.000.020.330.330.330.330.340.321.001.001.001.001.001.001.001.001.000.011.001.001.001.001.001.001.001.000.050.350.350.350.350.350.350.350.350.760.760</td><td>19001905191019151920192519301935194019450.420.380.420.380.420.380.420.380.420.380.420.500.000.000.000.000.000.000.000.000.000.000.001.000.860.860.790.710.570.430.290.551.000.990.990.980.970.960.940.920.890.870.710.680.650.610.580.530.470.420.370.310.000.000.000.000.000.000.000.000.000.001.000.870.810.750.730.730.650.580.480.381.000.330.330.030.040.400.640.380.370.200.330.330.330.040.400.640.101.001.001.001.001.001.001.001.001.001.000.010.020.030.030.030.030.040.440.410.020.030.030.030.030.040.040.040.000.000.020.030.030.030.350.350.330.220.011.001.001.001.001.001.001.001.001.00<</td><td>19001910191019101920192819201928193019401940194019500.420.380.420.380.420.380.420.380.420.500.420.000.000.000.000.000.000.000.000.000.000.001.000.860.860.790.710.570.430.290.890.570.710.680.650.610.580.530.470.420.370.310.000.030.310.730.730.730.550.580.480.380.331.000.870.810.750.730.730.730.400.400.660.940.920.390.380.370.360.350.340.320.390.490.920.390.380.370.370.360.350.340.320.390.491.001.001.001.001.001.001.001.001.001.000.390.380.370.370.360.350.340.320.390.490.491.001.001.001.001.001.001.001.001.</td><td>19001905191019151920192519301935194019451946195519560.420.380.420.380.420.380.420.580.500.520.000.000.000.000.000.000.000.000.000.000.001.000.860.860.790.710.570.430.290.890.870.500.250.710.680.650.610.580.530.470.420.370.310.260.160.00</td><td>1900 1910 1915 1920 1935 1940 1945 1946 1945 1956 1956 1956 0.42 0.38 0.42 0.38 0.42 0.38 0.42 0.50 0.00 0.</td><td>1900 1915 1920 1920 1920 1935 1940 1945 1950 1950 1966 0.42 0.38 0.42 0.38 0.42 0.38 0.42 0.50 0.42 0.25 0.42 0.25 0.42 0.25 0.42 0.25 0.41 0.30 0.00 0.</td><td>1900 1905 1910 1920 1930 <th< td=""><td>1906 1906 1915 1920 1930 1930 1940 1944 1950 1950 1956 1960 1965 1970 1975 0.00 0</td><td>1900 1905 1904 1904 1904 1904 1905 1905 1905 1970 1975 1980 0.42 0.38 0.42 0.46 0.44 0.38 0.42 0.53 0.42 0.54 0.54 0.52 0.05 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00
0.00 0.</td><td>1900 1905 1916 1917 1928 1938 1948 1958 1950 1957 1976 1975 1976 1976 1975 1976 1975 1976 1975 1976 1975 1976 1975 1976 1975 1976 1975 1976 1975 1976 <th< td=""><td>1900 1905 1916 1915 1926 <th< td=""><td>1900 1905 1905 1960 1965 1960 1965 1960 1965 1960 1965 1960 1965 1960 1965 1960 1965 1960 1965 1960 1965 1960 1965 1960 <th< td=""><td>1900 1900 1910 1913 1920 1933 1940 1945 1950 1960 1960 1980 1980 1980 1980 1980 1980 1990 100<td>1900 1910 <th< td=""><td>1906 1910 <th< td=""></th<></td></th<></td></td></th<></td></th<></td></th<></td></th<></td></tr<></td> | 19001905191019151920192519300.420.380.420.460.420.380.420.000.000.000.000.000.000.001.000.860.860.790.790.710.571.000.990.990.980.970.960.940.710.680.650.610.580.530.470.000.000.000.000.000.001.001.000.870.810.750.730.730.651.000.830.750.670.580.500.420.020.030.030.030.030.040.041.001.000.990.980.980.970.960.390.380.370.370.360.350.351.001.001.001.001.001.001.000.000.000.020.030.030.030.031.001.001.001.001.001.001.000.700.700.750.750.750.750.751.000.740.470.470.470.470.750.750.750.750.750.750.760.760.760.760.760.760.770.770.770.770.770.770.760.750.750.750.750.75 <tr<
