WATERBIRDS IN A CHANGING WORLD: EFFECTS OF CLIMATE, HABITAT AND CONSERVATION POLICY ON EUROPEAN WATERBIRDS

DIEGO PAVÓN JORDÁN

The Helsinki Lab of Ornithology
Finnish Museum of Natural History
University of Helsinki
Finland

Faculty of Biological and Environmental Sciences
Department of Biosciences
University of Helsinki
Finland

Doctoral Programme in Wildlife Biology Research (LUOVA)
Doctoral School in Environmental, Food and Biological Sciences (YEB)
University of Helsinki
Finland

ACADEMIC DISSERTATION

To be presented for public examination with the permission of the Faculty of Biological and Environmental Sciences of the University of Helsinki in Auditorium C205, Economicum (Arkadiankatu 7), on May 5th 2017 at 9:00 AM.

HELSINKI 2017

SUPERVISED BY: Dr. Aleksi Lehikoinen
Helsinki Lab of Ornithology
Finnish Museum of Natural History, Finland

REVIEWED BY: Dr. Alison Johnston
British Trust for Ornithology (BTO), United Kingdom

Dr. Kari Koivula
University of Oulu, Finland

EXAMINED BY: Prof. Johan Elmberg
Kristianstad University, Sweden

CUSTOS: Prof. Liselotte Sundström
University of Helsinki, Finland

MEMBERS OF THE THESIS ADVISORY COMMITTEE:

Assistant Prof. Jon E. Brommer
University of Turku, Finland

Dr. Mar Cabeza
University of Helsinki, Finland

Dr. Jukka Rintala
Natural Resources Institute Finland (LUKE), Finland

ISBN 978-951-51-3124-9 (paperback)
ISBN 978-951-51-3125-6 (PDF)
http://ethesis.helsinki.fi

Unigrafia

Helsinki 2017

To my family, the Finnish and the Spanish. No matter where you are, you are always with me.

“Mantén siempre a Ítaca en tu mente.

Llegar allí es tu destino.

Mas no apresures nunca el viaje.

Mejor que dure muchos años

y atracar, viejo ya, en la isla,

enriquecido de cuanto ganaste en el camino,

sin esperar que Ítaca te enriquezca.”

Κωνσταντίνος Π. Καβάφης, Ítaca, 1911

CONTENTS

LIST OF ORIGINAL PUBLICATIONS

The thesis is based in the following articles, which are referred to in the text by their Roman numerals:

I Fox, A. D., Jónsson, J. E., Aarvak, T., Bregnballe, T., Christensen, T. K., Clausen, K. K., Clausen, P., Dalby, L., Holm, T. E., **Pavón-Jordan, D.**, Laursen, K., Lehikoinen, A., Lorentsen, S. –H., Møller, A. P., Nordström, M., Öst, M., Söderquist, P. & Therkildsen, O. R. (2015) Current and potential threats to Nordic duck populations — a horizon scanning exercise. *Annales Zoologici Fennici,* 52: 193–220.

II **Pavón-Jordán, D.**, Clausen, P., Crowe. O., Dagys, M., Deceuninck, B., Devos, K., Encarnaçao, V., Fox, A. D., Frost, T., Gaudard, C., Hornman, M., Keller, V., Langendoen, T., Ławicki, Ł., Lorentsen. S. -H., Luigujoe, L., Meissner, W., Molina, B., Musil, P., Musilova, Z., Nilsson, L., Paquet, J. -Y., Ridzon, J., Stipniece, A., Teufelbauer, N., Wahl, J., Zenatello, M. & Lehikoinen, A. Large-scale winter weather conditions drive inter-annual and long-term density changes of entire biogeographical populations of a guild of conservation concern in Europe. *Manuscript*.

III **Pavón-Jordán**, **D.,** Fox, A. D., Clausen, P., Dagys, M., Deceuninck, B., Devos, K., Hearn, R. D., Holt, C. A., Hornman, M., Keller, V., Langendoen, T., Ławicki, Ł., Lorentsen, S. –H., Luigujoe, L., Meissner, W., Musil,P., Nilsson, L., Paquet, J. –Y., Stipniece, A., Stroud, D. A., Wahl, J., Zenatello, M., & Lehikoinen, A. (2015) Climate-driven changes in winter abundance of a migratory waterbird in relation to EU protected areas. *Diversity and Distributions,* 21: 571–582.

IV **Pavón-Jordán, D.,** Santangeli, A. & Lehikoinen, A. (2017) Effects of flyway-wide weather conditions and breeding habitat on the breeding abundance of migratory boreal waterbirds. *Journal of Avian Biology*, doi:10.1111/jav.01125.

Table of contributions

	I	II	III	IV
Original idea	ADJ	**DPJ**, AL, ADF	**DPJ**, AL, ADF	**DPJ**, AL
Data	ADJ, **DPJ**, JEJ, TA, TB, TJK, KKC, PC, LD, THE, KL, AL, SHL, APM, MN, MÖ, PS, ORT	PC, OC, MD, BD, KD, VE, ADF, MH, VK, TL, LLa, SHL, LLu, WM, BM, PM, ZM, LN, JYP, JR, ASt, NT, JW, MZ, AL	PC, MD, BD, KD, CAH, MH, VK, TL, LLa, SHL, LLu, WM, PM, LN, JYP, ASt, JW, MZ, AL	**DPJ**, AL
Analyses	-	**DPJ**, AL	**DPJ**, AL	**DPJ**, AL
Manuscript preparation	ADJ, **DPJ**, JEJ, TA, TB, TJK, KKC, PC, LD, THE, KL, AL, SHL, APM, MN, MÖ, PS, ORT	**DPJ**, AL, ADF	**DPJ**, AL, ADF, RH, DAS, PC	**DPJ,** AL, ASa

Diego Pavón-Jordán (**DPJ**), Aleksi Lehikoinen (AL), Anthony D. Fox (ADF), Tomas Aarvak (TA), Thomas Bregnballe (TB), Thomas Kjær Christensen (TKC), Olivia Crowe (OC), Kevin Kuhlmann Clausen (KKC), Preben Clausen (PC), Mindaugas Dagys (MD), Lars Dalby (LD), Bernard Deceuninck (BD), Koen Devos (KD), Vitor Encarnacao (VE), Teresa Frost (TF), Richard D. Hearn (RDH), Thomas Eske Holm (TEH), Chas A. Holt (CAH), Menno Hornman (MH), Jón Einar Jónsson (JEJ), Verena Keller (VK), Tom Langendoen (TL), Karsten Laursen (KL), Łukasz Ławicki (ŁŁ), Svein-Håkon Lorentsen (SHL), Leho Luigujoe (LL), Włodzimierz Meissner (WM), Blas Molina (BM), Anders Pape Møller (APM), Petr Musil (PM), Zuzana Musilova (ZM), Leif Nilsson (LN), Mikael Nordström (MN), Markus Öst (MÖ), Jean-Yves Paquet (JYP), Jozef Ridzon (JR), Andrea Santangeli (ASa), Pär Söderquist (PS), Antra Stipniece (ASt), Norbert Teufelbauer (NT), David A. Stroud (DAS), Ole Roland Therkildsen (ORT), Johannes Wahl (JW), Marco Zenatello (MZ)

ABSTRACT

Climate change has become a major threat for biodiversity in recent decades. Waterbirds, in particular, are very responsive to climate change compared to other avian species and have already shown changes in phenology and distribution. Such strong and rapid response of some species to climate change has motivated debate about the effectiveness of the site-safeguard network, as climate change may ultimately push species of conservation concern out of the protected areas. One such network, which aims to protect all European bird species, is the Special Protection Area (SPA), designated under the EU Birds Directive.

My thesis overviews the most important environmental factors acting upon Nordic waterbird populations now and in the future. In addition, I studied (i) the spatial changes in wintering abundances of 25 waterbird species in Europe in relation to weather conditions, (ii) the effectiveness of the SPA network delivering climate change adaptation for a protected waterbird species and (iii) the effects of weather conditions and habitat type on the abundance of 17 waterbird species breeding in Finland.

Results show differential response of 25 waterbird species (classified into five guilds) to inter-annual variation in weather conditions. The centre of gravity in abundance of dabbling ducks, diving ducks, swans and other waterbird species (non-Anatidae) moved southwestwards in cold winters. On the other hand, only the centre of gravity in abundance of dabbling and diving ducks moved northeastwards in warm, and *a priori* beneficial, winter weather conditions. In this case, diving ducks responded the fastest. There was no link between the movement of the centre of gravity in abundance of geese with winter weather conditions. These differences in responses to weather conditions are probably related to different food and habitat requirements during winter as well as to life-history traits.

Furthermore, while the centre of gravity in abundance of diving ducks showed a steadily long-term shift northeastwards over the past three decades, that of other waterbird species shifted southwestwards in recent years probably due to several consecutive cold winters. Dabbling ducks, swans and geese did not show long-term shifts. A detailed study about the wintering distribution of the smew *Megellus albellus* supports the above-mentioned findings and shows that the wintering numbers of this protected diving duck in the northeastern part of the wintering range increased from 6% of the total wintering population in the early 1990s to 32% in the early 2010s.

In this context of climate-driven redistribution of wintering waterbirds, the EU's SPA network facilitated the redistribution of wintering smew towards the northeast: smew wintering numbers increased twice as fast inside than outside SPAs. However, results also pinpointed big gaps in the SPA network in north European countries, as most of the individuals winter outside the network in Sweden (79%) and Finland (95%). This findings call for an urgent assessment of the network in northern Europe, where wintering numbers are rapidly increasing. Furthermore, due to the high flexibility in migration of this and other waterbirds according to current weather conditions, it is of paramount importance to maintain a cohesive and coherent site-safeguard network throughout the flyway, including cold weather refuge sites.

Lastly, the abundance of waterbird species breeding in Finland was higher after mild winters in western and northern Europe likely

due to improved survival. This beneficial effect of mild weather conditions was more apparent in eutrophic wetlands than in oligotrophic ones. However, my analysis of population trends in different habitat types revealed faster population declines in wetlands surrounded by agricultural and urban areas, possibly due to hyper-eutrophication processes that renders such wetlands unsuitable for waterbirds to breed. These findings suggest that the impact decreased habitat quality can overcome the positive effects of milder winters and cause populations to decline.

TIIVISTELMÄ

Ilmastonmuutoksesta on tullut merkittävä uhka luonnon monimuotoisuudelle. Vesilinnuilla on osoitettu ilmaston aiheuttamia muutoksia fenologiassa ja levinneisyydessä, ja ne reagoivat voimakkaammin muuttuvaan ilmastoon kuin monet muut lintulajiryhmät. Nopeat muutokset ovat käynnistäneet keskustelun suojelualueverkoston toimivuudesta ilmaston ja lajien levinneisyysalueiden muuttuessa, sillä ilmastonmuutos voi työntää suojeltavan lajin levinneisyyden suojelualueiden ulkopuolelle. Euroopan Unionin lintudirektiivin perusteella rauhoitetut SPA-alueet (Special Protection Areas) muodostavat merkittävän suojelualueverkoston.

Väitöskirjani koostuu neljästä osatyöstä ja näiden yhteenvedosta. Ensimmäinen osatyöni käsittelee tärkeimpiä Pohjoismaiden sorsakantoihin nyt ja tulevaisuudessa vaikuttavia tekijöitä. Loput kolme osatyötäni tarkastelevat (i) vesilintujen talvipopulaatioiden muutoksia Euroopassa 25 vesilintulajilla viime vuosikymmeninä, (ii) EU:n suojelualueverkoston tehokkuutta sopeutua vesilintujen talviaikaisiin levinneisyysmuutoksiin ja (iii) säätekijöiden sekä elinympäristön laadun yhteisvaikutusta 17 vesilintulajin pesimäpopulaatioihin Suomessa.

Tulokset osoittavat, että viiteen vesilintukiltaan jaetut 25 vesilintulajia reagoivat eri tavalla talven sääolojen vaihteluun. Puolisukeltaja- ja sukeltajasorsien ja joutsenten talviset runsauden painopisteet siirtyivät kohti lounasta kylminä talvina, mutta keskimääräistä lämpiminä talvina painopiste siirtyi kohti koillista vain puolisukeltaja- ja sukeltajasorsilla. Sukeltajasorsat olivat ainoa ryhmä, jolla talvirunsauden painopiste on siirtynyt kohti koillista viimeisen 25 vuoden aikana. Alueelliset muutokset lajien talvirunsauden muutoksista ja niiden yhteys talven sääoloihin riippunevat lajiryhmien ravinto- ja elinympäristövaatimuksista.

Erillinen tarkastelu EU:n lintudirektiivin erityissuojellulla sukeltajasorsalajilla, uivelolla, osoitti, että Pohjois-Euroopassa talvehtivien lintujen osuus koko talvikannasta on kasvanut 6 %:sta 32:een vuosina 1990–2011. Tulokset viittaavat, että EU:n suojelualueverkosto tukee lajin levittäytymistä kohti pohjoista, sillä Pohjois-Euroopassa talvikanta kasvoi lähes kaksi kertaa nopeammin EU:n SPA-alueilla. Tutkimukseni kuitenkin paljasti, että osassa Pohjois-Euroopan maissa lajin suojelutilanne on heikko: SPA-alueiden ulkopuolella talvehtivien lintujen osuus oli Ruotsissa 79 % ja Suomessa peräti 95 %. Tulosten perusteella suojelualueen kattavuutta tulisi päivittää säännöllisesti etenkin pohjoisilla alueilla, sillä ilmastonmuutoksen myötä lajien levinneisyysalueet ja runsaudet muuttuvat. Koska kylmät talvet työntävät vesilintuja talvehtimaan eteläisille alueille, eteläisten alueiden suojelu on edelleen tärkeää suojelualueverkoston joustavuuden kannalta.

