

Bird populations in a changing world: implications for North European conservation

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“Many of the things we need to know about for practical conservation purposes are sufficiently plain as to be revealed by studies with quite simple methodology”.

Colin J. Bibby – *Bird diversity survey methods*, in: Sutherland, W.J., Newton, I. & Green, R.E. (eds.), *Bird Ecology and Conservation: A Handbook of Techniques*, 2004

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

- I** **Fraixedas, S.**, Lehtikoinen, A., Piha, M. and Lindén, A. (Manuscript). A review on birds as indicators of biodiversity: advances, gaps, challenges, and future recommendations.
- II** Lehtikoinen, A., **Fraixedas, S.**, Burgas, D., Eriksson, H., Henttonen, H., Laakkonen, H., Lehtikoinen, P., Lehtomäki, J., Leppänen, J., Mäkeläinen, S., Niemimaa, J., Pihlajaniemi, M., Santaharju, J. and Välimäki, K. 2016. The impact of weather and the phase of the rodent cycle on breeding populations of waterbirds in Finnish Lapland. *Ornis Fennica* 93, 31–46.
- III** **Fraixedas, S.**, Lindén, A., Meller, K., Lindström, Å., Keiřs, O., Kälås, J.A., Husby, M., Leivits, M., Leivits, A. and Lehtikoinen, A. (Submitted, under review). Substantial decline of Northern European peatland bird populations: consequences of drainage.
- IV** **Fraixedas, S.**, Lindén, A. and Lehtikoinen, A. 2015. Population trends of common breeding forest birds in southern Finland are consistent with trends in forest management and climate change. *Ornis Fennica* 92, 187–203.
- V** **Fraixedas, S.**, Lehtikoinen, A. and Lindén, A. 2015. Impacts of climate and land-use change on wintering bird populations in Finland. *Journal of Avian Biology* 46, 63–72.

Table of contributions

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Study design	SF , AiL, ALi, MkP	AiL, SF	ALi, AiL, SF , KM	ALi, AiL, SF	ALi, AiL, SF
Data collection / management	SF	AiL, SF , DB, HE, HH, HL, PL, JoL, JeL, SM, JN, MrP, JS, KV	AiL, ÅL, OK, JAK, MH, ML, ALe	AiL	AiL
Analyses	SF , ALi	SF , AiL, DB	SF , ALi, KM, AiL	SF , ALi, AiL	SF , ALi
Manuscript preparation	SF , AiL, ALi, MkP	AiL, SF , DB, HH, JeL, PL, SM, KV	SF , ALi, AiL, KM, ÅL, OK, JAK, MH, ML, ALe	SF , ALi, AiL	SF , AiL, ALi

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ABSTRACT

The combined effects of climate and land-use change constitute a major threat to global biodiversity. Accurate tools to track changes in biodiversity have been largely called upon in order to address global conservation targets. In response to this, a range of ecological indicators have been developed to measure the state of biodiversity in a changing world. Because of their sensitivity to environmental changes, birds are increasingly used in the construction of multi-species indicators, which represent a powerful tool for decision-makers to assess conservation effectiveness.

This work aims to further our understanding of the general state of bird populations in Finland and the underlying ecological processes behind corresponding trends, covering different environments and with a special focus on some of the most threatened ecosystems of northern Europe.

Using data on common bird species, the effects of climate change and anthropogenic habitat degradation on bird populations are quantified for different habitat types and seasons of the year. Habitat-specific indicators are also produced to deepen knowledge about large-scale impacts taking place in the environment while allowing an evaluation of the conservation status of bird populations, thus helping target the most critical conservation issues. Although the effects of climate and land-use change on bird populations vary significantly with the habitat type and the life-history traits of the species (e.g. migration strategy), the conservation status of nearly all studied communities is considerably deteriorating in both Finland and its neighbouring Northern European countries. Peatlands and forests are of particular concern, given that intensive management actions are severely impacting the inhabiting bird communities.

TIIVISTELMÄ

Ilmastonmuutoksen ja maankäytön tehostumisen yhteisvaikutus uhkaa luonnon monimuotoisuutta maailmanlaajuisesti. Kansainvälisesti sovittujen luonnonsuojelutavoitteiden onnistumisen arvioimista varten tarvitaan luotettavia seurantamenetelmiä. Niinpä monia ekologisista indikaattoreita on kehitetty mittaamaan luonnon monimuotoisuuden tilaa muuttuvassa maailmassa. Linnut reagoivat nopeasti ympäristönmuutoksiin, minkä takia niitä käytetään yleisesti monista lajeista koostuvissa yleisindikaattoreissa, jotka toimivat tehokkaina työkaluina päätöksentekijöille luonnonsuojelun toimivuuden mittaamisessa.

Väitöskirjani tarkoituksena oli lisätä ymmärrystä lintukantojemme yleisestä tilasta Suomessa sekä ekologisista prosesseista, jotka selittävät kannanmuutoksia.

Mallinsin ilmastonmuutoksen ja lajien elinympäristöjen laadun heikkenemisen vaikutuksia yleisten lintulajien kannanvaihteluihin eri elinympäristöissä ja vuodenaikoina. Laskin myös elinympäristökohtaisia indikaattoreita, joiden avulla voi sekä seurata suuren mittakaavan muutoksia luonnossa että arvioida eri elinympäristöjen lintulajien suojelun tarvetta. Ilmastonmuutoksen ja maankäytön muutosten vaikutukset lintupopulaatioihin vaihtelivat selvästi eri elinympäristöissä ja lajien ominaisuuksien (esim. muuttostrategia) välillä. Silti lähes kaikissa tutkimissani lintulajiyhteisöissä Suomessa ja läheisissä Pohjois-Euroopan maissa lajien uhanalaisuusluokitukset olivat huonontuneet. Erityisesti soiden ja metsien lintujen tilanne on huolestuttava, koska tehometساتalous, soiden ojitus ja turvetuotanto ovat vaikuttaneet negatiivisesti lintuyhteisöihin.

SUMMARY

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1. INTRODUCTION

1.1. DRIVERS OF BIODIVERSITY DECLINE

Mounting scientific evidence shows that global biodiversity is decreasing at unprecedented rates (MA 2005, Butchart et al. 2010, Barnosky et al. 2011). As a result of a wide range of anthropogenic activities, an ever-increasing number of species is threatened with extinction, in a process that several authors have already defined as the sixth mass extinction in Earth's history (Wake and Vredenburg 2008, Dirzo et al. 2014, Ceballos et al. 2015). Such human-driven changes in the global biosphere erode the ecosystem services on which humanity depends (Hooper et al. 2012), threaten human well-being (Díaz et al. 2006, Hanski et al. 2012) and undermine the ability of humankind to adapt to global change (Cardinale et al. 2012).

The urgent need to reduce the rates of biodiversity loss has been widely recognized as a priority societal issue, resulting in a number of international conventions and agreements. In 2002, some 190 countries pledged, under the Convention on Biological Diversity (CBD), to tackle both human-induced extinction of species and the loss of natural habitats through a significant reduction of the current rate of biodiversity loss by 2010 (CBD 2002, Gregory 2006, BirdLife International 2013). An even stricter target was set the year before by European high-level delegations, who committed to halt biodiversity decline by 2010 (Pereira and Cooper 2006, Mace and Baillie

2007, van Strien et al. 2009, Pereira et al. 2010). However, none of the targets were met (Butchart et al. 2010, Rands et al. 2010), and similar – but more explicit – goals were adopted within the Strategic Plan for Biodiversity 2011–2020 (CBD 2010, Henle et al. 2013, SCBD 2014), widely referred to as the Aichi Biodiversity Targets (Tittensor et al. 2014). Such targets have been reinvigorated globally by the United Nations' 2030 Agenda for Sustainable Development (2030 Agenda) and its 17 Sustainable Development Goals, in recognition of the impact of biodiversity loss on human wellbeing (Griggs et al. 2013).

Despite the fact that habitat loss (destruction, degradation, and fragmentation of habitats) is generally considered as the most important driver of biodiversity loss (Hoffmann et al. 2010), with globally 60% of the world's ecosystem services being degraded or used at unsustainable rates (MA 2005), climate change is becoming paramount in projected future scenarios (Jetz et al. 2007, Pereira et al. 2010, Dawson et al. 2011). Poleward shifts of species' range margins have been regarded as one of the most common ecological responses due to climate change (Parmesan 2006, Jiguet et al. 2010), and evidence of climate change driven range shifts has mounted for many species, regions and habitats (e.g. Parmesan and Yohe 2003, Chen et al. 2011, Devictor et al. 2012). Besides spatial alterations (changing distributions), temporal alterations are also understood as climate change responses, for example through differences in the arrival or breeding time in relation to timings of weather

events or peaks in resource availability (Visser and Both 2005, Visser et al. 2012).