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Sandwich tern	0.40	0.23	0.01	0.11	0.30	0.33	0.52	0.80	1.00	0.63	0.81	0.82	0.34	0.06	0.05	0.12	0.21	0.26	0.27	0.31	0.39	0.45	0.47	0.43
Eurasian curlew	0.64	0.61	0.58	0.55	0.52	0.49	0.46	0.43	0.40	0.37	0.34	0.34	0.35	0.36	0.37	0.49	0.86	1.00	0.96	0.92	0.85	0.75	0.63	0.56
Little grebe	1.00	0.94	0.89	0.83	0.78	0.72	0.67	0.61	0.56	0.50	0.44	0.39	0.33	0.28	0.19	0.17	0.33	0.32	0.31	0.39	0.60	0.66	0.56	0.55
European stonechat	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.98	0.95	0.91	0.82	0.68	0.55	0.36	0.23	0.23	0.09	0.09	0.12	0.18	0.32	0.44	0.68	0.80
Woodlark	0.78	0.78	0.78	0.78	0.78	0.78	0.78	0.78	0.78	0.78	0.78	0.62	0.46	0.30	0.14	0.16	0.40	0.14	0.39	0.73	0.84	0.83	0.83	1.00
Northern goshawk	0.05	0.05	0.05	0.06	0.07	0.08	0.09	0.11	0.12	0.14	0.17	0.19	0.09	0.05	0.08	0.19	0.57	0.71	0.78	0.83	0.89	0.92	1.00	0.95
Common buzzard	0.11	0.11	0.11	0.11	0.11	0.10	0.09	0.07	0.07	0.06	0.06	0.06	0.04	0.02	0.03	0.14	0.17	0.20	0.54	0.71	0.84	0.91	0.99	1.00
Eurasian sparrowhawk	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.19	0.17	0.19	0.19	0.19	0.15	0.05	0.05	0.12	0.34	0.34	0.85	1.00	0.94	0.89	0.74	0.68
European herring gull	0.03	0.02	0.03	0.02	0.06	0.08	0.12	0.22	0.17	0.18	0.22	0.20	0.17	0.22	0.33	0.56	0.94	1.00	0.90	0.81	0.75	0.63	0.58	0.50
Black-tailed godwit	0.33	0.39	0.44	0.50	0.56	0.60	0.66	0.73	0.77	0.83	0.87	0.91	0.95	1.00	0.98	1.00	0.79	0.71	0.60	0.54	0.45	0.36	0.29	0.28
Black grouse	0.76	0.80	0.85	0.88	0.94	0.96	1.00	0.90	0.79	0.71	0.58	0.47	0.33	0.22	0.13	0.07	0.03	0.02	0.01	0.01	0.00	0.00	0.00	0.00
Ruff	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.80	0.60	0.50	0.40	0.23	0.13	0.10	0.06	0.04	0.02	0.01	0.00	0.00
Common tern	0.17	0.17	0.07	0.07	0.07	0.13	0.17	0.26	0.09	1.00	0.20	0.20	0.05	0.03	0.46	0.05	0.06	0.05	0.11	0.11	0.11	0.11	0.10	0.09
Greylag goose	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.03	0.05	0.13	0.19	0.28	0.56	1.00
Black Tern	1.00	1.00	1.00	1.00	1.00	1.00	0.90	0.90	0.85	0.95	0.90	0.70	0.50	0.35	0.25	0.13	0.10	0.10	0.09	0.09	0.08	0.08	0.08	0.08
Great Cormorant	0.17	0.17	0.17	0.17	0.17	0.17	0.17	0.17	0.17	0.17	0.17	0.07	0.09	0.07	0.11	0.17	0.26	0.48	0.65	0.78	0.78	1.00	0.91	0.96
Bluethroat	0.67	0.67	0.67	0.67	0.67	0.67	0.67	0.44	0.33	0.33	0.22	0.22	0.13	0.11	0.11	0.13	0.13	0.22	0.44	0.67	0.78	1.00	0.89	1.00
Rook	0.30	0.33	0.36	0.39	0.42	0.48	0.55	0.62	0.69	0.76	0.82	0.61	0.42	0.28	0.17	0.17	0.31	0.44	0.50	0.85	1.00	0.94	0.86	0.79
Black-crowned Heron	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.83	0.67	0.33	0.42	0.42	0.43	0.45	0.33	0.25	0.33	0.42	0.50	0.58	0.62	0.67