Viimeisessä osatyössäni selvitin, että vesilintulajilla pesimäkannat kasvoivat leutojen talvien jälkeen todennäköisesti parantuneen hengissäsäilyvyyden takia. Tämä leutojen talvien suotuisa vaikutus oli voimakkaampaa rehevillä kosteikoilla kuin karuilla vesillä. Elinympäristökohtainen tarkasteluni kuitenkin paljasti, että vesilinnut taantuivat kaikkein voimakkaimmin maatalousympäristöjen ja taajamien läheisillä kosteikoilla, todennäköisesti liiallisen rehevöitymisen takia. Tulokset osoittavat, että heikentynyt elinympäristön laatu voi kumota leudontuneen ilmaston positiiviset vaikutukset.

SUMMARY

Diego Pavón Jordán

The Helsinki Lab of Ornithology, Finnish Museum of Natural History, Helsinki, Finland.

Introduction

The environment in which species develop their life cycle is naturally dynamic in time and space. Individual species, thus, have to cope with variable levels of unpredictability with respect to their surroundings (Begon et al. 1994). Besides the natural fluctuations in environmental conditions, organisms have to cope with rapid changes in climatic conditions derived from human activities (IPCC 2012, 2013, EEA 2012). Effective evidence-based conservation can only be accomplished when the drivers of population change at local, country and global scales have been disentangled (Stroud et al 2004, Sutherland et al. 2004, Courchamp et al. 2015, Johnston et al. 2015, Fox et al. 2016a). Traditionally, continuous, profound and rapid human alteration of the original characteristics of most of Earth's habitats has been considered the most important cause of biodiversity loss at a planetary scale (Pimm et al. 2006). However, new evidence is accumulating that anthropogenic climate change has become a major threat for biodiversity in the past decades (Parmesan & Yohe 2003, Thomas & Williamson 2012). While some organisms may be unable to survive such changes, others have shown clear responses to changes in climatic conditions (Parmesan 2006, Mawdsley et al. 2009, Mawdsley 2011), for example by either altering the timing of some of their phenological events, such as flowering (Menzel et al. 2006, Frei et al. 2014, Amano et al. 2016) and migration time (Møller et al. 2008, Knudsen et al. 2011, Kelly et al. 2016) or by changing their distribution (Chen et al. 2011, Thomas et al. 2012, Amano et al. 2016, Santangeli & Lehikoinen 2017).

To quantify the impact of changes in environmental conditions on wildlife, one needs good quality, long-term monitoring data of species. Birds are unquestionably the taxon that has been most extensively monitored, over the longest time period, owing to tens of thousands of volunteer birdwatchers that participate in different monitoring schemes around the world. With these data, researchers have been able to show that some avian species have responded in different ways to climate change in the past decades (Møller et al. 2010, Pearce-Higgins et al. 2015). Some studies have shown evidence of the positive relationship between such responses and population trends: for instance, species that did not advance their spring migration declined in the 1990s, whereas those able to track climatic changes showed stable or increasing population trends (Møller et al. 2008). However, the direct benefits of advancing migration time is not always evident and changes in other environmental factors may have stronger impact on population trends (Ockendon et al. 2012 and references therein). The type, speed and strength of such responses to climate change are, therefore, highly species-specific. In particular, waterbirds have shown to be very responsive to climate change compared to other avian species (Brommer 2008, Bussière et al. 2015) and have shown changes in phenology (Lehikoinen et al 2006, Guillemain et al. 2013, Donnelly et al. 2015, Szostek et a. 2015) and distribution (Zipkin et al. 2010, Godet et al. 2011, Gunnarsson et al. 2012, Lehikoinen et al. 2013).

Waterbirds are defined as a group of bird species strictly reliant on aquatic environments, at least in some stage of their life cycle. Within waterbirds, one can find several groups of avian species. For example, the term *waterfowl* includes all species of the Orders *Gaviiformes, Podicipediformes* and *Anseriformes* as well as the Coot *Fulica atra* (del Hoyo et al. 1994). The term *waders* (or *shorebirds* in North America) refers to species belonging to the Order *Charadriiformes* (del Hoyo et al. 1994).

Many waterbirds are considered keystone species and have not only a crucial ecological role in the functioning of ecosystems (Green & Elmberg 2014, Arzel et al. 2015, Kleyheeg et al. 2017), but also a high economic and societal importance, specially relevant in the case of duck species (Green & Elmberg 2014). Waterfowl, in particular, are harvested as sources of eggs and down, comprising the main source of income sustaining certain communities in Norway and Iceland (e.g. Green & Elmberg 2014). In addition, ducks and waders are important game species (more than 7.6 million waterfowl and 4.2 waders are shot annually in Europe; Green & Elmberg 2014). Hunting is an old tradition and part of the culture of many countries in Europe and North America, as well as being a very profitable business worldwide (Black & Owen 1990, Glaeson et al. 2011, Green & Elmberg et al. 2014, Lindström et al. 2015). Moreover, waterbirds provide other ecosystem services that are beneficial and enhance people's welfare and day-to-day life, such as bird-watching, eco-tourism or enhancement of recreational areas (Glaeson et al. 2011, Green & Elmberg 2014, Arzel et al. 2015).

Waterbirds are usually considered indicators of wetland health and biodiversity (Guillemain et al. 2013, Green & Elmberg 2014, Arzel et al. 2014, but see Guareschi et al. 2015) and their abundance and diversity are often used as criteria to identify and qualify wetlands as internationally important and to designate as protected areas (Stroud et al. 2004, Glaeson et al. 2011, Wetlands International 2017). Hence, specific monitoring programmes targeting this group of birds have been running for many decades (Wetlands International 2017). Such schemes have revealed important population declines of many species in recent years in Europe (Holt et al. 2012, Waldeck & Larsson 2013, Wetlands International 2017) due to rapid habitat loss and exacerbated by ongoing climate change (Clausen et al. 2013, Guillemain et al. 2013, Márquez-Ferrando et al. 2014). For these and other reasons, most waterbird species and their key habitats are protected under international legislation and are included in conservation programs such as the RAMSAR Convention, African-Eurasian waterbird agreement (AEWA), the Convention on Migratory Species (CMS) and the Natura 2000 network, which combines the EU Birds Directive and the EU Habitats Directive (Wetlands International 2017).

Climate change & waterbird distributions

Although the future characteristics of the climate on Earth are difficult to anticipate, changes to date are beyond the expected natural variability (IPCC 2012, 2013). One of the main features of climate change is the increase in temperature (IPCC 2012). In this sense, the arctic and boreal zones are anticipated to experience the fastest changes (Jylhä et al. 2004, IPCC 2012). These two regions in particular, are used by many waterbird species as main breeding grounds (del Hoyo et al. 1994, Holopainen 2015, Lehikoinen et al. 2016a, Wetlands International 2017). Moreover, within the annual cycle, autumn, winter and spring temperatures have substantially increased in northern Europe and the Arctic region causing reductions in the Baltic Sea ice cover during the last decade and contributing to a 15–20% decrease in the circumpolar arctic ice cover over the past three decades (European Environmental Agency 2012, see also Tulp & Schekkermann 2008, Iverson et al. 2014, Prop et al. 2015). On the other hand, summer temperature increased only moderately compared to the other seasons in the past decade in Europe and this asymmetry is anticipated to increase in the future (Jylhä et al. 2004, European Environmental Agency 2012).

This variation in temperature change can have a profound impact on birds in general (Møller et al. 2010, Pearce-Higgins & Green 2014), and waterbirds in particular, because most of them are migratory species and therefore more vulnerable to the asynchrony of these changes (Guillemain et al. 2013, Donnelly et al. 2015, **I**). For example, some individuals may reduce their migration distance and spend the winter in newly available wintering grounds closer to the breeding sites. This is known as a short-stopping (see Elmberg et al. 2014) and is a direct consequence of the increase in temperature during winter in northern Europe, which creates new ice-free wetlands further north. The availability of new wintering sites may ultimately cause a shift northwards of the wintering range of some species (Lehikoinen et al. 2013, Fox et al. 2016b, **I, II, III**). Moreover, conditions in traditional wintering grounds are changing and, due to climate change previously unfavourable wintering sites may have become favourable for exploitation, causing a displacement of wintering sites (Austin et al. 2005, Maclean et al. 2008, see also Ockendon et al. 2012). Waterbirds, however, are also able to adjust their migration to current weather conditions and move further southwest along the flyway during harsh winters or unexpected cold-spells (Ridgill & Fox 1990, **II, III**). This phenomenon has recently given rise to concerns about the effectiveness of the current network of protected areas. Protected areas are static entities and may fail to protect those species of conservation concern as they change their distribution as a response to climate change (Araújo et al. 2011, Mawdsley 2011, Thomas et al. 2012, Johnston et al. 2013, **III**). Furthermore, changes in weather conditions during the non-breeding season can affect the abundance of waterbirds the following breeding season and ultimately the population dynamics of these species (Pöysä & Väänänen 2014, **IV,** see also Guillemain et al. 2005).

Climate change & wetland degradation

Aquatic ecosystems are especially threatened by climate change (Moss et al. 2011, Bellisario et al. 2014, Steen et al. 2016, Guareschi et al. 2015) which may accelerate the speed at which wetland dependent species such as waterbirds, lose their optimal habitat (Stoate et al. 2009, Gordo et al. 2011, Steen et al. 2014, 2016). Climate-driven alterations of wetland availability and quality have a sizable impact on waterbird distribution and abundance (Bellisario et al. 2014, Steen et al. 2014, 2016). In extreme cases, increased temperature and/or reduced rainfall may cause severe continuous droughts and loss of wetlands impacting the availability and distribution of both breeding and wintering habitats (Zwarts et al. 2009, EEA 2012, Steen et al. 2014, 2016).

Changes in climate may also alter the quality of wetlands. For example, increased temperature may unleash phytoplankton blooms, cause loss of food resources (i.e. underwater vegetation) and refugia from predators, increase water turbidity and outbreaks of diseases such as botulism; all symptoms of hyper-eutrophication (Moss et al. 2011, Guillemain et al. 2013, **I**). Traditionally, eutrophic wetlands have provided better breeding and wintering habitat for waterbirds than oligotrophic wetlands (Nilsson & Nilsson 1978, Kauppinen & Väisänen 1993). However, declines in waterbird populations have been associated with habitat degradation due to hyper-eutrophication of such wetlands in northern Europe (Fox et al. 2016a, Lehikoinen et al. 2016b, **I**, **IV**). Hyper-eutrophication of wetlands is a worrying problem at a planetary scale due to the high load of nutrients leaking from cultivated fields (Moss et al. 2011). Climate change, through the alteration of precipitation patterns, increased frequency of storms, increased soil temperature and favouring the melting of glaciers, will increase the damage caused by the runoff of nutrients from the catchment areas into wetlands (Moss et al. 2011). However, wetland management has been effective in restoring these habitats for waterbirds in several countries (Giles 1994, Holm & Clausen 2006, Ma et al. 2010, Gleason et al. 2011, Clausen et al. 2013, Bregnballe et al. 2014).

Aims & outline of the thesis

This project was born with the main goal of exploring the impacts of climate change on European waterbird populations, contributing to fill some gaps in our understanding of this complex process (Guillemain et al. 2013). In addition, it assesses the effectiveness of the EU conservation policy in the context of climate change. Because of the ecological and societal relevance of waterbirds, specific schemes have been running for decades to monitor their populations, especially outside the breeding season. Two of these schemes are, for example, the International Waterbird Census (IWC) which is coordinated worldwide since late 1960s (Delany 2005) and the Finnish breeding waterbird survey since 1986 (Koskimies & Väisänen 1991; see Methods below). These impressive datasets allow me to study processes occurring at large scales (e.g. flyway level; see Box 1 for useful definitions), which may provide valuable evidence for policy makers to propose efficient conservation measures. In conclusion, the availability of such long-term (several decades) and large-scale (whole of Europe) datasets on waterbird abundance coupled with the need of a better understanding of the drivers of change in waterbird populations at flyway scale motivated the start of this project.

This thesis could be divided in three thematic blocks:

The first block presents an overview of environmental and anthropogenic factors that currently impact Nordic waterbird populations as well as future threats that these may face in the near future (**I**). The main aim here was to put waterbirds in an environmental and climate change context to stimulate debate and to motivate further research. These would ultimately enhance our likelihood to succeed in maintaining and restoring waterbird populations through efficient conservations policies, now and in the future.

The second block describes responses of waterbirds during the wintering season to changes in weather conditions (North Atlantic Oscillation index, NAO), in general (**II**) and

Box 1. Short definition of flyway and other relevant terms in this thesis.

Flyway

"*The entire range of a migratory bird species (or groups of related species or distinct populations of a single species) through which it moves on an annual basis from the breeding grounds to non-breeding areas, including intermediate resting and feeding places as well as the area within which the birds migrate*" (Boere & Stroud 2006). In addition, flyways may be described for several species (multi-species flyways, Fig. 1a, Boere & Stroud 2006, BirdLife International 2010) or as species-specific flyways, also called '*population flyway*' or '*migration systems*' (e.g. Fig. 1b, Boere & Stroud 2006, Wetlands International 2017).There is a third type, called '*political flyway*', which includes all migration systems of all waterbird species that occur within the boundaries of international conservation agreements, such as the African – Eurasian Agreement on the conservation of migratory waterbirds (AEWA, Boere & Stroud 2006, Wetlands International 2017).