In general terms, significant shifts in communities have been reported for birds in different countries and at the European scale (Devictor et al. 2012, Lindström et al. 2013, Roth et al. 2014), with bird communities changing towards warm-dwelling species at all altitudes (Roth et al. 2014). Despite these shifts, birds often do not keep up with temperature increase (Devictor et al. 2012, Lindström et al. 2013). As for wintering areas, a strong community response of migratory species to recent climate change has been found for birds, especially species breeding in colder and/or northern areas (Godet et al. 2011). Northern latitudes have been identified as being particularly vulnerable to the effects of climate change given that temperatures in those areas have been predicted to increase more rapidly than elsewhere, particularly in winter (Gonzalez et al. 2010, Settele et al. 2014). The latest climatic predictions also point towards increased rainfall in higher latitudes because of milder winters increasing the levels of water vapour (EEA 2012, Pearce-Higgins and Green 2014). Given this context, climate change poses a serious threat to the ecosystem health of this region (Pachauri and Reisinger 2007), and therefore to the bird communities therein (Kujala et al. 2011, 2013, Laaksonen and Lehikoinen 2013, Lehikoinen et al. 2014).

Natural habitats are essential for bird survival, providing breeding and wintering areas, refugia from predators, and migration stopover sites, among other services (Lebbin et al. 2010, Pearce-Higgins and Green 2014). Not surprisingly, habitat loss poses numerous threats to bird communities worldwide (Jetz et al. 2007, Pearce-Higgins and Green 2014). For instance, the destruction of any of the habitats used by a bird can exert profound impacts at the population level (Lebbin et al. 2010). Indeed, the

IUCN Red List Index (RLI) indicates a global increase in the extinction risk of bird species during the last twenty years (BirdLife International 2013). Several declines of bird populations have been attributed to land-use changes in different habitats (particularly in farmland, woodland and open habitats) at different spatial units (Larsen et al. 2011, Lehikoinen et al. 2014, Herrando et al. 2016). One of the most well-known examples of the impacts of human land-use practices on biodiversity is the dramatic decline of common farmland birds across Europe (including Finland) as a consequence of increasing agricultural intensification (Donald et al. 2001, Gregory et al. 2005, Laaksonen and Lehikoinen 2013). During the period 1980–2013, numbers of common farmland bird species have decreased by 57% in all Europe (Pe'er et al. 2014). In addition, loss of resources in forest habitats (e.g. reduction in canopy and shrub food resources – invertebrate/seeds/plant material – due to reduced abundance of broadleaf species as a major change to forest habitats) is considered to be the main driver of decline for both resident and migrant forest birds in Europe (Wade et al. 2013).

The interaction between climate change and habitat loss especially has been argued to be a major cause of biodiversity loss (Thomas et al. 2004, Pearce-Higgins and Green 2014, Settele et al. 2014) – sometimes referred to as a “deadly anthropogenic cocktail” (Travis 2003, Kampichler et al. 2012). However, disentangling the factors driving population trends is not free from challenge. This is particularly true when it comes to quantifying the relative magnitude of different components of global change, as well as their interactions (Clavero et al. 2011), all of which show variation across ecosystems and biomes (Sala et al. 2000, Jetz et al. 2007). Despite multiple human stressors affecting bird populations, there is an urgent need to account for these

interactions both in ecological studies and conservation planning (Donald et al. 2007, Brook et al. 2008, Butchart et al. 2016).

Most of the studies on Finland's bird populations attribute declines to both land-use and climate change (Virkkala and Rajasärkkä 2011, Laaksonen and Lehikoinen 2013, Lehikoinen et al. 2014). Land-use changes in Finland, mostly due to the intensification of forest management practices (i.e. clearcutting), are affecting numerous breeding areas across the country. Habitat alterations in several wintering grounds and stopover sites along migratory routes also pose a serious threat to migrant birds, which are depending on a wide range of habitat types (Lebbin et al. 2010). In addition to habitat loss, climate change is also a recognized driver of bird population changes in the country (Tiainen et al. 2016). Some insights into how climate change and habitat loss are affecting bird populations specifically for Finland are provided in **Box 1**.

1.2. MEASURING BIODIVERSITY FOR CONSERVATION: BIRDS AS INDICATORS OF ECOLOGICAL CHANGE

In order to determine the impacts of diverse threats on biodiversity, as well as to objectively quantify progress towards different international environmental commitments (including the Aichi Biodiversity Targets), there is an urgent need to develop summary statistics to describe trends in components of biodiversity as accurately and robustly as possible. Findings of ecological change have allowed the faster development of biodiversity indicators into what is known as composite indices (also named multi-species indicators; Gregory et al. 2005, Maes and van Dyck 2005), with an index understood as a 'scaled measure for one or several concordant indicators' (Duelli and Obrist 2003). The purpose of composite indices is to integrate data of species and ecosystem

change in such a way that information is reduced into simple visual summaries (Gregory et al. 2003, Pereira and Cooper 2006). At the same time, such indicators should be useful and understandable for decision-makers, and tailored to their policy needs (Reid et al. 1993, Gregory et al. 2005). Along these lines, since 2003, biodiversity indicators have been developed and used to assess conservation targets (Mace and Baillie 2007) and have been argued to be essential in order to synthesize and communicate our current knowledge on the status and trends of biodiversity (Gregory et al. 2005). The key point here is to find a single species or a group of species that together accurately represent and reflect wider changes in the natural environment (Gregory 2006, van Strien et al. 2009). Also, indicators should deliver scientifically robust information to support the formal assessment of conservation actions to reduce biodiversity loss in policy-relevant ways (van Strien et al. 2009). However, it is difficult to come up with a single biodiversity indicator satisfying all the required properties to consider it effective (Noss 1990, Bibby 1999, Büchs 2003), especially because they need to meet both scientific (i.e. peer review process) and practical criteria (i.e. relatively easy to understand by general audiences; Bibby 1999, van Strien et al. 2009).

Ideally, indicator species, either a single species or a group of species, should be sensitive to changes in the ecosystem and their biology reasonably well known (Rolstad et al. 2002). In this sense, birds are an excellent candidate for several reasons. First, they are a widespread and diverse group (roughly 10 000 species) living in large parts of the globe (Gregory et al. 2005, Gregory 2006). Second, they have long been monitored in many countries, and therefore they constitute one of the taxonomic groups for which most long-term data series are available (Bibby 1999, Schmeller et al. 2012).

Box 1. Direct and indirect causes of biodiversity loss and ecosystem degradation: threats to bird populations in Finland

In Finland, one of the main threats to bird populations is change in **forest habitats (Chapters IV, V)**, for instance due to commercial use of forests (Rassi et al. 2010). Modern large-scale forestry was developed following the Second World War, and in Finland its effects on birds were already addressed at the end of the 1970s (e.g. Järvinen et al. 1977). The decline in the proportion of mature forests and the increase in the proportion of young age classes have been going on for decades in Finland (Parviainen and Västilä 2012). Intensified forestry has resulted in the loss of native habitats, with consequent responses on bird communities (Schmiegelow and Mönkkönen 2002, Kuuluvainen 2009). Old-growth forest specialists and resident species (e.g. grouse) have been particularly affected by forest management (Helle 1985, Väisänen et al. 1986, Hildén 1987). Nevertheless, although several studies concerning the impacts of forestry on bird populations have been carried out in northern Finland (e.g. Järvinen and Väisänen 1978, Virkkala 1987), where forest areas have been strongly altered since the 1950s (Schmiegelow and Mönkkönen 2002), the effects of forest management on bird populations in southern Finland (an area with less than 1% of old-growth forests; Virkkala et al. 2000) have been far less explored. Besides old-growth forests, **peatlands (bogs, mires and fens; Chapter III)** are probably one of the most threatened ecosystems in Finland, notably due to drainage (Rassi et al. 2010). Approximately 60% of the original peatland cover has been drained mostly for forestry (Vasander 1996, Peltola 2004). Drainage associated with historical ditching (developed extensively since the 1960s; Vasander et al. 2003) slowly degrades the habitat, gradually leading into afforestation of open peatland areas, increased tree height and reduced wetness. Finland is considered to be the country with the highest proportion of peatlands worldwide (32% of the land area; Vasander et al. 2003), covering one third of the peatlands of the European Union (EU) (Montanarella et al. 2006). Peatlands cover about 60% of the world's wetlands (Silva et al. 2007), and are key habitats for many breeding bird species, especially waders (Littlewood et al. 2010).