Table A3. Species categorization

Species	Salt marches	Open water, marches	Streams and rivers	Estuaria	Wet open dune	Raised bog	Wet heathland	Dry heath, inland dune	Urban areas	Open grassland	Open arable land	Cultural landschape	Shrubland	Deciduous forest	Mixed forest	Coniferous forest	Not threatened	Red list species	Carnivore	Insectivore	Piscivore	Herbivore	Omnivore	Hunting, persecution	Pollution	Eutrophication	Weather extremes	Disturbance	Habitat loss	Habitat fragmentation	Desiccation	Diseases
European rabbit								x	x			x	x				x					x		x		x			x			x
Eurasian beaver		x	x															x				x		x						x		
Eurasian		~	~															~				~		~						~		
otter Lesser		х	х															х			х			х	х	х		х	х	х		
horseshoe																																
bat Geoffrov's																		х		х					х			х	х			
bat																		х		х									х			
Grey seal Harbor seal	X X			X X														X X			x x			X X	x x			x x	x			
European																																
badger European							х	х				х	х	х	х	х	х						х	х				х	х	х		
roe deer					х		х	х				х	х	х	х	х	х					х		х				х		х		
Red fox	x	х			X X	х	X X	x	х	х	x	x	х	x	x	x	х	х	х			х		х		х		х	х		х	x
European																																
nare Wild boar	x							х		х	х	х		x	x		X X					х	x	х					х	x		x
Harbour																																
porpoise Atlantic				х														х			х				х			х				
salmon			х	х														х	х					х	х				х	х		
sturgeon			х	x														x			x			х	x				х	x		
European																																
eei Burbot			X X	x x														x x	X X					х	x x	х			x x	х		х
Atlantic																																
Atlantic cod			х	x													х	х	X X					X X								
Common																																
sole European				х														х	х					х								
plaice				х													х		х					х								
Allis shad Twait shad			х	x x													х	x	X X						х				х			
Sea trout			х	х														х	х													
spotted																																
catshark				х													х		х													
Spotted ray Thornback				х															х													
ray				х															х													
marsh																																
harrier		х			х												х		х					х	х				х			
plover	x																	x	x	x								x	x			
Eurasian		\ <i>.</i>																														
Common		х																х	X		х						x		х		х	
kingfisher		х	х														х				х				х		х		х			

Eurasian spoonbill	x	x		x												x		x						х			x	x		
White stork Red-backed		х						х	х							х		х										х		
shrike Eurasian				х	х	х					х	х					х	x	х									х		
oystercatch																														
er	х			Х					х	х						х		х	х									Х		
Grey neron Great		х							х				х			х		x		х			х	х		х				
crested																														
grebe		х														х				х			х		х					
Grey																														
partridge Sandwich				х		х	х		х	х	х						х				х	х						х	х	
tern Eurasian	x																х			х				х				х		
curlew				х	х	х	х		х	х	х						х	х	х											
Little grebe European		х		х	х	х										х		х								х				
stonechat				x	x	x	¥		x		x	x				x			x									Y		
Woodlark				Ŷ	~	x	Ŷ		~		~	~		x	x	Ŷ			x							x		x		
Northern				^		^	^							^	^	Â			^							^		^		
goshawk Common																х		х					х	х						
buzzard													х	х	х	х		х						х						
Eurasian																														
sparrowna											v		v	v	v	v		v						v						
W											^		^	^	^	^		^						^						
herring gull								х			х		х	х		x		x				x	x					х		
Black-tailed																														
godwit Black	х	х		х	х	х			х								х		х								х		×	K
grouse					х	х	х										х				х							х		
Ruff Common	х			х	х				х								х		х						х		х		×	K
tern	x	х	х	х					х								х			х				х						
Greylag		v														v					v		v					v		
Black Torn		Ŷ				v			v							^	v	v	v		^		^					^		
Great		~				X			٨								X	^	٨											
Cormorant		х														x				х										
Bluethroat		х			х	х						х				х			х			х								
Rook											х	-	х			x						x								
Black-																``														
crowned																														
Heron		x															v	v		v										

Appendix II: Calculation weighted terrestrial index

In the weighted terrestrial index the population series are weighted by the size of various ecosystems in 1900 and 2000. For each ecosystem, the average (relative) species abundance of indicator species is taken. See table A3 for the categories of species occurring in the specific ecosystems (habitats). Then, the average species abundance of each ecosystem is weighted by the seize in 1900 and 2000, respectively. See table A4 for the surface areas of the respective ecosystems in 1900 and 2000. The respective indices, i.e. weighted based on 1900 and 2000, are presented with 1900 as a base year (=1).

	1900	2000
Salt marches	24000	11990
Marches	36000	21010
Grassland	13475	15254
Arable land	8968	8885
Raised bogs	33000	160
Forest	248000	328660
Heathland	377000	35750
Total	740443	421709

Table A4. Development surface area habitats 1900-2000

Appendix III: Calculation similarity index

For each disaggregated index the similarity in species composition between 1900 and 2015 was calculated to assess the level of species turnover. The similarity index provides a number between 0 and 1, with 0 representing no change in species composition and 1 representing maximum change (see appendix IIIV for calculation details).

$$\frac{\sum_{i=1}^{n} |(SPi_{2015} - SPavg_{2015}) - (SPi_{1900} - SPavg_{1900})|}{N} \times 100$$

N is number of species in the index, SP_i is the relative species abundance of species i in either 2015 or 1900, SP_{avg} is the average species abundance in either 2015 or 1900.