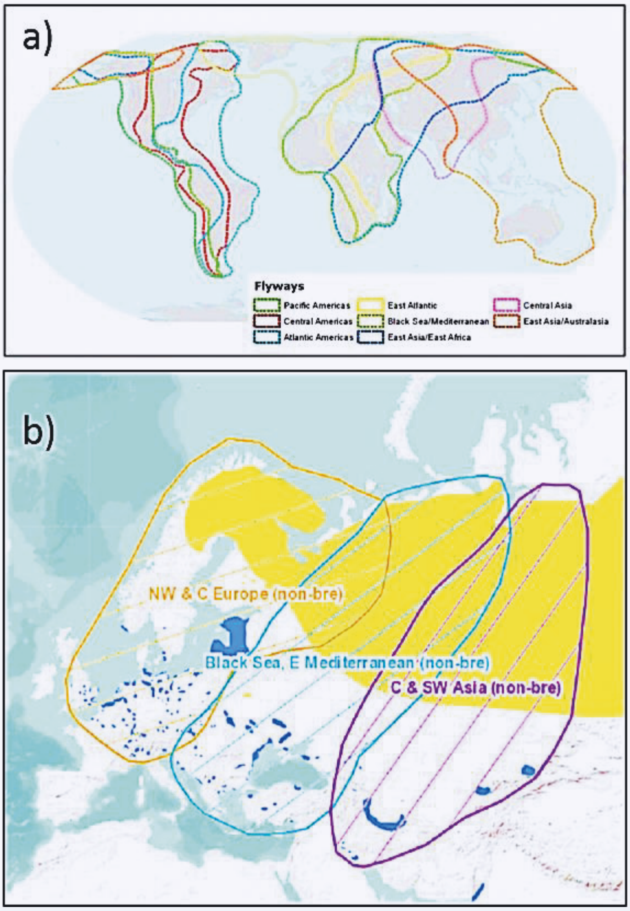

Figure 1. a) *Multi-species flyways (Boere & Stroud 2006, BirdLife International 2010).* ***b)*** *Three population flyways (or migration systems) defined for smew (Mergellus albellus) in Eurasia (Wetlands International 2017). Breeding range (in yellow) and wintering sites (in blue) are shown (map from csntool.wingsoverwetlands.org).*

Flyway population

Refers to all individuals of a species that breed, migrate and winter within the same *Population flyway* (or *migration system*, See e.g. Fig. 1b). It can be used as a synonym of '*biogeographical population*' (Wetlands International 2017). Most species have several *population flyways* or *migration systems* (see Fig. 1b for an example; Boere & Stroud 2006). Some of the population flyways might coincide neatly with a multi-species flyways (Fig. 1a), but this is rarely the case.

Regional population

In this thesis, *regional population* of a given species relates to the ‘population’ in the 21 European countries included in the analyses in **Chapter II**. Although the 21 countries cover the entire western and central Europe, from Spain and Portugal in the south to Norway and Finland in the north (see Fig. 2), ‘*regional population*’ differs from ‘*flyway population*’ (see above): important numbers of certain species wintering in Africa might be missed and in some other cases this ‘regional population’ might include birds that in reality should be classified as part of another ‘*flyway population*’ (different *population flyways* overlap, e.g. Fig. 1b).

EU Birds Directive

The European Union’s Birds Directive (2009/147/EC) aims to protect all bird species naturally occurring at any stage of the annual cycle in any EU Member State.

Special Protection areas (SPAs)

The Birds Directive recognizes habitat loss and degradation as the major threat for European wild bird species. Special Protection Areas (SPAs) are designated under this Directive to protect the most valuable habitats of endangered and migratory bird species. SPAs are also included in the Natura 2000 ecological network, set up under the Habitats Directive (92/43/EEC). All Member States are committed to designate as SPAs any site (e.g. wetland) that meets the classifying criteria described in the Directive (see also Stroud et al. 2004).

Annex I (EU Birds Directive)

There are 194 species and sub-species included in the Annex I of the Birds Directive, which are categorized as particularly threatened. Member States must designate Special Protection Areas (SPAs) for their survival. Species studied in this thesis such as smew *Mergellus albellus*, whooper swan *Cygnus cygnus*, Bewick’s swan *Cygnus columbianus*, black-throated diver *Gavia arctica* and the Slavonian grebe *Podiceps auritus* are included in the Annex I.

North Atlantic Oscillation index (NAO)

The winter North Atlantic Oscillation index (NAO) can be used as a proxy of general climatic conditions during winter across Europe. The NAO is calculated as the difference between the normalized sea level pressures in Iceland and Portugal since 1864 (Hurrell et al. 2016). Positive values of NAO are associated with higher winter temperature and precipitation than average in western and northern Europe as well as to drier than average winters in southern Europe. Hence, one could assume winters with positive NAO values to be ‘beneficial’ for waterbirds, especially those wintering in the western and northern Europe but potentially harmful for individuals wintering in the Mediterranean region due to drought (**II**, **IV**). Consequently, negative values of NAO describe cold winter conditions, and the more negative the value, the harsher the winter. Therefore, negative NAO could represent, in general, 'detrimental' winter weather conditions for waterbirds.

Climate change adaptation strategies

Climate change adaptation strategies are practical approaches in climate change science and policy aiming to reduce or ameliorate the anticipated adverse impacts of climate change (Mawdsley et al. 2009).

Northeasterness

We defined *Northeasterness* as the distance moved by the centre of gravity in wintering abundance towards the northeast in two consecutive years. Therefore, northeasterness will be positive if the centre of gravity in year *t* has move predominantly towards the northeast respective to the coordinates in year *t – 1,* and negative if the movement has been predominantly towards the southwest.

temperature, in particular (**III**). Specifically, this block aims to shed new light on the role of weather conditions driving changes in waterbird abundances within their wintering range in Europe. National case studies have shown that species may respond differently to changes in climate (e.g. Välimäki et al. 2016). However, this has rarely been examined at continental scale and has never been tested explicitly for waterbird populations.

In **Chapter II**, I study the regional population (see Box 1) of 25 waterbird species to investigate potential differences in the (a) annual responses (changes in local abundance) of five different feeding guilds of waterbirds to changes in winter weather conditions (NAO) and (b) long-term changes in wintering distributions over 24 years. Waterbirds are highly responsive to changes in weather conditions, which cause their local abundances to change rapidly. Such responses might render conservation efforts ineffective as species of conservation concern might move out of those protected areas specifically designated to protect them. In **Chapter III**, I present a case study of a species listed in the Annex I under the European Union's Birds Directive (species of conservation concern) where, in addition to study the effects of changes in early winter temperature in northern Europe on the winter abundance across its entire north-west and central European flyway, I also assess the effectiveness of the Special Protection Area (SPA) network (designated under the EU's Birds Directive) delivering climate change adaptation at flyway scale by comparing population trends inside and outside SPAs in different parts of the wintering range (i.e. southwest, centre and northeast).

Lastly, the third block provides new insight into the relationship between waterbird breeding abundance, climatic factors during breeding and non-breeding season and the type of breeding habitat (**IV**). The likely synergistic effect that weather conditions (NAO) and habitat characteristics may have on the breeding abundance of waterbirds has rarely been modelled. Specifically, we first investigate differences in the impact that changes in weather conditions during breeding and non-breeding season may have on the abundance of 17 waterbird species breeding in Finland over three decades. Second, we explore potential differences in the impact of such changes in weather conditions on waterbirds breeding in different habitat type (see Methods below) and assess potential differences in long-term population trends across these habitat types.

Methods

Data for the review

I, together with other Nordic waterbird researchers and colleagues, collected the relevant data from scientific articles found in Google Scholar and the Web of Knowledge (and the references listed in those articles) as well as from national and international reports.

Waterbird abundance data

In this thesis, I used two different dataset on waterbird abundance. The first dataset (**II**, **III**) are counts of wintering waterbirds from censuses organized within the IWC. The second dataset are counts of breeding pairs of waterbirds in Finland (**IV**).

International Waterbird Census (IWC) - Wetlands International

The main objective of the IWC is to monitor the status and distribution of waterbird populations and to help to identify internationally important wintering areas for these species (Delany 2005).

Thus, the information derived from the IWC is highly relevant for policy-making statutory agencies (van Roomen et al. 2012). In the last years, 143 countries have taken part in the IWC around the world. The IWC is carried out by tens of thousands of experienced volunteer birdwatchers in a standardized way. Censuses are done in January in all European countries, with a single visit to each wetland which, ideally, should be repeated every year. The IWC constitutes one of the largest citizen science programmes in the world and it is coordinated by Wetlands International. Although the IWC started in late 1960s, many countries joined the programme later. As a trade-off between spatial coverage and length of the time series, I used only data from 1990 until 2013 (**II**) and until 2011 (**III**).

In **Chapter II**, I included data on 25 waterbird species classified into five feeding guilds: dabbling ducks (northern pintail *Anas acuta,* northern shoveler *Anas clypeata,* Eurasian teal *Anas crecca,* Eurasian wigeon *Anas penelope,* mallard *Anas platyrhynchos,* gadwall *Anas strepera,* shelduck *Tadorna tadorna)*, diving ducks (common pochard *Aythya ferina,* tufted duck *Aythya fuligula,* red-crested pochard *Netta rufina,* common goldeneye *Bucephala clangula,* goosander *Mergus merganser,* red-breasted merganser *Mergus serrator,* smew), geese (greater white-fronted goose *Anser albifrons,* greylag goose *Anser anser,* brent goose *Branta bernicla,* barnacle goose *Branta leucopsis*), swans (Bewick’s swan, whooper swan, mute swan *Cygnus olor*) and other waterbirds (grey heron *Ardea cinerea,* coot *Fulica atra,* great cormorant *Phalacrocorax carbo*, great crested grebe *Podiceps cristatus*).

Data came from 21 countries: Finland, Sweden, Norway, Estonia, Latvia, Lithuania, Denmark, Germany, Poland, Slovakia, Austria, Czech Republic, Netherlands, Belgium, UK, Ireland, France, Switzerland, Italy, Spain and Portugal. Overall, more than 10 000 sites were surveyed every year and more than 213 million waterbirds counted over the study period (Fig.

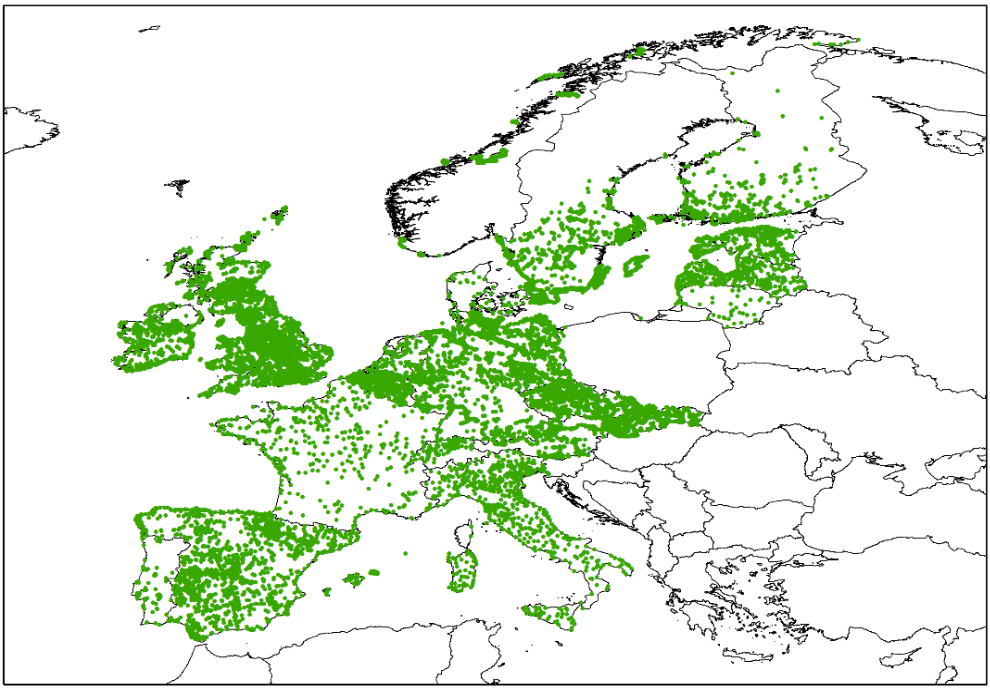

Figure 2. *Monitoring sites of the IWC data used in the* ***Chapter II****. Data (in green) show the distribution of sites that had mallard at least once during the study period to illustrate the spatial coverage in the chapter.*

2). While analysing entire biogeographical or flyway populations (see Box 1) would be ideal for a complete understanding of global drivers of population change, delimiting such population boundaries is not a trivial task (Boere & Stroud 2006, BirdLife International 2010, Wetlands International 2017). The dataset used in this chapter covers the regional population of the 25 species in the 21 countries (Fig. 2, Box 1). Nevertheless, the spatial and temporal coverage of the dataset on waterbird abundance analysed in this chapter allow me to assess the impacts of climate change on wintering populations and its consequences at large scales.

In **Chapter III**, I focused on the smew, which is listed in the Annex I of the EU Birds Directive and thus has high conservation status within EU (see Box 1). The data came from 16 countries: Finland, Sweden, Norway, Estonia, Latvia, Lithuania, Denmark, Germany, Poland, Czech Republic, Netherlands, Belgium, UK, France, Switzerland and Italy. In this study, more than 6 833 sites were monitored and over 291 000 (average annual count = 13 258 ± 3 840 SD) wintering smew counted over the study period (1990–2011) across the entire north-west and central European flyway (Fig. 1b). The data were classified in three categories based on the conservation status of the wetland it came from: SPA with smew as classifying species, other SPA or non-SPA (see Box 1).

Breeding waterbirds surveys (LUOMUS and LUKE)

Finland is one of the few countries in Europe where breeding waterbirds are regularly monitored at large scale. This active monitoring scheme has been running since 1986 and coordinated by the Finnish Museum of Natural History (LUOMUS) and the Finnish Game and Fisheries Research Institute (currently renamed as Natural Resources Institute Finland; Finnish acronym LUKE). In this thesis, however, I only analysed data from LUOMUS' database (**IV**).