All the above-mentioned habitat modifications have caused and are still causing declines in birds dependent on forests and peatlands. Lastly, **urbanization (Chapter V)** understood as the process implying increasingly urban land use but also as a level of development (Blair 2004) may primarily be regarded as a threat to bird populations. However, recent estimates for Finland indicate a notable decline in the urban human population growth since the 1960s (World Bank 2015). Not all the effects of urbanization are necessarily negative, e.g. supplemental food provided by humans improves the survival of some urban bird species and can also increase the reproductive output in the following breeding season (Robb et al. 2008).

Bird populations are not just responding to land-use practices, but they show a linear graded response across their European thermal range due to climate change (Jiguet et al. 2010). Thus, the observed decline of northern species and increase in southern species are in accordance with the predictions of range shifts for this species group under a warming climate, as earlier studies have shown also for Finland (Kujala et al. 2011, 2013, Virkkala and Rajasärkkä 2011, Brommer et al. 2012). Distributional shifts are being particularly observed for wintering waterbirds in northern latitudes, which depend on open water environments (**Chapter V**).

Waterbirds have already experienced rapid responses to recent increasing early-winter temperature during the last three decades, with north-eastwards shifts confirmed for many European waterbirds, including waders (Maclean et al. 2008) and ducks (Lehikoinen et al. 2013). These responses in waterbirds are most likely due to the fact that initial harsh ice conditions have been unsuitable for wintering (Dalby et al. 2013, Lehikoinen et al. 2013). On the other hand, bird species breeding in the northernmost limit of their distribution have restricted dispersal movements. Consequently, their ranges tend to contract rather than shift (Engler et al. 2011, Gottfried et al. 2012). One example is Finnish birds breeding in sub-Arctic areas (**Chapter II**), key habitats for many waterbird species such as waders and ducks (Wetlands International 2006). As an illustration of the pervasive effects of climate change upon Arctic wildlife, common alpine tundra bird species in Fennoscandia have declined about 30% in the last ten years along with increasing temperature and rainfall (Lehikoinen et al. 2014). Moreover, not only ecological barriers but also habitat fragmentation may hamper species possibilities to spread into new areas (Thomas et al. 2004). Habitats lagging behind climate change (i.e. not shifting fast enough) might represent a further complication for migrants. Given that wintering areas do not shift at the same rates than breeding areas do, birds are faced with increasing travelling distances to find suitable breeding sites (Lebbin et al. 2010, Devictor et al. 2012, Potvin et al. 2016).

Other indirect effects of climate change may be, for instance, the predicted increase in both forest productivity and the proportion of broadleaf trees in primarily coniferous forests (Kellomäki et al. 2005, Parviainen and Västilä 2012), which has been suggested to affect the structure of North European forest bird communities (Virkkala 2004, Felton et al. 2013). As another example, the dampening of peak years in rodent cycles, which has occurred in several areas in Europe (Cornulier et al. 2013), has been suggested to be linked to climate change (Kausrud et al. 2008). Potentially continuous low rodent levels (i.e. changes in predation-prey interactions) could lead to declines in productivity of Arctic waterbirds (Zydelis et al. 2006, Hario et al. 2009, Guillemain et al. 2013, Fox et al. 2015), which in combination with changes in weather, as for instance increased summer rainfall, may translate into long-term population declines in the future.

Third, they are fairly easy to detect and identify, census methods are well developed and relatively cheap, and many volunteers are willing to count birds (Koskimies 1989, Venier and Pearce 2004, Gregory et al. 2005, Gregory 2006, Pereira and Cooper 2006). Fourth, our understanding of their population biology, behaviour and life history (in Europe but not in the tropics; Xiao et al. 2016) is very accurate (Venier and Pearce 2004, Gregory et al. 2005). Fifth, they tend to be high up in food chains, thus being especially sensitive to climate and land-use changes (Koskimies 1989, Gregory et al. 2005, Gregory 2006). Moreover, given that bird trends often reflect changes in other animal and

plant taxa, they are well-positioned to further our understanding of wider changes in the natural environment (Järvinen and Väisänen 1979, Gregory 2005, 2006).

1.3. BIRD POPULATION TRENDS AND THEIR RELEVANCE FOR EUROPEAN ENVIRONMENTAL POLICY

Trend data are essential for setting priorities for bird species conservation (Gregory et al. 2004). The population trend of a particular bird species can be obtained through repeated surveys (Gregory et al. 2004). A composite trend indicator (Gregory et al. 2005, 2008) is formed

when a group of species population trends are taken as a whole. The main goal is to reflect the population's overall status and trends, while also acting as a surrogate for ecosystem health (Caro and D'Oherty 1999, Gregory et al. 2005, 2008). Probably the best-known example among birds is the Wild Bird Index (WBI; Gregory et al. 1999, 2003). This index is one of the most advanced summary statistics available at global scale (Gregory et al. 2008, Butchart et al. 2010, Sheehan et al. 2010). Wild bird indicators have been adopted by the EU and incorporated in the "abundance and distribution of selected species", one of the Streamlining European Biodiversity Indicators (SEBI) set to address the EU biodiversity targets (EEA 2012). Importantly, these indicators can be used to improve current management practices, as is the case of the European Farmland Bird Indicator (EFBI; Butler et al. 2010). Composite indices have been further developed to describe the impacts of climate change on biodiversity. Some examples include the Community Temperature Index (CTI; Devictor et al. 2008, 2012) and the Climate Impact Indicator (CII; Gregory et al. 2009, Stephens et al. 2016). The latter, so far designed for birds, has been also taken up by the EU (SEBI 011) under the name "impacts of climate change on bird populations" (EEA 2012).

Bird trend data can also be used to monitor the status and trends of the world's Important Bird Areas (IBAs), comprising some of the most important sites for bird conservation worldwide (BirdLife International 2013). The continuous monitoring of trends in bird population numbers in IBAs can provide valuable information to track threats and pressures over time, and analyse the effectiveness of these sites in buffering biodiversity loss. Indeed, IBA indices are contributing to move towards the global biodiversity targets by promoting the expansion of the protected area networks at IBAs, particularly targeted at "especially areas of

particular importance for biodiversity" (BirdLife International 2013, Butchart et al. 2012). At the European level, Special Protection Areas (SPAs) are designated by the EU Member States through the Birds Directive. The establishment of SPAs (included in the Nature 2000 ecological network set up under the Habitats Directive; European Commission 2016a) is mostly based on Annex I bird species subject to special protection (Pearce-Higgins and Green 2014). Species conservation status is determined by trends in bird populations reported by all Member States (European Commission 2016b), which can also be used to analyse the success of bird protection efforts (e.g. Sanderson et al. 2015).

All this makes bird indicators particularly important as a tool to track changes in biodiversity at different temporal and spatial scales, as well as to evaluate the effectiveness of different European environmental policy instruments. Despite the potential of developing bird indicators as a tool to inform environmental decision-making, there are still some methodological gaps, as is the case of species selection procedures that challenge their widespread application in the policy arena (see **Box 2**). Other additional problems of current bird indicators like species representativeness and seasonal biases are also covered in the following sections.

1.4. COMMONNESS AND CONSERVATION EFFECTIVENESS

Changes in the availability of birds' preferred habitats (habitats of highest density) can be an important driver of population changes in bird species (Helle and Järvinen 1986). Whereas generalist species able to thrive in human-modified landscapes are at an advantage, more specialized species are more vulnerable to habitat loss or fragmentation (Lebbin et al. 2010).

Common (generally abundant) species occur in a range of different habitat types. Due to their commonness in the data, bird indicator trends tend to represent the status of the more widespread bird community (Gregory et al. 2005). On the other hand, very uncommon or scarce species are more associated with pristine

habitats and are therefore more sensitive to environmental changes (Battisti and Fanelli 2016). One important consideration is the inclusion of these species in the indicators, since their omission can produce an over-optimistic assessment of the health of the ecosystem (Renwick et al. 2012).

Box 2. Species selection and importance of peer review processes

Wild bird indicators have experienced a remarkable improvement in particular as regards the approach to indicator species selection (Gregory et al. 2005), with methods that have evolved and moved from lists compiled by a sample of experts (potentially biased due to subjectivity, or to contrasting species habitat preferences between European countries, among others; Gregory et al. 2005, Larsen et al. 2011) towards more quantitative assessments based on empirical data (Carignan and Villard 2002). However, there are still some cases where species are selected by expert judgment (EBCC 2016). Several studies have demonstrated that when species selection criteria are involved in identifying the potential indicator species pool, this results in more accurate and representative indices of the wider community (Butler et al. 2012, Pakkala et al. 2014, Wade et al. 2014). Therefore, species selection procedures are a key element in the design of indicators.