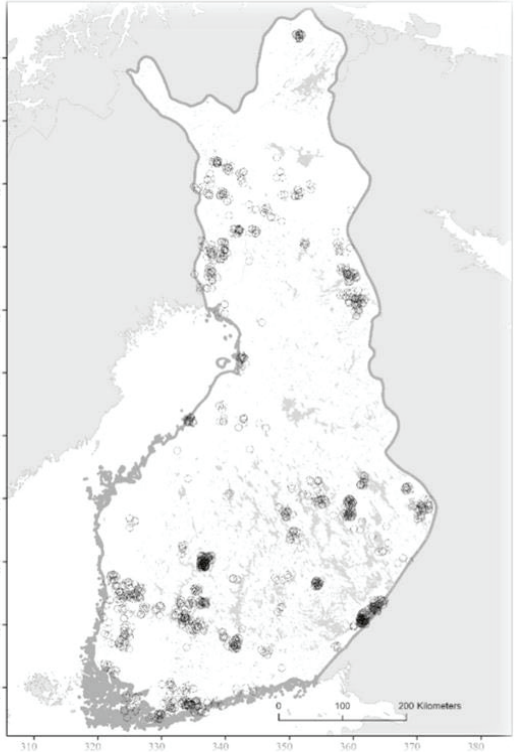

Figure. 3. *Location of the 1280 wetlands surveyed during breeding season in 1986–2015.*

This census is carried out by experienced volunteer birdwatchers, who survey the chosen wetlands twice a year; the first visit is in early May and second in late May. I personally participate in the data collection in one census site in the Helsinki area. Although all species are recorded in both visits, the aim of these two visits to the same site each year is not to have repeated counts (two counts per year for each species) but rather to account for differential timing of breeding in different species. Thus, during the first visit, the focus is on species that breed early in the season such as mallard, common pochard or common goldeneye. In the second visit the main objective is to record late breeding species such as Eurasian wigeon, tufted duck or red-breasted merganser. In other words, when reporting the final abundance of early breeding species, only counts in the first visit will be considered. Consequently, the total abundance of late breeding species will be the sum of the counts only in the second visit. Both visits are carried out well before the fully-grown reed beds reduce the visibility, thus maximising detection (the detailed census method is described in Koskimies & Väisänen [1991]).

In **Chapter IV**, I analysed data containing 110 077 records of breeding pairs of 17 species in 1280 sites distributed across Finland (Fig. 3) during 1986–2015. The species included in this analysis are regular breeders in Finland: northern pintail, northern shoveler, Eurasian teal, Eurasian wigeon, mallard, garganey *Anas querquedula*, common pochard, tufted duck, common goldeneye, goosander, red-breasted merganser, whooper swan, coot, black-throated diver, great crested grebe, Slavonian grebe and red-necked grebe *Podiceps grisegena*.

Habitat type data

Another feature of the Finnish breeding waterbird census is that birdwatchers are asked to record the habitat type of the surveyed wetlands they are surveying. Wetlands can be classified in eight categories based on their nutrient status and location (inland or coastal): (1) barren oligotrophic lake or pond without vegetation, (2) deep partly eutrophic lake with wide reed beds in bays, (3) shallow eutrophic lake with forest or peatland shores, typically horsetail *Equisetum* spp. vegetation, (4) relatively shallow eutrophic lake with extensive reed beds in agricultural or urban area, (5) barren oligotrophic sea coast (equivalent to (1) in inland lakes), (6) relatively eutrophic sea coast, with some reed beds, (7) eutrophic sea bay with large reed bed vegetation, (8) other (e.g. artificial pond, river) (see Koskimies and Väisänen 1991, Lehikoinen et al. 2016b). For the sake of simplicity, to analyse the phenomena we were interested in and to increase the interpretability of the results, in **Chapter IV**, we merged these categories into three clearly defined habitat classes: (a) oligotrophic wetlands with relatively low amount of vegetation, (b) naturally eutrophic wetlands surrounded mainly by forests and peatlands or reed beds and (c) eutrophic wetlands with extensive reed beds surrounded by agricultural land or urban areas where the eutrophication process has been at least partly caused by human actions.

Weather data

In this thesis, I used data on winter North Atlantic Oscillation (NAO) (**II**, **IV**), mean early winter temperature in northern Europe (**III**) and summer temperature in Finland (**IV**).

North Atlantic Oscillation index (NAO)

The winter North Atlantic Oscillation index (NAO) was used as a proxy of general weather conditions in the main wintering areas used by the waterbird species considered in **Chapter II** and **Chapter IV** throughout Europe (see Box 1). Monthly NAO data related to Western Europe were downloaded from http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml. In order to obtain a single value for the "general winter climate conditions in the main wintering sites in Europe", we averaged the NAO values of December and January (before and during the IWC; **II**), and December, January and February (**IV**) each winter during 1990–2013 and 1986–2014, respectively.

Winter temperature

In **Chapter III**, I used the mean temperature during early winter (first half of the winter, 16th November to 15th January) in southern Finland as a proxy of the general winter conditions in northern Europe. These data were calculated by the Finnish Meteorological Institute (FMI), by interpolating data from ca. 100 weather stations to a 10 x 10 kilometres grid of virtual weather stations (Venäläinen et al. 2005). Then I calculated the mean winter temperature for southern Finland during early winter for each year (1990–2011). Winter temperature in southern Finland correlates with a large area in northern Europe (Lehikoinen et al. 2013) and therefore can be used as a proxy of the general winter conditions in the north-eastern part of the smew's wintering range.

Summer temperature

The summer temperature was downloaded from www.cru.uea.ac.uk. This database consists of temperature data in 5° x 5° grids. In **Chapter IV**, I used data from the two grids that cover most of Finland and averaged the June temperature for each year (1986–2014). I then used this annual average as a proxy of weather conditions during the fledgling phase of most species of waterbirds in Finland.

Statistical analyses

In this thesis, I carried out a variety of statistical analyses with the goal of obtaining the most realistic and robust results as well as reducing the potential biases in these. The modelling approaches used in the different chapters were selected based on the characteristics of the data to be analysed and the hypothesis to be tested. I mainly followed the recommendations and protocol described in Zuur et al. (2009, 2010, 2014), Zuur & Ieno (2016a, b), Bolker (2008) and Bolker et al. (2008). Date were analysed in R 3.2.2 (R Core Team 2015) using specific packages (**II, III, IV**) and the TRIM software (Pannekoek & van Strien 2004; available at www.ebcc.info; **III**). I also used the super computers at the CSC – IT Centre for Science (www.csc.fi) when high computing power was needed (**II**, **IV**).

Chapter II

The two main objectives in this chapter required two different statistical approaches. First, I modelled the inter-annual variation of the centre of gravity in abundance of 25 waterbird species as a response to changes in winter weather conditions during 1990–2013 and if these responses differed between five feeding guilds of waterbirds. I calculated the annual centre of gravity in abundance for each species (eqn. 1 & 2 in **Chapter II**) and then calculated how much this centre of gravity predominantly moved towards the northeast in two consecutive years. We called this movement *Northeasterness* (see also Box 1). Then, I built a Generalized Additive Mixed Model (GAMM) to model the non-linear relationship between *Northeasterness* and the interaction between NAO and feeding guild (Zuur et al. 2014), using species as a random term (see eqn. 3 in **Chapter II** for the full model description).

Second, I assessed the existence of a long-term trend in the movement of the centre of gravity in abundance towards the northeast and whether this trend differed between the five feeding guilds. To achieve this goal, I merged the data and constructed eight periods of three years in order to minimise the 'noise' from the large inter-annual variation in the *Northeasterness*, which could mask the long-term trend (period 1 = 1990–1992, period 2 = 1993–1995, …, period 8 = 2011–2013).

Then, I calculated the centre of gravity in abundance in these eight periods and assess the long-term trend by also fitting a GAMM to the data (Zuur et al. 2009), using species as a random effect (see eqn. 4 in **Chapter II** for the full description of the model).

Chapter III

In **Chapter III**, I carried out three different analyses: First, I used the software TRIM, designed to calculate abundance indices from count data, to assess the population growth rate over the study period (1990–2011) in different countries, regions of the wintering range of the smew (southwestern, central and northeastern) and at the entire flyway level. TRIM uses a generalized estimating equation (GEE) algorithm to estimate the abundance indices (Pannekoek & van Strien 2004).

Second, I built two Generalized Liner Model (GLM) to assess the effect of changes in early winter temperature in northern Europe on the annual abundances at the southwestern, central and northeastern part of the smew's wintering range (see formulae (1) & (2) in **Chapter III** for the model details).

Lastly, I compared population trends inside and outside Special Protection Areas (SPAs) in these three regions and at the entire flyway level using a Wald's Test (implemented in the TRIM software).

Chapter IV

The main goal in this chapter was to assess the effect of winter NAO, summer temperature, habitat type and the interaction between them on 17 waterbird species breeding abundance in Finland. To achieve this goal, I fitted a GLMM to the breeding counts, with 'Year' as a random effect and 'Species' nested within 'Site' (see eqn. 1 in **Chapter IV** for the detailed model specification).

Results & discussion

Threats and drivers of waterbird population change

Together with other researchers, I identified several anthropogenic and environmental factors that are currently affecting waterbird populations and pinpointed the consequences of the major changes that will most likely occur in their ecosystems during the next 50 years (**I**). This assessment, however, did not cover all possible drivers acting upon waterbird populations, nor was it the intention.

Nevertheless, reviews like **Chapter I** are very valuable and are needed in order to raise awareness of what drives population dynamics of different species, what are the likely scenarios that species may face in the future, to stimulate debate and research and, ultimately to provide policy makers with enough essential knowledge to propose efficient management and conservation measures (see also Sutherland & Woodroof 2009, Sutherland et al. 2012a, b).

In the context of climate change, dynamic management and conservation efforts should have as one of the main goals the provision and maintenance of a coherent network of key habitats to support current and future levels of waterbird populations. However, to succeed, the extent and ‘*philosophy’* of the current protected area network, especially in northern Europe, needs to be improved to be able to cope with current and anticipated changes in waterbird abundances and distributions. Therefore, monitoring programmes are an essential tool for evaluating and assessing the impact of management and conservation policies on waterbird populations at different spatial scales (from local to flyway level). Different monitoring programmes continuously provide data that increase our understanding of the drivers of population change and allow us to generate and test new hypotheses in which to develop new recommendations to improve management policies. However, the creation of new internationally coordinated monitoring programs that provide, for example, basic demographic data during the breeding season would allow to increase our understanding of drivers of population change at a flyway level.

Effect of winter weather conditions on waterbird winter abundance and distribution

There is ample evidence that some species respond to changes in weather conditions by moving to new regions that have become suitable (e.g. Chen et al. 2011). In this thesis, I show that this is also the case for several waterbird species which main wintering areas are located across Europe (**II**, **III**). However, the strength of such responses are not universal within waterbirds and differ between feeding guilds (**II**). Furthermore, I show that there are two different processes acting upon waterbirds that may have different conservation implications (**II**, **III**).

Inter-annual variation in waterbird abundance during the non-breeding season

Some waterbirds responded rapidly to the annual variation in winter weather conditions, in general (**II**), and temperature, in particular (**III**), over the past three decades in Europe causing fluctuations in local winter abundances between years (**II**, **III**).

In **Chapter II**, I analysed the regional populations (see Box 1) of 25 waterbird species classified in five feeding guilds and showed how the centre of gravity in abundance of these guilds moved between consecutive years in response to changes in winter weather

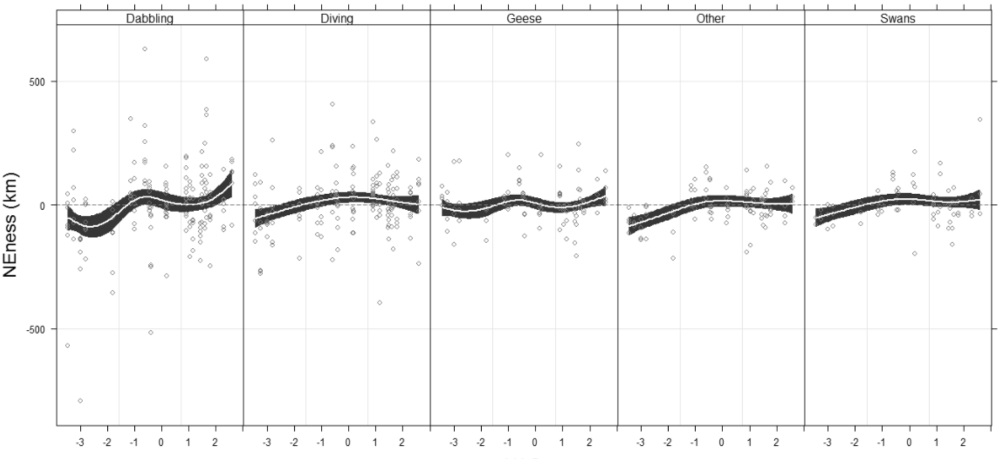

Figure 4. *Inter-annual variation in northeasterness (**II**). From left to right, smoothed annual changes in the centre of gravity in abundance of dabbling ducks, diving ducks, geese, other waterbirds and swans, as a function of winter weather conditions (NAO).*

conditions (NAO) during 1990–2013. In general, waterbirds were more responsive to colder weather conditions (i.e. negative NAO) than to mild weather conditions (i.e. positive NAO) and such responses were non-linear (Fig. 4). Hence, the centre of gravity in abundance shifted southwestwards (respective to the preceding year) in cold winters in western and northern Europe (depicted by negative NAO, see Box 1). This pattern, however, was not apparent for geese, which *Northeasterness* was not associated with the NAO index (Fig. 4, **II**). Moreover, the strength of the responses to cold weather conditions also differed between feeding guilds: the centre of gravity in abundance of dabbling ducks and other waterbird species (see Methods, section 3.2.1.) moved towards the southwest sooner (higher NAO values; Fig. 4) than that of other guilds (**II**).