Obtaining information on species habitat use may be a good way to deepen knowledge and understanding of the major causes for the loss of biodiversity and come up with more robust indicators for the development of sound conservation policies (Gregory et al. 2005, Wade et al. 2013). In this sense, determining species' preferences in relation to their habitat (e.g. requirements of large enough areas of suitable habitat, association with old-growth forests, and dependence on decaying wood for foraging; Schmiegelow and Mönkkönen 2002) could be an effective tool to help complementing prioritization within ecosystems, both in terms of conservation and restoration (Sergio et al. 2004, Noss et al. 2009). Several studies have quantified bird species habitat preferences (Gregory et al. 2005, Wade et al. 2013). Some examples include the calculation of an inclusion ratio (i.e. species have to either meet or exceed a certain preference ratio in relation to the study habitat for their inclusion in the indicator) using species densities (e.g. van Strien et al. 2016) or abundances (e.g. Relative Habitat Use index RHU; Larsen et al. 2011). Regardless of whether there is need to engage experts in species selection procedures, indicators of biodiversity should include standards that involve editorial and technical quality control, including peer review (Costello et al. 2013). Moreover, cross-validation with other biodiversity indicators is also essential when interpreting results (Bailey et al. 2007, European Communities 2009) because birds may respond differently to environmental factors compared to other taxa (Gregory and van Strien 2010).

However, current monitoring schemes may not have sufficient coverage to track population changes in rare species because they are more difficult to detect (Gregory et al. 2005, Dupuis et al. 2011). Rare species that are not yet the focus of any specific conservation action may thus be the “losers” in biodiversity action plans (Studený et al. 2013). Although there is an inherent challenge in identifying declines in bird populations for rare species (Lebbin et al. 2010), methodological advances are moving towards this direction (e.g. hierarchical multi-species models; Ovaskainen and Soininen 2011; goodness-of-fit biodiversity measures; Studený et al. 2013, Harrison et al. 2014).

Despite the fact that wild bird indicators inform about the general state of common birds, even subtle changes in the abundance of certain common species could already be a symptom of ecosystem disturbance (Gregory et al. 2003, Gregory and van Strien 2010, Koch et al. 2011). Diverting increasing conservation resources to generalist species (instead of specialist ones) is misadvised (Lebbin et al. 2010), but it is nevertheless worth mentioning that commoner species may co-occur in rare or threatened habitats, and so their preservation may help to conserve other bird species with similar needs (Lebbin et al. 2010).

1.5. WINTERING POPULATIONS AND MIGRATORY BEHAVIOUR

There is a great body of literature investigating the combined effects of climate and land-use change on animal populations (Warren et al. 2001, Jetz et al. 2007, Eglinton and Pearce-Higgins 2012). Nevertheless, most long-term population studies have concerned data collected during the breeding season, whereas wintering population changes, and wintering ecology in general, have been much less explored. So far, studies dealing with wintering bird populations have basically examined

diversity and abundance of species according to different landscape variables (Pearson 1993, Smith 2003). More recent research has focused on shifts in distributions and species’ ranges in response to climate, urbanization and supplementary feeding (La Sorte and Thompson 2007, Zuckerberg et al. 2011, Paprocki et al. 2014). Nonetheless, the majority of the studies analysing wintering bird populations in Europe concentrate on waterbirds (Crowe et al. 2008, Musgrove et al. 2011, Hornman et al. 2012, Lehikoinen et al. 2013). In contrast to breeding populations, the composition of wintering populations is to a great extent determined by migratory behaviour.

Some wintering bird species are partial migrants, i.e. one part of the population is wintering in the breeding areas and another is migratory (Berthold 2001, Newton 2008). Climate change has been suggested to increase the proportion of resident individuals of such species as winters become milder, since a decreasing part of their populations is predicted to migrate due to more favourable wintering conditions in the north (Berthold 2001, but see Nilsson et al. 2006). In this sense, the same phenomenon is expected to occur for short-distance migrants (Berthold 2001).

Winter is a critical period for population regulation because of decreased food availability compared to other seasons (Lahti et al. 1998). While resident species spend the winter in the same breeding areas, including winters when resources are typically scarce, purely migratory species can find higher quantities of food from southern latitudes during the non-breeding season (Newton 1998, 2008). However, not only have populations of resident species been declining over the last few decades, but also long-distance migrants (e.g. Hildén 1987, Gregory et al. 2007, Laaksonen and Lehikoinen 2013). In addition to the effects of climate change and habitat loss taking place on

the breeding areas (e.g. asynchrony between the timing of arrival, breeding, and peak in resource availability; Visser et al. 2004, Jonzén et al. 2006, Visser et al. 2012), long-distance migrants may be potentially facing other problems, such as mortality during migration or in their wintering grounds (Sanderson et al. 2006, Vickery et al. 2014). In the case of farmland birds, the quality of wintering habitats has been shown to affect their breeding population trends (Gillings et al. 2005). The existing literature on the topic points particularly towards the decline in breeding populations of long-distance migrant birds (e.g. Sanderson et al. 2006, Gregory et al. 2007). In Finland, migratory strategy has proved to be one of the components explaining changes in bird populations, both during the breeding and wintering seasons (e.g. Laaksonen and Lehikoinen 2013, Virkkala et al. 2013).

Last, populations of species display natural fluctuations (Ranta et al. 2006, Gallego Zamorano et al. 2017). In many species, annual wintering numbers fluctuate according to the availability of fruits and seed crops of trees per year (Hildén 1987, Newton 1998, Virkkala 2004). In this case, species are adapted to exploit seasonal peaks in food, and they can be distinguished between irruption species (e.g. Bramblings *Fringilla montifringilla* and Bohemian Waxwings *Bombycilla garrulus*) and nomadic species (e.g. Crossbills). Nomadic behaviours are often the result of annual changes in food availability, whereas irruption species generally escape from seasonal food scarcity (Berthold 2001). Rowan berry crops have been shown to affect the migratory behaviour of berry-eating species like Fieldfare *Turdus pilaris* and Bohemian Waxwing (Newton 2008). As a consequence, the introduction of berry trees to gardens and parks in urban areas may have population consequences even on birds breeding outside these habitats.

2. AIMS OF THIS THESIS

This work aims to further our understanding of the general state of bird populations in Finland and the underlying ecological processes behind their trends, covering different environments and with a special focus on some of the most threatened ecosystems of northern Europe. Using data on common bird species, the effects of climate change and anthropogenic habitat degradation on bird populations are quantified for different habitat types and seasons. Based on different statistical analyses, I examine the mechanisms affecting bird population trends in a large number of species occurring in the same geographical area. This method enables us to combine species into groups according to their ecological and life-history traits, and habitat requirements, which helps deepen the knowledge about large-scale impacts taking place in the environment while allowing an evaluation of the conservation status of bird populations. Moreover, this thesis also aims to produce habitat-specific bird indicators that can be adopted by environmental authorities, for instance through national online platforms such as biodiversity.fi, as one of the key indicators for monitoring biodiversity based on Society's Commitment to Sustainable Development (Sustainable Development Strategy Group 2016). In addition, these indicators can be used as tools to identify the most critical conservation issues, having important implications at national level. The main study questions that I seek to answer are:

1. What is our ability to measure progress towards biodiversity targets?
2. Is climate change, land use practices or both processes driving changes in bird populations in the studied environments?

3. What is the conservation status of bird populations in the studied environments?
4. Which are the most affected habitats and/or groups of species within the studied environments, and what can be done to reverse ecosystem degradation?