This result mirrors that of **Chapter III** showing that the abundance of smew (a diving duck) in the southwestern part of the wintering range was higher in winters with low early winter temperature in northern Europe. Furthermore, there were interesting between-guild differences also in the response to mild weather conditions (**II**). Dabbling and diving ducks were the only guilds that responded to mild winter weather conditions (positive NAO; Fig. 4, **II**). However, their response also varied between guilds: while diving ducks responded fast to increasing winter mildness (the centre of gravity in abundance already shifted northeastwards at NAO values around 0; Fig. 4, **II**), dabbling ducks only moved northeastwards in very mild winters (Fig. 4, **II**).

Harsh winter weather conditions (negative NAO values) force many waterbirds to migrate larger distances and settle further to the southwest along the flyway (Ridgill & Fox 1990). A possible explanation for the differential responses to cold weather conditions between guilds may be that dabbling ducks and other waterbird species may tolerate less well cold weather conditions due to their feeding and habitat requirements (e.g. Ridgill & Fox 1990), causing their centre of gravity in abundance to shift southwestwards earlier than those of diving ducks and swans (**II**). On the other hand, the centre of gravity in abundance of dabbling and diving ducks shifted towards the northeast with increasing NAO, but diving ducks responded faster than dabbling ducks, which

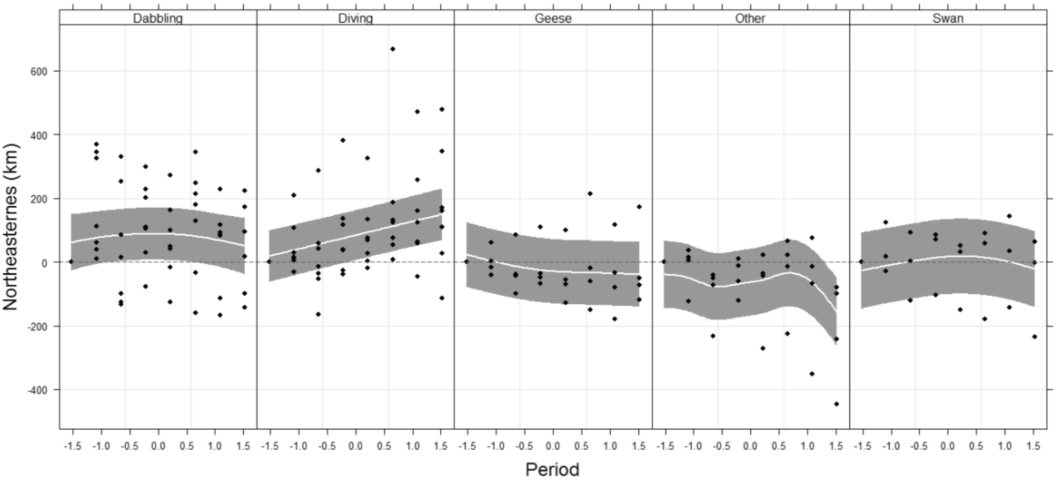

***Figure 5**. Results of the long-term trend in northeasterness **(II)**. Smoothed long-term trend in northeasterness (Y-axis) during the eight 3-year periods from 1990 to 2013. Period (X-axis) is standardized (e.g. period 1 = -1.5,..., period 8 = 1.5; see Methods). Panels from left to right show the different long-term trends of dabbling ducks, diving ducks, geese, other waterbirds and swans.*

may be also related to their food and habitat requirements. In this sense, only under extremely mild winter weather conditions do dabbling ducks attempt to winter closer to the breeding grounds (Fig. 4, **II**) perhaps to avoid shortage of food during unexpected cold spells (**II**).

Detecting positive response to 'beneficial' winter weather conditions in northern Europe (positive NAO), however, may be challenging, not only because of waterbirds' site-fidelity to the wintering sites (e.g. Owen & Black 1990), but also because northeastern movements may be driven by young individuals exploring newly available wintering sites or males attempting to winter closer to the breeding grounds (Nilsson 1970). This may be specially true for geese and swans, which family ties (Owen & Black 1990) may slow down the shift northeastwards.

Long-term shifts in waterbird winter abundance

In addition to the impact of inter-annual variation in winter weather conditions that may cause immediate response from waterbirds regarding their choice of wintering sites, the second process acting upon these species is the long-term effect of climate change.

There were marked differences in the long-term responses to changes in weather conditions between the five feeding guilds (**II**). While most guilds showed no significant long-term trends in the movement of their centre of gravity in abundance towards the northeast (*Northeasterness*) over the study period, diving ducks steadily moved towards the northeast since 1990 (Fig. 5).

Matching this result, wintering numbers of smew increased in the northeastern part of the wintering range in the early 2010s, compared to the early 1990s (Fig. 6), suggesting a long-term redistribution of individuals towards the northeast (**III**). In the early 1990s, only 6% of the flyway population of smew wintered in the northeastern part of the range whereas in the early 2010s, 32% of the entire flyway wintering population settled their wintering grounds in this region (**III**). Interestingly, and contrary to expectations, the centre of gravity in abundance of other waterbird species moved southwestwards in the last part of the study period (Fig. 5).

Milder winters allow individuals to stay closer to the breeding grounds through reduced thermoregulation costs (Ridgill & Fox 1990, Dalby et al. 2013) but also by providing ice-free wintering sites that were completely frozen and thus unavailable for waterbirds some decades ago (Lehikoinen et al. 2013, **I**, **II**, **III**). Open water is one of the main habitat requirements for waterbirds to settle and increasingly milder winters in northern Europe in the past three decades have provided waterbirds with new habitat to exploit during the non-breeding season closer to the breeding grounds. The guild of diving ducks has responded the fastest to recent changes in weather conditions and have undergone a long-term shift in their abundance towards the northeastern part of their wintering range since the 1980s (Lehikoinen et al. 2013) and the 1990s (**II**, **III**), despite the occurrence of cold winters in recent years (**II**). These recent cold winters, however, may be one of the causes of the shift southwestwards observed in other non-Anatidae waterbird species (Fig. 5, **II**). Some life-history traits of diving ducks may allow them to exploit changes in the environment faster than other guilds (**II**). For instance, while other waterbird species use coastal and inland waters or farmland for grazing, diving ducks are able to exploit off-shore and/or deeper waterbodies, which generally freeze later or may remain opened during mild winters.

All these changes in winter abundances, either long-term shifts or inter-annual fluctuations in local abundances have important ecological consequences as they may potentially

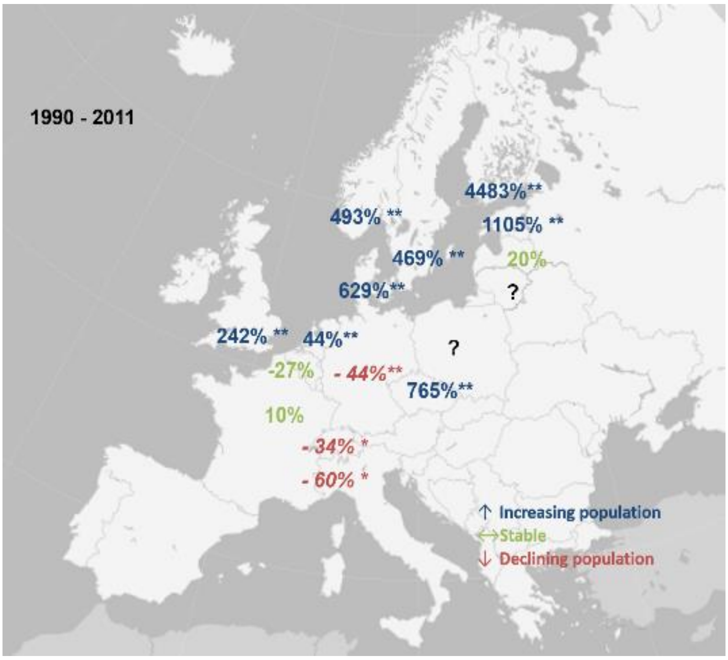

Figure 6. *Total change (%) of smew's wintering abundance between 1990 and 2011 in all 16 countries covering its entire north-west and central European flyway (**III**).*

alter intra- and inter-specific interactions and the dynamics in some wetlands (and farmland areas, e.g. Ramo et al. 2015, Podhrázský et al. 2016). Furthermore, it also has conservation implications because the differential response to climate change showed by the different guilds suggests that ‘less flexible’ guilds (e.g. geese, **II**) may be more threatened than others (e.g. diving ducks, **II**, **III**) which should be taking into account when planning conservation and management actions. In any case, these changes in abundances and distributions of several species may affect the effectiveness of the current network of protected areas safeguarding important wetlands and species of conservation needs.

Effectiveness of the Special Protection Area (SPA) network delivering climate change adaptation

There is increasing debate about the effectiveness of the current network of protected areas providing climate change adaptation to species of conservation concern (Donald et al. 2007, Araújo et al. 2011, Thomas et al. 2012). The EU Special Protection Area (SPA, see Box 1) network that were designated using smew (listed in the Annex I) as a qualifying species, provided climate change adaptation by accommodating part of the rapidly increasing wintering numbers of this species in the northeastern part of the north-west and central European flyway (Fig 1b, Fig. 7a, **III**). In addition, wintering numbers in the northeastern part of the wintering range increased almost twice as fast inside SPAs than outside SPAs (Fig. 7, **III**).

Smew also benefited from the existence of other SPAs across the flyway (Fig. 7b), even if these were not specifically designated for it (**III**). This suggests that the overall network of protected areas may have beneficial effects for other species to those which they classified for, which is important in the context of climate-driven changes in species distributions and abundances. Importantly, there are considerable gaps in the SPA network in north European countries, such as Finland, Sweden and Latvia (**III**). This is worrying because it is in the northeastern part of the wintering range where numbers are increasing and even though the rate of increase in numbers is higher inside SPAs than outside them, in absolute numbers, large proportion of the wintering populations winters outside the entire SPA network, for example, in Finland (95%) and Sweden (79%). This finding, therefore, calls for an urgent re-assessment of

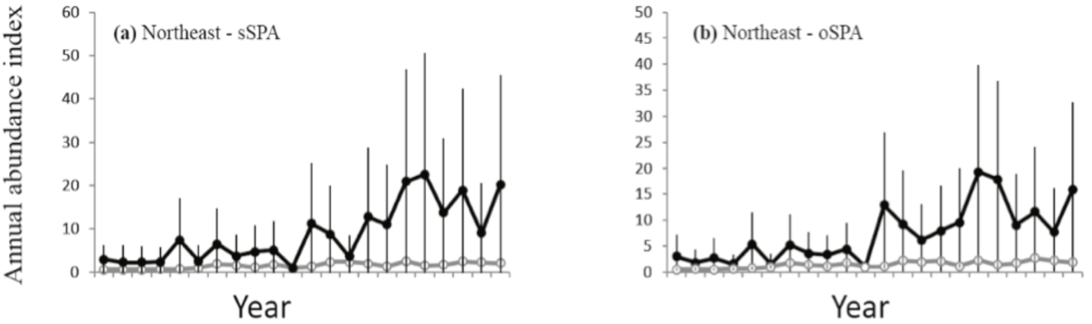

Figure 7. Annual winter abundance indices of smew Mergellus albellus (and 95% confidence intervals) in the northeastern part of the north-west and central European flyway during 1990–2011. Population trends inside (black line and filled circles) and outside (grey line and open circles) of (a) smew-specific SPA (sSPA) and (b) the overall SPA (oSPA) network.

the current SPA network, particularly at northern latitudes.

Given the '1% criterion' that classifies wetlands as internationally important under the Birds Directive (2009/147/EC) and the Ramsar Convention (e.g. Stroud et al. 2004), climate-driven changes in abundances and distributions of species may jeopardize the conservation status of some protected areas if the abundance of classifying species declines below such threshold. The large fluctuations in wintering abundances showed by some waterbirds in relation to the weather conditions experienced each winter (**II**, **III**) highlights the necessity of maintaining a coherent network of protected areas throughout the entire flyway of the species, including 'cold weather refuge sites' that may have lost required numbers in recent years (see Koffijberg et al. 2013). On the other hand, some wetlands may increase their 'ecological value' if increasing abundance of such species start to winter regularly in them. This may be the case of new wintering sites adopted by waterbirds in the northern archipelago of the Baltic Sea that were often frozen in the 1980s and the 1990s, when the network was created, but have become available as increasing winter temperatures keep them ice-free during the winter.

These new wintering sites, which may already be or become internationally important in the near future due to the fast changes in abundances of some species (**II**, **III**), are highly vulnerable to direct human disturbance and land-use change. This highlights the importance of carrying out regular assessments of sites through internationally coordinated monitoring programs to identify such areas on time.

Effects of winter and summer weather conditions on the breeding abundance of waterbirds in Finland

Changes in weather conditions do not only affect distributions of species, but also impact their breeding performance and population dynamics (Møller et al. 2010, Pearce-Higgins & Green 2014, **I**). **Chapter IV** shows that weather conditions was one of the drivers of changes of breeding numbers of the 17 most common waterbird species in Finland in the past three decades (1986–2015). In particular, mild weather conditions in winter (positive values of NAO) acting in the wintering grounds across their flyway had a positive effect on the abundance of waterbirds the following breeding season in Finland during the study period. Possibly, mild winters enhance waterbirds' over-winter survival by (i) reducing thermoregulatory costs (Guillemain et al. 2010, Gunnarsson 2012, Dalby et al. 2013), (ii) making available new wintering sites that allow individuals to short-stop during migration (Elmberg et al. 2014) and (iii) improving feeding opportunities in the wintering areas situated in western Europe that allow individuals to get better body conditions (Guillemain et al. 2010, see also Fox & Walsh 2012).