The present thesis consists of five chapters, each addressing at least one of the above questions (see **Table 1** and **Fig. 1** for more details). As shown in the Introduction, policy efforts are being made to address the current rates of biodiversity loss, however resulting in only a few local accomplishments and increasing responses (e.g. protected area extent and biodiversity coverage; Butchart et al. 2010). Given the importance of indicators to track progress towards the Aichi Biodiversity Targets, **Chapter I** critically examines efforts to measure the state and trends of biodiversity at the global level by revising the recent literature on state indicators (built on species' population trends covering the main habitat types) and pressure indicators (i.e. climate change impacts). Multi-species indicators have shown to be an effective means for analysing the state of biodiversity and the pressures upon it, particularly in the context of climate change. Northern ecosystems are predicted to be highly impacted under most climate change scenarios, and therefore the population trends of tundra and alpine bird species breeding in Arctic areas will be particularly affected. Along these lines, **Chapter II** studies species' ability to cope with changes in the environment by investigating how environmental factors are affecting Arctic breeding waterbird populations in the Finnish Lapland. Regardless of the growing evidence on the impacts of climate change on biodiversity (e.g. changes in species distributions), habitat loss is shown to be the most significant threat to bird populations. This is especially true for peatland ecosystems, where historical drainage

has been responsible for the loss of a large part of the original peatland cover (**Box 1**). Although peatlands are one of the most threatened ecosystems in Finland, there is surprisingly meagre research on the status of bird species relying on peatland habitats. **Chapter III** aims to increase our current ecological knowledge of boreal peatland birds by constructing the first bird status indicators covering Northern Europe and exploring whether aspects mostly related to peatland habitat quality and climate change (i.e. species range shifts) are responsible for changes in breeding bird species densities. Finnish forests have also been heavily impacted by land-use change. Changes in forest habitats are considered the main cause of threat to biodiversity in Finland, having particularly affected resident species and old-growth forest specialists (**Box 1**). Given that the effects of forest management on bird population trends in southern Finland has received scant attention up to date, **Chapter IV** evaluates the conservation status of common breeding forest birds in this particular region by investigating patterns of population change (species habitat requirements and traits) and developing three multi-species indicators that facilitate the monitoring of the observed patterns. Compared to the breeding season (when bird numbers increase because reproduction exceeds mortality), the non-breeding season is a crucial period for birds since mortality during this time is primarily responsible for declines in their numbers (Newton 1998). In temperate regions, these declines can be associated with hard winters and/or non-renewable food resources (Pearce-Higgins and Green et al. 2014). However, climate change and human impacts may modify this pattern with milder winters and winter feeding improving the habitat conditions for both landbirds and waterbirds, potentially causing changes in migration behaviour and significantly altering regional abundances (Lehikoinen et al. 2013, 2016).

Table 1. The specific objectives and main study questions addressed in the five chapters of this thesis.

Chapter	Specific objectives	Geographical extent	Main study question
I	Evaluate the recent advancements in the development of biodiversity indicators Identify main knowledge gaps, challenges and limitations of current biodiversity indicators Make recommendations for the future construction of biodiversity indicators	Global	1
II	Analyse the impact of weather and the phase of the small rodent cycle on breeding Arctic waterbirds	Finnish Lapland	2
III	Construct the first bird status indicators reflecting the state of peatland bird populations Identify the habitat requirements of common peatland bird species Determine whether climate change is driving peatland bird populations	Northern Europe	2, 3, 4
IV	Investigate patterns of population change relating them to species' habitat preferences and traits Construct multi-species indicators based on forest successional stages and latitudinal distribution	Southern Finland	2, 3, 4
V	Investigate patterns of population change relating them to species' habitat preferences and traits Construct multi-species indicators for urban, forest, and open water environments	Finland	2, 3, 4

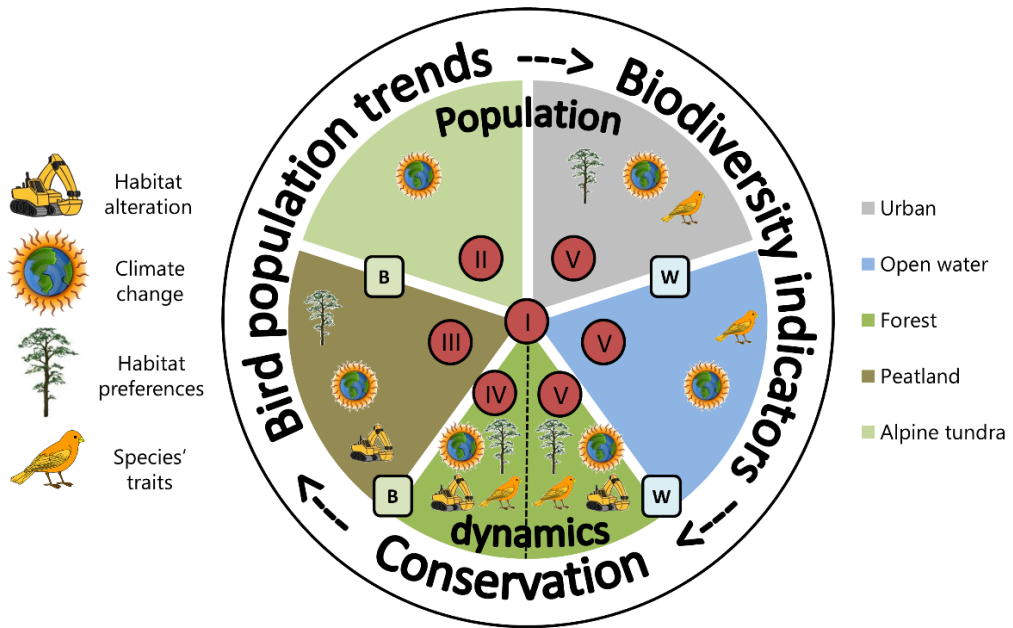


Fig. 1. This thesis assesses the general state of Finland’s bird populations in five different environments: urban, open water, forest, peatland and alpine tundra. Most of the chapters focus on breeding season data (B) and on a single environment (**Chapters II–IV**), whereas **Chapter V** explores three environments in the wintering season (W). In addition, **Chapter I** is based on a review covering several different environments. To investigate the potential drivers of population dynamics, the effects of climate change (weather, distributional shifts, predator-prey interactions), and habitat alteration by human activities are examined together or separately depending on the environment being evaluated. Habitat requirements as well as species’ ecological and life-history traits (i.e. species’ habitat preferences, species’ flexibility in habitat use and migratory strategy) help target those specific habitats and groups of species in need of urgent conservation action, while also allowing the construction of more robust indicators based on bird population trends. Altogether, the present work represents a broader evaluation of the current conservation status of biodiversity in Finland and the pressures upon it, contributing to the implementation of Society’s Commitment to Sustainable Development at national scale, and the Strategic Plan for Biodiversity 2011–2020 at global level.

While there is a plethora of studies examining breeding bird populations in Finland (e.g. Laaksonen and Lehikoinen 2013, Virkkala and Lehikoinen 2014, Välimäki et al. 2016), the winter ecology of Finnish birds remains largely under-studied. To fill this gap, **Chapter V** investigates the potential drivers of wintering bird population trends in Finland taking into account species traits and the type of habitat

where they occur. In addition, three multi-species habitat-specific indicators are constructed for urban, forest and open water environments.

3. MATERIAL AND METHODS

3.1. STUDY AREA

This thesis is mainly focused on how climate and land use changes affect bird populations in Finland. Therefore, most of the present work has been done at national scale either covering the whole territory (**Chapters III, V**) or a certain area (**Chapters II, IV**). In **Chapter III**, additional data were used from other countries in northern Europe (Sweden, Norway, Estonia and Latvia) which altogether cover approximately 70% of the peatland area in Europe (Montanarella et al. 2006), whereas **Chapter I** includes various spatial scales, from national to continental (see **Table 2**). Local studies encompassed an area of 43 and 230,000 km² (**Chapters II, IV**, respectively). The geographical extent of **Chapters II–V** is visualized in **Fig. 2**.

3.2. DATA

This thesis combines data from the three most common bird census methods: mapping, line and point transects (**Chapters II–V**). In **Chapter I**, the main advances, knowledge gaps, and research challenges and limitations of current bird indicators are synthesised in a literature review, giving recommendations for the construction of future biodiversity indicators. Additional sources of data are also presented.

3.2.1. Field methods

Long-term data are necessary for measuring changes in bird populations (Gregory et al. 2004, Lebbin et al. 2010), and Finland is one of the countries in the world with the longest bird datasets currently available (Lehikoinen 2016). In my thesis, I mainly used data coming from long-term bird monitoring schemes coordinated by the Finnish Museum of Natural History and conducted mostly by volunteers. Observers have not only counted the birds, but also classified the habitat types of survey sites. Habitat data have

been recorded since 1986 both during the non-breeding and the breeding season, including habitats of the counted birds as well as the amount of habitat along the routes. Based on wintering and breeding censuses it is possible to obtain information on annual population development for more than 60 and 130 species since late 1950s and mid-1980s, respectively.

a) Monitoring method during winter season

Since the winter of 1956/1957, the abundances of wintering birds in Finland have been monitored using line transects (**Chapter V**), which have an average length of ten km and are freely chosen by volunteers. There are three census seasons currently applied, but I used the season around New Year, also known as mid-winter censuses (during 25 December to 7 January), which has the best census coverage through the monitoring period. In winter, habitat data are classified in eight different land cover categories: a) dumping ground or fur farm, b) urban settlement, c) rural settlement, d) arable land, e) forest, f) clear-cut area or stand of saplings, g) reed-bed or shore scrub, and h) other. The last category contains birds in water areas, in active migration flight, and those cases in which habitat classification has not been possible to determine (Koskimies and Väisänen 1991).

b) Monitoring methods during breeding season in Finland

During the study period two different schemes have been run in the country for monitoring breeding abundances of birds: the line transect census and the point count census. Both schemes primarily aim to monitor landbirds (**Chapters III, IV**). In this thesis I also used data collected through a modified version of territory mapping (**Chapter II**).

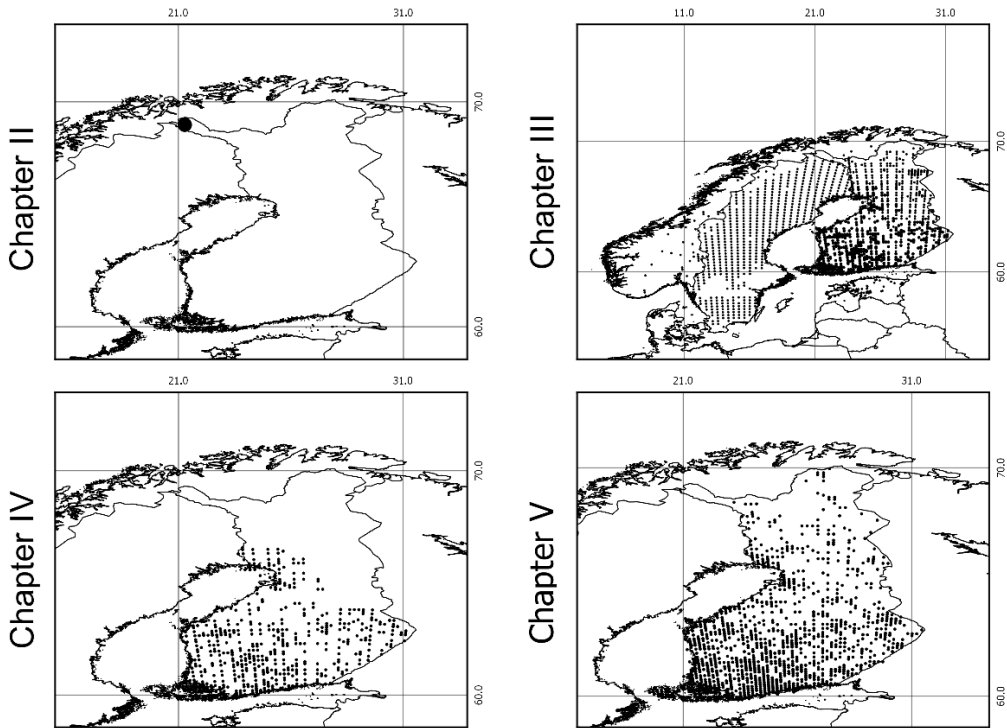


Fig. 2. Geographical extent and distribution of bird survey sites of **Chapters II–V** (coordinates in WGS84). Total number of sites used in these chapters: Chapter II = 1, Chapter III = 1398, Chapter IV = 868, and Chapter V = 3840 (see **Table 2** for more details).

The line transect census of landbirds has been carried out since 1975 (a new system of fixed routes was established across the whole country in 2006; Väisänen 2006). Along the line transect routes, which are approximately six km long each, birds are recorded according to their distance to the transect line. Two distance belts are distinguished: the main belt (25 + 25 m wide) and the supplementary belt, including pairs observed > 25 m from the route and all flying individuals (Koskimies and Väisänen 1991, Laaksonen and Lehikoinen 2013). Line transect habitat data are structured in twelve categories: a) spruce, b) pine, c) mixed (broadleaf-conifer stands), and d) broadleaf forests, e) bushes (tree height < 5 m, except for mountain birch forests), f) clear-cuts, g) pine mires, h) open mires, i) arable land, j) settlements, k) mountain areas,

and l) other. Few birds fall into the last category, which contains habitats such as industrial land and parking areas (Koskimies and Väisänen 1991). Finland's bird census data are unique in its kind because they allow to establish direct associations between the bird observations and the habitat types, thus obtaining relative densities (individuals or pairs / km; Järvinen and Väisänen 1975, Järvinen 1978).

The point count census for landbirds started in 1984. One point count route includes 20 points, each of which is located in a uniform habitat (within a 50-m radius) and separated by 250 m in forests and 350 m in open areas (Koskimies and Väisänen 1991, Laaksonen and Lehikoinen 2013).

Table 2. Details of the different bird census methods. Total number of survey sites (line transects and point counts) for Finland: Chapter III = 729 and Chapter IV = 868.

Method	Location	Study period	Census period	Census unit	No. sites	Chapter
Modified version of territory mapping	Finnish Lapland	2005–2015 (2006 excl.)	Early Jul	No. of pairs	1	II
Line transect census	Finland	1981–2014 (habitat data since 1986)	Late May–early Jul	No. of pairs	641	III
	S Finland	1984–2013 (habitat data since 1986)			677	IV
	Sweden	1997–2014		No. of adult individuals	561	III
	Estonia	1981–2014		62	III	
	Latvia	2003–2014		1	III	
Point count census	Finland	1984–2014	Late May–early Jul	No. of pairs	88	III
	S Finland	1984–2013			191	IV
	Norway	2006–2014			45	III
Winter transect census (mid-winter)	Finland	1959–2012 (habitat data since 1986)	Late Dec–early Jan	No. of individuals	3840	V

Each point is surveyed for five minutes, and observed birds are classified as inside or outside a 50-m radius from the point (Koskimies and Väisänen 1991). While habitat data are also provided in point count routes, the precision is lower compared with those gathered from line transects (e.g. average tree height or average size for open areas is not specified). The habitat of each point is classified into 17 different habitat categories.

The third census method used in this thesis was a modified version of territory mapping

(**Chapter II**; Koskimies and Väisänen 1991), which is a useful method to survey birds at temperate regions during the breeding season, when many individuals are actively defending their territories or spending much time around the nesting site (Gregory et al. 2004). Theoretically, territory mapping provides fairly accurate estimates of population size since the total number of pairs or territories of the surveyed species can be directly estimated (Gregory et al. 2004). More details about the bird census methods used in this thesis can be found in **Table 2**.

c) Census methods outside Finland

The chapter examining bird populations in peatlands (**Chapter III**) included data from four other Northern European countries (besides Finland): Sweden, Norway, Estonia and Latvia.

In Sweden, data originate from the so-called fixed routes (Lindström et al. 2013). There are in total 716 fixed routes, each of eight km in length, distributed evenly across the country (Lindström et al. 2013). A total of 561 routes were regarded as peatland routes, with bird data covering the period from 1996 to 2014 (**Table 2**). Censuses were carried out from mid-May (southernmost Sweden) to early July (northernmost Sweden), and there was no indication of a temporal trend in the annual-average survey dates (Lindström et al. 2013).

In Norway, common bird monitoring data are collected from almost 500 sites which are randomly selected among 1030 sites distributed evenly over the country in an 18 km north-south and 18 km east-west network (Husby and Kålås 2011, Lehikoinen et al. 2014, Lindström et al. 2015). Bird counting consists of point counts, each route containing 20 points (5 min counting period at each point) situated 300 apart and forming a 1.5×1.5 km square. In addition, all observations of non-passerine birds (and a few pre-selected passerine species) observed while moving between the counting points are recorded (Lehikoinen et al. 2014, Lindström et al. 2015). After habitat selection the Norwegian dataset consisted of 45 routes censused from 2006 to 2014 (**Table 2**).

In Estonia, regular annual censuses of mire birds begun in 1968 in Nigula bog (Irtd and Vilbaste 1974). In this bog area of approximately 2000 ha, up to ten transects were censused per year with an average length of 5.5 km. Since 1986 other census sites started to be surveyed especially using line transects (Laitinen et al.

2007, Leivits et al. 2013). Overall, data included altogether surveys of 62 different sites and it was assumed that censuses were random samples from the mires. The study period comprised years from 1981 to 2014 (**Table 2**).