Summer temperature, on the other hand, did not have statistically significant effect on breeding numbers the following breeding season in Finland (**IV**). It seems, therefore, that changes in winter weather conditions across species' wintering ranges may have larger impact on species' population dynamics than summer weather conditions at the breeding sites, which should be taken into consideration for an effective international and coordinated conservation plan.

Population dynamics in different breeding habitat

Breeding waterbird abundance is generally higher in eutrophic than in oligotrophic boreal lakes (Nilsson & Nilsson 1978, Kauppinen & Väisänen 1993). **Chapter IV** corroborates that this is true for Finnish wetlands across the entire country, where eutrophic lakes hosted, on average, larger number of pairs of the 17 most common breeding waterbird species in the past three decades (see Table 1 in **Chapter IV**).

Interestingly, the increase in breeding numbers in Finland associated with mild winter weather conditions in western and northern Europe (see above) was more evident in eutrophic wetlands compared to oligotrophic ones (**IV**). However, the eutrophication process in boreal lakes in Finland has increased in the past decades, mainly due to agricultural intensification (Ekholm & Mitikka 2006, Niemi & Raateland 2007). Therefore, despite the apparent beneficial environmental conditions for waterbirds breeding in Finland (milder winter weather conditions and nutrient-rich wetlands), waterbird populations have declined in Finland in the past decades (Lehikoinen et al. 2016b), and especially so during the last years (**IV**). The observed pattern may be driven by hyper-eutrophication of boreal lakes, which renders such breeding sites unsuitable for many waterbird species. Indeed, the fraction of the population breeding in wetlands surrounded by agricultural and urban landscapes, which are supposed to have the highest eutrophication level, showed more negative trends than populations breeding in oligotrophic or 'naturally' eutrophic wetlands (Table 1 in **IV**). This suggests that the quality of Finnish wetlands may be deteriorating, and some may be reaching levels of hyper-eutrophication. This is particularly alarming given that such wetlands support the largest breeding numbers in Finland. These findings highlight the need for effective management actions that restore the quality of wetlands for breeding waterbirds (see Lehikoinen et al. 2017), taking into account not only the lake itself but also the management of the entire catchment area.

Conclusions

My thesis provides new evidence on the importance of weather conditions as a key driver of waterbird population change at large scale (**II**, **III**) as well as on the interactive effect that weather conditions and habitat characteristics, including protection status, have on the population dynamics of waterbirds (**III, IV**). Furthermore, it gives a case study to illustrate the impact of climate change on a protected species and the effectiveness of the European Union conservation policy in such context (**III**). At the same time, it provides an overview of other anthropogenic and environmental factors that are also likely to currently have an impact on waterbird populations and the most likely changes in their environment that this guild will have to face in the near future (**I**).

The review (**I**), therefore, describes major drivers of changes in waterbird population dynamics that are likely to be important by the second half of this century. As highlighted in the review, the creation and management of a coherent site safeguard network that provides sufficient high quality habitat for waterbirds is essential for their conservation, regardless of the future characteristics of the surrounding ecosystem. However, one such network, the Special Protection Area (SPA) network, needs improvement in the coverage and scope to be able to deliver the expected results in the context of climate-driven changes in waterbird distributions, especially in northern Europe (**I**, **III**). Some waterbirds have proved to respond fast to changes in weather conditions, causing large fluctuations in annual winter abundances as well as long-term movements towards northeastern Europe (**II**, **III**). However, not all guilds are equally flexible (**II**) and conservation management should also account for these differences. Hence, conservation effort and resources should be targeted to those species already with poorest conservation status (see e.g. Fox et al. 2016a). However, adaptive management should take also into account that, on one hand, some species are less responsive to changes in climate (e.g. geese and swans; **III**) and are, thus, more bounded to traditional areas which must be maintained in optimal conditions. On the other hand, the relatively high flexibility showed by some species in terms of migration and wintering sites (e.g. diving ducks; **II**) compared to others may help them to adapt to changes in climate. However, this should be also taken into consideration when planning conservation measures, as large numbers may rapidly move outside the site safeguard network. This highlights the need for regular assessments of sites through extensive monitoring. In addition, due to this high flexibility shown by some waterbirds, the maintenance of a cohesive and comprehensive network of high quality habitat throughout the species' flyway (including 'cold weather refuges') is of paramount importance (**I**, **II**, **III**).

Winter weather conditions in western Europe not only drive annual changes in waterbirds' distribution during the non-breeding season, but also have considerable impact on the waterbird abundance at the breeding grounds in Finland (**IV**). Waterbird breeding numbers are higher after mild and wet winters in their main wintering areas in western and northern Europe (depicted by high values of NAO). However, long-term population trends are driven by habitat characteristics. The quality of the breeding habitat has decreased in Finland due to hyper-eutrophication of boreal wetlands in recent times. This seems to be the main cause of the observed declines in waterbird breeding populations (Pöysä et al. 2012, Lehikoinen et al. 2016, **IV**). Indeed, in many waterbird species, the fraction of the population breeding in wetlands surrounded by agricultural fields and urban areas, which are thought to be the ones with higher risk of hyper-eutrophication, has declined the fastest in the past 30 years. Restoration of such wetlands and new management regulations on the entire catchment area are needed to revert this situation. Due to the large proportion of the entire flyway population of several species breeding in Finland, the poor conservation status of waterbird species breeding in Finland have conservation implications at national and international level. Therefore, changes in the population dynamics of waterbirds breeding in Finland may have far-reaching consequences, affecting the dynamics of the species at the flyway level (see e.g. Fox et al. 2016a, b, **IV**). Although my thesis is based on well-monitored waterbird species the main conclusions may apply also to other migratory populations. Understanding the drivers of change in populations at local, national and flyway level throughout the annual cycle is essential to maintain healthy waterbird populations. In this sense, my thesis provides a clear example of how spatio-temporal studies at large scale can make a difference in the context of climate change.

Acknowledgements

Finalising a PhD thesis is an interesting experience. It is like a real rollercoaster. However, I have not ridden it alone and I have been very lucky to be surrounded by amazing people since I first stepped in Finland. This thesis has, thus, a little bit of all of you in it. Firstly, I owe the greatest thank to my supervisor (and friend) Dr. Aleksi Lehikoinen. Aksu, you rescued when my boat was sinking

and I was drowning at the end of 2012. You offered me the possibility to (re)start a PhD project at LUOMUS when I was struggling to get funding for my previous project in Viikki. I will never forget that morning in December 2012 when you called me and asked me if I would be interested in joining the project that you just got funded. I was born again. Thank you! In these past four years, not only have you guided me during the journey of doing a PhD, but also made me finish it: you came to my office one morning and said “ok, now we have to set a date for your defence. Is the 5th of May okay with you? I will contact Johan (Elmberg) to see if he is available”. And that was it. The process had really begun in that exact moment and the deadline was set. Thanks for that, by the way! Otherwise, I would still be wondering when to defend. You introduced me to the world of waterbirds and waterbird researchers; which now, I have to say, it is great! Thanks for giving me this opportunity. I admire the massive knowledge about ecology, in general, and birds, in particular, that you have. I admire your capability to combine work with your passion; bird watching. No matter where you are birding that you always have time to reply an email or comment on texts. But I won’t comment on you birding skills… oh man, that is insane. Since I met you (and the other hardcore birdwatchers living in Finland), I stopped calling myself a ‘birdwatcher’. No way. Lastly, and perhaps most important, you have managed to be the leader of your own research group, but you are always so close to us that it feels like you are another PhD student. This is how you do it and how you keep a great working atmosphere in the group! I have enjoyed going with you to birding trips in Finland, pre- and post-conference (birding) trips in Romania, Iceland and Spain, as well as discussing about music and the world beyond birds while drinking some beers. Thanks also for promoting social events with us! I think that I have been extremely lucky having you as supervisor. You are a clear example of how a supervisor should act and treat his/her students. Kiitos plajon!

I would like to show my gratitude to Prof. Johan Elmberg who accepted the task of acting as my opponent. I knew that May was probably not the most suitable period for you to spend time reading my thesis and travelling to Finland; yet you agreed to do it. Tack! I am equally indebted to Dr. Alison Johnston and Dr. Kari Koivula for acting as pre-examiners and providing excellent comments that improved the earlier version of this thesis. Furthermore, Alison also babysat me during my visit to Cambridge University and the BTO. Thank you so much for expending your time organizing my visit there and for the nice and useful discussion. I really enjoy reading and listening to you!

Huge thanks goes also to Assistant Prof. Jon E. Brommer, Dr. Mar Cabeza and Dr. Jukka Rintala, members of my thesis Advisory Committee, who contributed to the completion of this PhD by helping me to draw the route map towards the final dissertation and providing useful comments at several stages during my studies. Thanks for sharing your knowledge and the fruitful discussions during those meetings. Dank je wel; gràcies; kiitos. I would like to stress here how important were Jon and Dr. Hannu Pietiäinen, from the extinct Bird Ecology Unit at the university of Helsinki, for my career. Jon and Hannu, you allowed me to land in Finland to start a PhD here in 2010, when I just had finished my MSc. Your level of knowledge and expertise mesmerised me (and scared me!). It was also very nice to race around in dirty forest roads in Lahti and Heinola checking Ural owl’s nest boxes in spring and trapping voles in nice, cold and rainy days in May and September. I tried to absorb all the wisdom that came out from your mouths. I will be always grateful to you both for opening me the doors to the path that led now to this PhD thesis. Big thanks to you two. I would also thank Prof. Veijo Kaitala for answering all the emails about bureaucracy, which was essential to meet all the faculty deadlines. Kiitos. Thanks also to Prof. Liselotte Sundström, who accepted to act as Custos in my dissertation, even when we asked on such short notice. Tack. When writing about 'paper work' and 'help' there is the face of one person that comes to my mind. And I guess to every single PhD student's mind. This is Dr. Anni Tonteri's face. I definitely could not have finished (or even started) my thesis without the enormous help, advise and support that Anni has given me in the past seven years. Anni, you are a treasure for any PhD student, especially for foreigners like me. Please, do not leave us/them alone. Kiitos paljon!

Speaking about essential people, I owe my respect to thousands of volunteer birdwatchers that have been gathering the data used in this thesis since the 1980s. Honestly, I most sincerely thank all these enthusiasts, whose passion is then used to increase our scientific knowledge that ideally would help to conserve what they love the most. I am also thankful to all the national coordinators of the International Waterbird Census (IWC), who manage locally this census, and to Tom Langendoen, who coordinates and maintains the centralised database at Wetlands International. Thank you Tom for your help providing the data! All national coordinators form the 21 countries included in this thesis have contributed also during the manuscript preparations. I have greatly benefited from their expertise and knowledge about waterbird ecology. Thank you so much for your comments and discussion that have always improved earlier versions of the manuscripts. In addition to national coordinators of the IWC, I am also extremely grateful to the other collaborators that have provided insight and motivate discussion when preparing the manuscripts. Thank you Dr. David Stroud, Dr. Richard Hearn, and merci Dr. Matthieu Guillemain and Dr. Frédéric Jiguet. I must do a special section here to thank Prof. Anthony D. Fox. When I started this PhD project in January 2013 I knew nothing about waterbirds. Two months later, in March, Aksu sent me to Trondheim to meet all the waterbird experts and present my PhD project in the NOWAC meeting. I still knew nothing about waterbirds and I had to go and talk to experts. However, you warmly welcomed me and made me feel like I was an old member of the group. You took me under your wing. I felt safe. Since then, we have met in several occasions. No matter where you are or how busy you are, you have always had time to comment on the drafts and discuss about the results and to translate those from 'my' English to 'real' English. Thanks you so, so much for everything. You have been fundamental in this thesis, which, literally, would not exist without you.

Another co-author that deserves special mention is Dr. Andrea Santangeli. Andrea, you are an example of perfect researcher; talented and hard-worker. Your insights in our common paper were amazing and you are always up for discussion… and for making maps. I really hope we can keep discussing and working together in the future. Besides working 'stuff' it was also nice to go and play football together every now and then to burn a little bit of stress out. Grazie. Andrea was also a PhD student at the Museum of Natural History – University of Helsinki. This community of PhD students (and post-Docs) it is amazing. I have been so lucky to meet you all during this journey. I would first like to thank Dani, Ed, Jaana, Patte and Pekka, former PhD students at the Bird Ecology Unit. You guys were amazing and welcomed me to your research group back in 2010 with big smiles on your faces. You were very supportive and helped me with all the practicalities during the first months. I am so glad you were there when I started in Viikki. You made the adaptation period much easier. It amazes me how people like Dani and Ed can always be in great mood, smiling no matter what. This is something that I love about them. I am so glad that Ed came to the museum as a post-doc so that I could take some of his positive energy in cloudy days. Thanks for that, Ed and for the road trips to Germany, Turku and Halias, pub meetings and for showing me great music bands! It is always nice to have a chat with you about music and football with a beer in the hand.. In my 'Viikki years' a shared room with Patte, Jaana and Jenni. This was an awesome room to work in. Thanks a lot! Also, I must thank Alexandre, Bineet, Christina, Enrico, Eva, Guillaume, Heini, Joona, Jussi, Marco, María, María del Mar, Martin, Peter, Petra, Ricardo, Tanjona, Tobi, Ulisses and Vilppu. I have spent great time talking, eating, drinking, partying and even playing basketball with you. I had so much fun with you! You definitely have made me happy in these past 7 years. Thanks a lot! In 2013 I started my 'LUOMUS years'. The Museum of Natural History (LUOMUS) it is a wonderful place to work in (and even to get married in!). I felt wonderful when I started this PhD project there. For the first months, I couldn't sleep at night because I wanted to go back to the office. Its walls ooze out wisdom and its crunchy wooden floors made me feel like I was travelling to the past. Great feeling. Thanks Aksu for bringing me in! Besides the magic atmosphere at the museum, there is also great people working there. I would like to thank Porf. Leif Schulman and Dr. Aino Juslén, Director of LUOMUS and the Head of the Zoology Unit, respectively. It has been great to work in such institution excellently driven by you. Great work and thanks! Another positive aspect of LUOMUS is the amazing PhD students (and now post-docs) working under its roof. I do not know enough English words to describe how talented you are and how much I have learned from you. I have enjoyed every single second with you. Thanks a ton Aino, Annina, Eeva-Maria, Gosia, Hanna, Heidi, Juho, Kalle, Mari, Maria He, Maria Hä, Marianna and Sanna. Special mention also for Sara, my PhD sister. We started the same day in January 2013 and we finished the same day on the 5th of May 2017. We have lived in the same office during 4.5 years, sharing good and bad mood, laughter and sorrow, calm and stress. We have shared trips to conferences, we have tried to cope together with the hardcore birdwatchers around us during endless birding days and now we both close this book together. Thanks for bringing the light and the southern European attitude to the office. I wish you the best for you and Álvaro! Gràcies als dos!