In Latvia, data were collected entirely in the Ķemeru Mire, one of the largest raised bogs in the country located in the Ķemeri National Park (Bambe et al. 2008). This site was censused yearly in mid-May and consisted of a total of 13 consecutive line transects across the terrain covering typical open raised bog habitat. The study period ran from 2003 to 2014 (**Table 2**).

d) Survey effort and detectability

The census methods described above do not reveal the absolute unbiased abundances of species, nor the exact boundaries between the habitats used by birds (e.g. due to species- and habitat-specific differences in detectability). Nevertheless, most of the data can be used to reliably describe the spatial and temporal variation in the general distribution of birds in the study areas (Väisänen and Lehikoinen 2013) and in different environments (winter and line transect census methods; Koskimies and Väisänen 1991), with a higher level of accuracy in the case of territory mapping. Also, despite visiting the study sites only once and not finding all breeding pairs, the survey effort in **Chapter II** was the same each year, making the annual values comparable under the assumption that detectability remained constant.

Although several sources of bias can be reduced with standardized methods (effort and speed of surveying, time of the day, weather conditions, etc.; Gregory et al. 2004), others may be more difficult to account for. For instance, changes in species-specific differences in detectability (e.g. due to earlier phenology) could cause spurious patterns and correlations. However, a study carried out by Lehikoinen (2013) showed that

only three of the 73 studied Finland's breeding landbird species showed an annual trend in the proportion of main belt observations (line transect data; **Chapters III, IV**) from 1987 to 2010. This suggests that temporal change in detectability is at most a minor problem in trend estimation. Similarly, no temporal trend in the annual average latitudinal position or annual average census date of the line transects was found for the same study period (Lehikoinen 2013). As for the winter period, survey effort, spatial and temporal coverage were maximized by selecting the mid-winter transect routes (**Chapter V**). In addition, mid-winter transects are little affected by late autumn migration and early spring migration. Similarly, there was no temporal trend in the annual average latitudinal position of the censused sites during the study period (1959–2012). On the other hand, while there was no temporal trend in the number of sites surveyed annually for this period (linear regression, $b = 0.28 \text{ transect yr}^{-1} \pm 0.47 \text{ SE}$, $F_{1,52} = 0.34$, $p = 0.56$), the number of line transects surveyed during the breeding season increased from 1980 to 2014 (linear regression, $b = 4.99 \text{ transect yr}^{-1} \pm 0.87 \text{ SE}$, $F_{1,33} = 32.64$, $p < 0.001$). Line transects constituted most of the data used in **Chapter III** (Finland, Sweden and Latvia: 86%; Finland only: 88%) and **Chapter IV** (78%) (see **Table 2**).

3.2.2. Bird indicator data from literature

Chapter I is a literature review of recent studies published on bird indicators during the period 2011–2016. With the aim to analyse the current bird indicators used to evaluate the state of biodiversity (species' population trends) and the pressures upon it (climate change impacts), the following information is extracted from the ISI Web of Science database – two different combinations of key words used; birds + indicators + biodiversity, and birds + multi-

species + indices – for a total of 128 indicators from 25 different studies: a) the type of indicator (state or pressure), b) a brief description of the indicator, c) the study period, d) the type of data used (abundance or presence-absence data), e) the season of the year, f) the study area, g) the type of habitat, h) the type of driver thought to affect the indicator, i) the number of species involved, j) whether site selection was applied to develop the indicator, k) whether species selection was applied to develop the indicator, l) whether expert opinion was used in the species selection procedure, and m) the general outcome of the indicator. Although I did not consider grey literature (i.e. reports, government documents, etc.), the obtained sample can be regarded as representative of the current scientific literature available on the subject of study.

3.2.3. Additional data

Additional data are listed in **Table 3**.

3.3. SITE AND SPECIES SELECTION

Three of the five chapters belonging to this thesis established some kind of protocol (or more than one) for selecting the sites with sufficient bird observation data for estimating population trends. Site selection relied on: i) whether a site was considered to be part of the species' core distribution range (Minimum Convex Polygon method; **Chapter III**); ii) the number of times a transect was repeated or visited during the study period (**Chapters III, IV**); iii) the transect coverage of a certain habitat type (**Chapter III**); iv) the presence of a particular species representative of the study habitat (**Chapter III**); v) the location of sites (**Chapter IV**); and vi) the quality and quantity of the censuses (i.e. coverage over the longest study period and best sampling effort; **Chapter V**).

Table 3. Supplementary datasets used in this thesis. The number of sites used to extract the information for latitudinal data is indicated in brackets.

Data	Period	Description	Source	Chapter
Migratory data	—	Migratory strategies of the study species	Cramp et al. 1977–1994	IV, V
Latitudinal data	1970–2012	Latitudinal distribution of the study species (n = 4625)	Virkkala & Lehtikoinen 2014	IV
	1956–1969	Former latitudinal distribution of the study species (n = 5755)	Finnish Museum of Natural History	V
Rodent data	2005–2015 (2006 excl.)	June rodent density indices	H. Henttonen & J. Niemimaa	II
Weather data 10 × 10 km grid	2005–2015 (2006 excl.)	Average temperature & sum of rainfall Jun–Jul	Finnish Meteorological Institute	II
	1984–2013	Average temperature Mar–Jul & Dec–Feb		IV
	1961–2011	Average temperature mid-Nov–end Dec		V

Different procedures were also employed to choose the study species. However, all the studies (**Chapters II–V**) had to have a minimum number of observations as a requirement for a certain species to be included in the analyses (e.g. average annual number of pairs in **Chapter II**, or number of winters where the species was observed in **Chapter V**). Species were chosen not only on the basis of their occurrence in the datasets to ensure good data quality when estimating trends. In **Chapter III** and **Chapter IV**, habitat preferences of bird species were quantified by estimating a preference ratio using species densities from line transect habitat data (i.e. preference of a species for the study habitat over the non-study habitat). Species had to either meet or exceed a certain preference ratio threshold for their inclusion, but also meet the

required minimum number of observations. In some cases, although species fulfilled these requirements, they were finally excluded because they showed a highly variable spatio-temporal pattern of fluctuations, which is known to be driven by food availability. In other cases, species could not be considered to represent the studied habitat type *per se* (**Chapter III**). Hence, in **Chapter III**, expert opinion was used to complement the automatic species selection procedure when formulating the inclusion criteria for selecting species.

All the methods applied regarding site and species selection contributed to guarantee the representativeness of the study habitat among the selected sites, as well as the association of

the species and observed individuals with their corresponding habitats.

On this basis, a total of ten waterbird species (three ducks and seven wader species) were used in **Chapter II**, 13 species (three passerines and ten waders) in **Chapter III**, 32 common breeding forest land bird species in **Chapter IV** and 63 species (11 waterbirds and 52 landbirds) in **Chapter V**.

3.4. STUDY UNITS AND VARIABLES

All the chapters of the present thesis used bird species as the taxonomic study unit. However, there was one exception (**Chapter I**) where the study unit was bird indicators selected based on the literature review. The number of species studied varies across chapters depending on the geographical extent, type of habitat studied, season of the year, bird census method, and procedure employed for site and species selection. Also, the number of species differs according to the purpose of both the main analyses (i.e. studying how environmental factors relate to bird populations) and the indicators. Complementary information of this section can be found in **Table 4**.

The response variables of **Chapters IV–V** were mainly species' temporal logarithmic trends computed using log-linear Poisson regression with TRIM. The TRIM software (TRends and Indices for Monitoring data; Pannekoek and van Strien 2005) handles missing data (e.g. routes not censused every year) through imputation and it accounts for both overdispersion and temporal autocorrelation. In the model applied, the expectation of the natural logarithm of the counts (response variable) is explained with the fixed effect factor variables *year* and *site*. This is equivalent to a multiplicative model for the untransformed expected counts (van Strien et al.

2004). In **Chapter IV**, a bivariate response was used to give more flexibility in the trends. Population growth rate was the dependent variable in **Chapter II**, i.e. the natural logarithm of the rate of change in bird numbers $\ln(N_t / N_{t-1})$, whereas **Chapter III** used bird counts for each year and peatland route (effectively densities; pairs / km) obtained from line transect habitat data. Population indices constituted the response variables in the trend analyses, where *year* was set as a continuous variable (**Chapters III–V**; see below). As for the explanatory variables, while **Chapter II** used mostly variables related to other sources than bird census data, many of the variables included in **Chapters III–V** were extracted or built on habitat data either from line transects (eight in **Chapter III**, four in **Chapter IV**) or winter bird counts (one in **Chapter V**).

3.5. INDICATORS

Indicators of biodiversity change were developed in **Chapters III–V** (see **Table 5**). These chapters present habitat-specific indicators to evaluate the general state of biodiversity in different environments (state indicators), but additionally, one indicator in **Chapter IV** illustrates the relative representation of southern and northern species. Because any change in the bird community towards southern latitudes (i.e. southern species becoming more common) would presumably be associated with climate change shifting species' ranges northward (Kujala et al. 2011, 2013, Virkkala and Rajasärkkä 2011, Brommer et al. 2012), this indicator can be regarded as a pressure indicator.