In these 7 years of research activity in Finland, I have met other researchers and people that have had a significant contribution in my life and career. I would like to thank Aki, Andy, Dominique, Ed (yes, again), Jari, Jarko, Jeremy, Juha, Kimi, Markus, Noora, Päivi, Pepe, and William for great times at the office and nice discussions during HelLO group meetings, but most important, outside having beers in the bar. Thanks also Pedro Cardoso, Jaakko Kullberg and Lauri Kaila for nice discussions and very constructive comments during my presentations at the Museum's seminars.

Besides the 'local ones', I have met incredible researchers in conferences, workshops, courses and research visits that have expired me in many different ways. Thanks Anders Pape Møller, Alan Zuur, Álvaro Soutullo, Bill Sutherland, Dario Massimino, David Noble, Eric Le Tortorec, Heikki Helänterä, Hannu Pöysä, Helena Ieno, Jérôme Guélat, Jón Einar Jónsson, Jose Manuel Cano, Juan Carlos del Moral, JuanMa Pérez, Luis Cadahía, Mar Cabeza, Marc Kéry, Markus Öst, Matti Koivula, Mikael Kilpi, Oscar Gordo, Pascual López, Petri Nummi, Rubén Limiñana, Ruud Foppen, Sergi Herrando, Szabolcs Nagy, Tatsuya Amano, Toni Laaksonen, Veli-Matti Väänänen, Vicente Urios and Wesley Hochachka. I would like to take a moment here to remember Prof. Ilkka Hanski, source of inspiration and wisdom and an amazing human being. Thanks Ilkka for all you have done for science and for the PhD students at the University of Helsinki. You will be remembered for many years to come.

But not everything in life is Academia. Surely not. I am extremely grateful to all the new friends that I made in Finland and abroad in these past 7 years. I have to thank the friends from the football team, many Spaniards and Latin-Americans, who share same culture, hobbies, doubts and worries as me as expat. It was great to meet them, play football and forget about everything. In those moments, I felt like playing in my old neighbourhood back in Spain. Such a refreshing atmosphere! Thanks Ander, Alberto, Álex, Álvaro, Carlos, Felipe, Fonseca, Jesús 'Chuchi', Maikel, Mario, Michalis, Pablo, Unai and Victor. In addition, I want to thank my friends from the basketball team, Yökoris. By far, the best team in Helsinki. Such a great group of people. You cheered me up when I was a bit down with your positivism and happiness. Thank you Arsene, Daniele, Daniel, Erlis, Gabri, Javi, Jayson, Joonas P., Joonas G., Masi, Marko aka Signmark, Olsi, Santo, Themba, Timmy and Ville.

Last, but not least, I would like to thank my family. In 2010, I left behind my parents and sister when I decided to fledge and migrate northeastwards to breed (and study) in Finland. However, I would have never reached this stage in my life without their constant support from the South. I just want to say that everything I am today is thanks to you. I could never express in words (or characters in this case) the love I feel for you. In the breeding grounds, Finland, I found the best mate I could dream of. I would like, first, to express my gratitude to my 'in laws', Colin and Heidi, the kids Dylan, Sky and Zoe, and grandma Sirpa. I always enjoy so much our family gatherings around a table full of food and drinks. Thanks a lot for making me really feel part of this great family! Second, Nina, *mi amor*, you have been my boatswain during this odyssey, helping and supporting me from day 1 (thanks for leaving the key to the apartment and a sack of porridge in the locker at the airport for my late arrival). We have an amazing family, with two awesome boys, Emil and Aleksi. I love you and I love our boys! You have been always there during those moments of mental instability. I really appreciate that you are there when I really need you. We have fought together many battles in stormy waters. I really hope you can keep watching my back in the ones to come and continue sailing together towards new ventures. This metaphor reminds me the words in the poem *Ithaka* (Kavafy 1911),

"Keep Ithaka always in your mind.

Arriving there is what you're destined for.

But don't hurry the journey at all.

Better if it lasts for years,

so you're old by the time you reach the island,

wealthy with all you've gained on the way,

not expecting Ithaka to make you rich.

Ithaka gave you the marvellous journey.

Without her you wouldn't have set out.

She has nothing left to give you now.

And if you find her poor, Ithaka won't have fooled you.

Wise as you will have become, so full of experience,

you'll have understood by then what these Ithakas mean."

You all made of this journey the greatest experience in my life. Love.

References

Amano, T., Freckleton, R. P., Queenborough, S. A., Doxford, S. W., Smithers, R. J., Sparks, T. H. & Sutherland, W. J. 2014. Links between plant species' spatial and temporal responses to a warming climate. *Proceedings of the Royal Society B.*, 281:20133017.

Araújo,M.B., Alagador, D., Cabeza, M., Nogués-Bravo, D & Thuiller, W. 2011. Climate change threatens European conservation areas. *Ecology Letters*, 14: 484–492

Arzel, C. Elmberg, J., Guillemain, M., Lepley, M., Bosca, F., Legagneux, P. & Nogues, J. -B. 2008. A flyway perspective on food resources abundance in a long-distance migrant, the Eurasian teal (*Anas crecca*). *Journal of Ornithology*, 150: 61–73

Arzel, C., Rönkä, M., Tolvanen, H., Aarras, N., Kamppinen, M. & Vihervaara, P. 2015. Species diversity, abundance and brood numbers of breeding waterbirds in relation to habitat properties in an agricultural watershed. *Annales Zoolici Fennici,* 52: 17–32

Austin, G. E. & Rehfisch, M. M. 2005. Shifting nonbreeding distribution of migratory fauna in relation to climate change. *Global Change Biology*, 11: 31–38.

Begon, M., Harper, J. L. & Townsend, C. R. 1996. Ecology. – Oxford, Blackwell.

Bellisario, B., Cerfolli, F. & Nascetti, G. 2014. Climate effects on the distribution of wetland habitats and connectivity in networks of migratory waterbirds. *Acta Oecologica*, 58: 5-11.

BirdLife International. 2010. The flyways concept can help coordinate global efforts to conserve migratory birds. Presented as part of the BirdLife State of the world's birds website. AVAILABLE AT http://datazone.birdlife.org/sowb/casestudy/the-flyways-concept-can-help-coordinate-global-efforts-to-conserve-migratory-birds

Black, M. & Owen, M. J. 1990. Ecology of waterfowl. Blackie.

Boere, G. C. & Stroud, D. A. 2006. The flyway concept: what it is and what it isn't. Waterbirds around the world. Eds. G.C. Boere, C.A. Galbraith & D.A. Stroud. The Stationery Office, Edinburgh, UK. pp. 40-47.

Bolker, B. M. 2008. Ecological models and data in R. Princeton University Press.

Bolker, B. M., Brooks, M. E., Clarck, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H. & White, J.S.S. 2008. Generalized linear mixed models: a practical guide for ecology and evolution. *TREE* 24(3):127-135.

Bregnballe, T., Amstrup, O., Holm, T. E., Clausen, P. & Fox, A. D. 2014. Skjern River Valley, Northern Europe's most expensive wetland restoration project: benefits to breeding waterbirds. *Ornis Fennica* 91:231–243.

Brommer, J. E. 2008. Extent of recent polewards range margin shifts in Finnish birds depends on their body mass and feeding ecology. *Ornis Fennica* 85, 109–117.

Bussière, E. M, Underhill, L. G. & Altweeg, R. 2015. Patterns of bird migration phenology in South Africa suggest northern hemisphere climate as the most consistent driver of change. *Global Change Biology*, 21: 2179-2190.

Chen, I. –C., Hill, J. K., Ohlemüller, R et al. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* 333:1024–1026.

Clausen, K. K., Stjernhom, M. & Clausen, P. 2013. Grazing management can counteract the impacts of climate change-induced sea level rise on salt marsh-dependent waterbirds. *Journal of Applied Ecology*, 50: 528-537.

Courchamp, F., Dunne, J. A., Le Maho, Y., May, R. M., Thébaud, C. & Hochberg, M. E. 2015. Fundamental ecology is fundamental. *TREE*, 30:9–16.

Dalby L., Fox A. D., Petersen I. K., Svenning J. -C. & Delany S. 2013b. Temperature does not dictate the wintering distributions of European dabbling duck species. *Ibis,* 155: 80–88.

Delany, S. 2005. Guidelines for participants in the International Waterbird Census (IWC). Wetlands International. Wageningen.

Donald, P. F., Sandersons, F., J., Burfield, I., J., Bierman, S., M., Gregory, R., D. & Waliczky, Z. 2007. International conservation policy delivers benefits for birds in Europe. Science, 317:810–813

Donnelly, A., Geyer, H. & Yu, R. 2015. Changes in the timing of departure and arrival of Irish migrant waterbirds. *PeerJ*, **3**:e726

Ekholm, P. & Mitikka, S. 2006. Agricultural lakes in Finland: current water quality and trends. *Environmental Monitoring and Assessment,* 116, 111–135.

Elmberg, J., Hessel, R., Fox, A. D. & Dalby, L. 2014. Interpreting seasonal range shifts in migratory birds: a critical assessment of ‘short–stopping’ and a suggested terminology. *Journal of Ornithology,* 155:571–579.

European Environment Agency (EEA). 2012. Climate change, impacts and vulnerability in Europe 2012. EEA Report 12/2012, Paris.

Fox, A. D. & Walsh, A. J. 2012. Warming winter effects, fat store accumulation and timing of spring departure of Greenland White-fronted Geese *Anser albifrons flavirostris* from their winter quarters. *Hydrobiologia* 697: 95-102.

Fox, A. D., Caizergues, A., Banik, M. V., et al. 2016a. Recent changes in the abundance of Common Pochard Aythya ferina breeding in Europe. *Wildfowl*. 66: 22–40.

Fox, A. D., Dalby, L., Christensen, T. K., et al. 2016b. Seeking explanations for recent changes in abundance of wintering Eurasian Wigeon Anas penelope in northwest Europe. *Ornis Fennica,* 93:12–25.

Frei, E. R., Ghazoul, J., Matter, P., Heggli, M. & Pluess, A. R.. 2014 Plant population differentiation and climate change: responses of grassland species along an elevational gradient. *Global Change Biology* 20, 441 – 455.

Giles, N. 1994 Tufted Duck *Aythya fuligula* habitat use and brood survival increases after fish removal from gravel pit lakes. *Hydrobiologia* **279–280**:387–392.

Gleason, R. A., Euliss, N. H., Tangen, B. A., Laubhan, M. K. & Browne, B. A. 2011. USDA conservation program and practice effects on wetland ecosystem services in the Prairie Pothole Region. *Ecological Applications* 21: S65–S81.

Godet, L., Jaffré, M. & Devictor, V. 2011. Waders in winter: long-term changes of migratory bird assemblages facing climate change. *Biology Letters,* 7, 714–717.

Gordo, O., Barriocanal, C & Robson, D. 2011. Ecological impacts of the North Atlantic Oscillation (NAO) in Mediterranean ecosystems. – In Vicente-Serrano, S.M. and Trigo, R.M. (Eds.) Hydrological, socioeconomic and ecological impacts of the North Atlantic Oscillation in the Mediterranean region. Springer.

Green, A. J. & Elmberg, J. 2014. Ecosystem services provided by waterbirds. *Biological Reviews,* 89: 105-122.

Guareschi, S., Abellán, P., Laini, A., Green, A. J., Sánchez-Zapata, J. A., Velasco, J. & Millán, A. 2015. Cross-taxon congruence in wetlands: Assessing the value of waterbirds as surrogates of macroinvertebrate biodiversity in Mediterranean Ramsar sites. *Ecological indicators,* 49: 204-215.

Guillemain, M., Sadoul, M. & Simon, G. 2005. European flyway permeability and abmigration in teal *Anas crecca*, an analysis based on ringing recoveries. *Ibis* 147:688–696

Guillemain, M., Elmberg, J., Gauthier-Clerc, M., Massez, G., Hearn, R., Champagnon, J. & Simon, G. 2010b. Wintering French Mallard and Teal are heavier and in better condition than 30 years ago: effect of a changing environment? *Ambio* 39: 170-180.

Guillemain, M., Pöysä, H., Fox, A. D., et al. 2013. Climate change and European ducks: what do we know and what do we need to know? *Wildlife Biology,* 19: 404-419.

Gunnarsson, G., Waldeström, J. & Fransson, T. 2012. Direct and indirect effects of winter harshness on the survival of Mallards Anas platyrhynchos in northwest Europe. *Ibis*, 154, 307–317.

Holopainen, S. 2015. Duck habitat use and reproduction in boreal wetlands: importance of habitat quality and population density. PhD thesis. Dissertationes Forestales 190.

Holm, T. E. & Clausen, P. 2006: Effects of water level management on autumn staging waterbirds and macrophyte diversity in three Danish coastal lagoons. *Biodiversity and Conservation* 15: 4399-4423

Holt C. A., Austin G. E., Calbrade N. A., Mellan H. J., Hearn R. D., Stroud D. A., Wotton S. R. & Musgrove A. J. 2012. Waterbirds in the UK 2010/11: The Wetland Bird Survey. BTO/RSPB/JNCC, Thetford. UK.

del Hoyo, J., Elliott, A. & Sargatal, J. 1994. Handbook of the birds of the world. Lynx Edicions, Barcelona.

Hurrell, J. and National Center for Atmospheric Research Staff (Eds). Last modified 02 Mar 2016. "The Climate Data Guide: Hurrell North Atlantic Oscillation (NAO) Index (station–based). Retrieved from https://climatedataguide.ucar.edu/climate–data/hurrell–north–atlantic–oscillation–nao–index–station–based.

Intergovernmental Panel on Climate Change (IPCC) 2012. Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation. A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change. Cambridge Univ. Press.

Intergovernmental Panel on Climate Change (IPCC) 2013. Observations: atmosphere and surface. In: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge Univ. Press.

Iverson, S. A., Gilchrist, H. G., Smith, P. A., Gaston, A. J. & Forbes, M. R. 2014. Longer ice-free seasons increase the risk of nest depredation by polar bears for colonial breeding birds in the Canadian Arctic. *Proceeding of the Royal Society B,* 281: 20133128.

Johnston, A., Ausden, M., Dodd, A. M. et al. 2013. Observed and predicted effects of climate change on species abundance in protected areas. *Nature Climate Change*, 3, 1055–1061.

Johnston, A., Fink, D., Reynolds, M. D., Hochachka, W. M., Sullivan, B. L., Bruns, N. E., Hallstein, E., Merrifield, M. S., Matsumoto, S. & Kelling, S. 2015. Abundance models improve spatial and temporal prioritization of conservation resources. *Ecological Applications*, 25(7): 1749–1756.

Jylhä, K., Tuomenvirta, H. & Ruosteenoja, K. 2004. Climate change projections for Finland during the 21st century. *Boreal Environmentl Research,* 9: 127–152.

Jylhä, K., Fronzek, S., Tuomenvirta, H., Carter, T.R. & Ruosteenoja, K. 2008. Changes in frost, snow and Baltic sea ice by the end of the twenty-first century based on climate model projections for Europe. *Climate Change,* 86: 441–462.

Kauppinen, J. & Väisänen, R.A. 1993. Ordination and classification of waterfowl communities in south boreal lakes. *Finnish Game Research,* 48: 3–23.

Kelly, F. K., Horton, K. G., Stepianan, P. M., de Beurs, K. M., Fagin, T., Bridge, E. S. & Chilson, P. B. 2016. Novel measures of continental-scale avian migration phenology related to proximate environmental cues. *Ecosphere,* 7: e01434.

Kleyheeg, E., van Dijk, J.G.B., Tsoponglou-Gkina, D., Woud, T.Y., Boonstra, D.K., Nolet, B.A. and Soons, M.B. 2017. Movement patterns of a keystone waterbird species are highly predictable from landscape configuration. *Movement Ecology,* 5:2.

Knudsen, E., Lindén, A., Both, C., et al. 2011: Challenging claims in the study of migratory birds and climate change. *Biological Reviews,* 86: 928-946.

Koffijberg, K., van Winden, E. & Clausen, P. 2013. The Netherlands as a winter refuge for light-bellied brent geese *Branta bernicla hrota*. *Wildfowl*, 3: 40-56.

Lehikoinen, A., Kilpi, M. & Öst, M. 2006. Winter climate affects subsequent breeding success of common eiders. *Global Change Biology,* 12: 1355–1365.

Lehikoinen, A., Jaatinen, K., Vähätalo, A. V., et al. 2013. Rapid climate-driven shifts in wintering distributions of three common waterbird species. *Global Change Biology*, 19: 2071–2081.

Lehikoinen, A., Fraixedas-Nuñez, S., Burgas, D., et al. 2016a. The impact of weather and the phase of the rodent cycle on breeding population of waterbirds in Finnish Lapland. *Ornis Fennica,* 93: 31–46.

Lehikoinen, A., Rintala, J., Lammi, H. & Pöysä, H. 2016b. Habitat–specific population trajectories in boreal waterbirds: alarming trends and bioindicators for wetlands. *Animal Conservation,* 19: 88–95.

Lehikoinen, P., Lehikoinen, A., Mikkola-Roos, M. & Jaatinen, K. 2017: Counteracting wetland overgrowth increases breeding and staging bird abundances. *Scientific Reports,* 7:41391.

Lindström, Å., Green, M., Husby, M., Kålås, J.A. & Lehikoinen, A. 2015. Large-scale monitoring of waders on their boreal and arctic breeding grounds in northern Europe. *Ardea,* 103: 3–15.

Ma, Z., Cai, Y., Li, B. & Chen, J. 2010. Managing wetland habitats for waterbirds: an international perspective. *Wetlands,* 30: 15–27.

Maclean, I. D., Austin, G. E., Rehfisch, M. M., et al. 2008. Climate change causes rapid changes in the distribution and site abundance of birds in winter. *Global Change Biology*, 14: 2489–2500.

Márquez-Ferrando, R., Figuerola, J., Hooijmeijer, J. & Piersma, T. 2014. Recently created man-made habitats in Doñana provide alternative wintering space for the threatened Continental European black-tailed godwit population. *Biological Conservation,* 171: 127–135.

Mawdsley, J. R., O'Malley, R. & Ojima, D. S. 2009. A Review of Climate-Change Adaptation Strategies for Wildlife Management and Biodiversity Conservation. *Conservation Biology*, 23 (5): 1080–1089

Mawdsley, J. R. 2011. Design of conservation strategies for climate adaptation. *WIREs Climate Change,* 2, 498–515.

Menzel, A., Sparks, T. H., Estrella, N., et al.. 2006. European phenological response to climate change matches the warming pattern. *Global Change Biology,* 12(10), 1969 – 1976.

Møller, A. P., Rubolini, D. & Lehikoinen, E. 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. *PNAS,* 105: 16195–16200

Møller, A. P., Fiedler, W. & Berthold, P. 2010. Effects of Climate change in Birds. Oxford University Press.

Moss, B., Kosten, S., Meerhoff, M., et al. 2011. Allied attack: climate change and eutrophication. *Inland Waters,* 1: 101–105

Niemi, J. & Raateland, A. 2007. River water quality in the Finnish Eurowaternet. *Boreal Environment Research*, 12, 571-584.

Nilsson, L. 1970. Local and seasonal variation in sex-ratios in diving ducks in south Sweden in the non-breeding season. *Ornis Scandinavica*, 1, 115 – 128.

Nilsson, I. G. & Nilsson, I. N. 1978. Breeding bird community densities and species richness in lakes. *Oikos*, 31:214:221.

Ockeldon, N., Hewson, C. M., Johnston, A. & Atkinson, P. W. 2012. Declines in British-breeding populations of Afro-Palaearctic migrant birds are linked to bioclimatic wintering zone in Africa, possibly via constraints on arrival time advancement. *Bird Study*, 59:2, 111-125

Pannekoek, J. & van Strien, A. 2004. TRIM 3 manual (TRends & indices for monitoring data). Statistics Netherlands, Voorburg.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Reviews in Ecology, Evolution and Systematics,* 37: 637–669.

Parmesan, C. & Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature,* 421, 37-42.

Pearce-Higgins, J. W. and Green, R. E. 2014. Birds and climate change: impacts and conservation responses. Cambridge Univ. Press

Pimm, S., Raven, P., Peterson, A., Sekercioglu, C. H. & Ehrlich, P. R. 2006. Human impacts on the rates of recent, present, and future bird extinctions. *PNAS*, 103:10941–10946.

Podhrázský, M., Musil, P., Musilova, Z., Zouhar, J., Adam, M., Zavora, J. & Hudec, K. 2016. Central European Greylag Geese *Anser anser* show a shortening of migration distance and earlier spring arrival over 60 years. *Ibis*, 159: 352 – 365

Pöysä H. & Väänänen V.M. 2014. Drivers of breeding numbers in a long-distance migrant, the Garganey (*Anas querquedula*): effects of climate and hunting pressure. *Journal of Ornithology,* 155:679–687.

Prop, J., Aars, J., Bårdsen, B. -J., et al. 2015. Climate change and the increasing impact of polar bears on bird populations. *Frontiers in ecology and evolution*, 3: 114 – 125.

R Core Team 2015. R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. URL https://www.R-project.org/.

Ramo, C., Aguilera, E., Figuerola, J., Máñez, M. & Green, A. J. 2013. Long-term population trends of colonial wading birds breeding in Doñana (SW Spain) in relation to environmental and anthropogenic factors. *Ardeola*, 60: 305-326.

Ridgill, S. G. & Fox, A. D. 1990. Cold weather movements of waterfowl in Western Europe. International Wetlands and Waterbirds Research Bureau, Slimbridge

van Roomen M., Hornman M., Flink S., Langendoen T., van Winden E., Nagy S. & van Turnhout C. 2012. Flyway-trends for waterbird species important in Lakes IJsselmeer and Markermeer. Sovon-rapport 2012/22, Sovon Dutch Centre for Field Ornithology, Nijmegen - the Netherlands

Santangeli, A. & Lehikoinen, A. 2017: Are winter and breeding bird communities able to track rapid climate change? Lessons from the high North. *Diversity and Distribution*, 23: 308 – 316.

Steen. V., Skagen, S. K. & Noon, B. R. 2014. Vulnerability of Breeding Waterbirds to Climate Change in the Prairie Pothole Region, U.S.A. *PLoS ONE,* 9(6): e96747.

Steen, V. A., Skagen, S. K. & Melcher, C. P. 2016. Implications of Climate Change for Wetland-Dependent Birds in the Prairie Pothole Region. *Wetlands*, 36(Suppl 2): 445

Stoate, C., Báldi, A., Beja, P., Boatman, N. D., Herzon, I., van Doorn, A., de Snoo, G. R., Rakosy, L. & Ramwell, C. 2009. Ecological impacts of early 21st century agricultural change in Europe – a review. *Journal of Environmental Management*, 91:22–46.

Stroud, D. A., Davidson, N. C., West, R., Scott, D. A., Haanstra, L., Thorup, O., Ganter, B. & Delany, S. (compilers) on behalf of the International Wader Study Group. 2004. Status of migratory wader populations in Africa and Western Eurasia in the 1990s. International Wader Studies 15: 1-259.

Sutherland, W. J., Pullin, A. S., Dolman, P. M. & Knight, T. M. 2004. The need for evidence-based conservation. *TREE*, 19 (6): 305-308.

Sutherland, W. J. & Woodroof, H. J. 2009. The need for environmental horizon scanning. *TREE,* 24 (10): 523 – 527.

Sutherland, W. J., Aveling, R., Bennun, L., et al. 2012a. A horizon scan of global conservation issues for 2012a. *TREE,* 27: 12–18.

Sutherland, W. J., Alves, J. A., Amano, T., et al. 2012b A horizon scanning assessment of current and potential future threats to migratory shorebirds. *Ibis,* 154: 663–679.

Szostek, K. L., Bouwhuis, S. & Becker, P. H. 2015. Are arrival dates and body mass after spring migration influenced by large-scale environmental factors in a migratory seabird? *Frontierns in Ecology and Evolution*, 3:42.

Thomas, C. D. & Williamson, M. 2012. Extinction and climate change. *Nature,* 482:E4–E5.

Thomas, C. D., Gillingham, P. K., Bradbury, R. B., et al. 2012. Protected areas facilitate species' range expansions. *PNAS,* 109: 14063-14068.

Välimäki, K., Lindén, A. & Lehikoinen, A. 2016: Velocity of density shifts in Finnish land bird species depends on their migration ecology and body mass. *Oecologia*, 181: 313–321.

Venäläinen, A., Tuomenvirta, H., Piirinen, P., & Drebs, A. 2005. A Basic Finnish climate dataset. 1961 – 2000 – Description and illustrations. Finnish Meteorological Institute.

Wetlands International 2017. Waterbird Population Estimates. Available at: wpe.wetlands.org (accessed 13 January 2017).

Zipkin, E. F., Gardner, B., Gilbert, A. T., O'Connell, A. F., Royle, J. A. & Silverman, E. 2010. Distribution patterns of wintering sea ducks in relation to the North Atlantic Oscillation and local environmental characteristics. *Oecologia*, 163, 893–902.

Zuur, A. F., Ieno, E.N., Walker, N. J., Savaliev, A. A. & Smith, G. M. 2009. Mixed effects models and extensions in ecology with R. Springer, New York

Zuur, A. F., Ieno, E. N. & Elphick, C. S. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1: 3–14.

Zuur, A. F., Saveliev, A. A. & Ieno, E. N. 2014. A Beginner's Guide to Generalized Additive Mixed Models with R. Highland Statistics Ltd.

Zuur, A. F. & Ieno, E. N. 2016a. Beginner's guide to zero-inflated models in R. Highland Statistics Ltd.

Zuur, A. F. & Ieno, E. N. 2016b. A protocol for conducting and presenting results of regression-type analyses. *Methods in Ecology and Evolution*, 7, 636–645.

Zwarts, L., Bijlsma, R. G., van der Kamp, J., Wymenga E., 2009. Living on the edge: Wetlands and birds in the changing Sahel. KNNV Publishing, Zeist. 564pp.