The construction of habitat specific indicators was done using the geometric mean of relative abundance (G ; method described by Gregory et al. 2005).

Table 4. List of explanatory variables used in the thesis organized in three different blocks: whether variables have been used only in the main analyses (**MA**), in both the main analyses and the construction of indicators (**MA & I**), or only in the construction of indicators (**I**).

	Chapter and data	Variable name	Type	Description
MA	II. Territory mapping	N_{t-1}	Continuous, numerical	Population size/density in the previous year
	II. Rodent data	Rodent _{<i>t</i>}	Continuous, numerical	Rodent abundance the same year
		Rodent _{<i>t-1</i>}	Continuous, numerical	Rodent abundance the year before
	II. Weather data	Temp _{<i>t</i>}	Continuous, numerical	Average temperature the same year
		Temp _{<i>t-1</i>}	Continuous, numerical	Average temperature the year before
		Rain _{<i>t</i>}	Continuous, numerical	Average sum of rainfall the same year
		Rain _{<i>t-1</i>}	Continuous, numerical	Average sum of rainfall the year before
	II. Territory mapping & III. Line transects	Species-ID	Factor, categorical	Species identity
		Year	Discrete, numerical	Temporal trend & random intercept
	III. Line transects		Factor, categorical	Spatio-temporal trend
		Latitude	Continuous, numerical	Spatio-temporal trend
	III. Habitat data		Continuous, numerical	Spatio-temporal trend
		Site	Factor, categorical	Random intercept between sites
		Open	Dummy, numerical	Open peatlands
	III. Habitat data	Ditched	Dummy, numerical	Ditched forested peatlands
Peat extraction		Dummy, numerical	Peat extraction areas mostly for energy production	

Table 4. Continued

	Chapter and data	Variable name	Type	Description
MA	III. Habitat data	Wetness	Dummy, numerical	Degree of wetness for wet, 'intermediate' and dry peatlands
		Area size	Continuous, numerical	Average \log_{10} area size of peatland
		Length	Continuous, numerical	Length of peatland route walked (km)
	III. Habitat data & IV. Habitat data	Tree height	Continuous, numerical	Average tree height of the observed species
	IV. Habitat data	NPH	Continuous, numerical	Species preference for nutrient-poor habitats
		Habitat evenness	Continuous, numerical	Flexibility of species in habitat use
	IV. Migratory data & V. Migratory data	Migration strategy	Factor, categorical	Migratory strategies of the study species
V. Latitudinal data	Latitude	Continuous, numerical	Average latitudinal distribution of species	
MA & I	IV. Latitudinal data	Latitude	Continuous, numerical	Average latitudinal distribution of species
	IV. Habitat data	LSH	Continuous, numerical	Species preference for late successional habitats
	V. Habitat data	Urbanity	Continuous, numerical	Species relative use of urban habitats
I	IV. Weather data &	Temp _b & Temp _w	Continuous, numerical	Average breeding & winter temperature
	V. Weather data	Temp _{ew}		Average early-winter temperature
	III. Line transects & IV. Line transects & V. Mid-winter counts	Year	Discrete, numerical	Temporal trend

G is a common measure employed to examine trends in biological diversity (Buckland et al. 2011, Harrison et al. 2014). This measure combines multiple species trends based on yearly relative abundance indices to generate a composite population index (Buckland et al. 2005), giving an indication of whether a population is increasing, decreasing or stable (Gregory et al. 2004). The index is directly proportional to changes in population size, i.e. if the population doubles, so does the index (Gregory et al. 2004). In this sense, the geometric mean has good mathematical properties compared to other measures of species diversity when it is balancing and halving species trends (Buckland et al. 2011, van Strien et al. 2012).

G can be estimated by back-transforming the arithmetic mean (common average) of the log-scale indices of m species per year:

$$G_j = \exp \left[(1/m) \sum_i \log(d_{ij}/d_{i1}) \right]$$

where d_{ij} is the abundance of species i in year j , and d_{i1} the abundance in year 1; d_{ij}/d_{i1} constitute the relative abundance indices.

Species-specific annual indices of relative abundance and standard errors of the parameter estimates were obtained from TRIM (see previous section). Standard errors of species annual abundance indices were used to calculate an estimate of the standard error for G . Finally, indices were produced combining G and its standard error approximation (see formula used for calculating the variance for G in Gregory et al. 2005).

On this basis, a total of nine indicators were related to habitat trends and one indicator to changes in climate. In two cases, annual estimates of species relative abundance were used to calculate a weighted geometric mean (species abundances weighted by the LSH

variable) or a weighted arithmetic mean to describe the average latitudinal distribution of the community (**Chapter IV; Tables 4, 5**). In **Chapter III**, no weights were applied in the construction of the North European peatland bird indicator because the area of peatland habitat per number of routes was very similar in Finland, Sweden and Estonia. Indicators were built based on the aforementioned species preference ratios, urbanity index (to distinguish between urban and forest species; **Chapter V**), latitudinal distribution and migratory strategy (**Tables 4, 5**).

3.6. STATISICAL MODELLING

Apart from the methods used for analysing trends and for constructing the indices (TRIM; see section 3.4.), this thesis incorporated a set of different statistical models with special features, including: multivariate linear mixed models (LMMs; **Chapter II**), generalised linear mixed models (GLMMs) fitted using Markov Chain Monte Carlo (**Chapter III**), multivariate linear models (LMs; **Chapters IV, V**), and generalized least squares (GLS) for incorporating measurement error and phylogenetic autocorrelation (**Chapter V**). Ordinary and segmented linear models were used to analyse temporal trends in species' populations and in the indicators (**Chapters III–V**), given that segmented analysis offers more complex patterns of dynamics to be potentially explained compared to a uniform trend.

Most statistical inference in this thesis used a frequentist approach. To test the null hypothesis of no influence of the explanatory variables on the response variable, Wald tests (**Chapter V**) and Likelihood Ratio Tests (LRT; **Chapters III–V**) were applied. LRT was used in the indicators to compare the segmented regression approach with the null model, where the trend was constant throughout the period.

Table 5. Characteristics of indicators developed in **Chapters III–V**. For the MF-index, the final species set was obtained through two species selection processes: 1) initial species preference ratio for forest over non-forest habitats; and 2) a second species preference ratio based on the LSH variable only including species preferring old stands. Meaning of the acronyms in alphabetical order: BAT = Baltic, CLI = Community latitude index, EE = Estonia, F = Finland/Finnish, LSH-index = Late successional habitat index, LV = Latvia, MF-index = Mature forest index, NE = North European, NO = Norway, PR = Pressure, S = Southern, SCAND = Scandinavian, SE = Sweden, ST = State.

Name	Type	Scale	Period covered	Basis species selection	No sp.	Habitat	Weights	Chapter
NE peatland bird indicator	ST	NE	1981–2014	Sp. pref. ratio FI & expert opin.	15	Peatland	—	III
FI peatland bird indicator	ST	National	1981–2014	Sp. pref. ratio FI & expert opin.	15	Peatland	—	III
SCAND peatland bird indicator	ST	Regional (SE & NO)	1997–2014	Sp. pref. ratio FI & expert opin.	12	Peatland	—	III
BAT peatland bird indicator	ST	Regional (EE & LV)	1981–2014	Expert opin.	9	Peatland	—	III
LSH-index	ST	National	1984–2013	Sp. pref. ratio	32	Forest	LSH variable	IV
MF-index	ST	National	1984–2013	Sp. pref. ratio	13	Forest	—	IV
CLI	PR	National	1984–2013	Sp. pref. ratio	32	Forest	Latitude variable	IV
Urban indicator	ST	National	1959–2012	Urbanity index > 0.66	19	Urban	—	V
Forest indicator	ST	National	1959–2012	Urbanity index < 0.33	17	Forest	—	V
S waterbirds indicator	ST	National	1959–2012	Lat. distribution & Migr. strategy	10	Water	—	V

To account for model uncertainty, and to evaluate the most parsimonious subset of predictors, information theoretical model selection was used (**Chapters II, IV**). *Post-hoc* tests (**Chapter II**) were performed based on the results from the information theoretical model selection. For analysing habitat preferences in

Finnish peatlands (**Chapter III**), a Bayesian approach for fitting the GLMMs was applied. In these analyses statistical inference was based on 95% credibility intervals of the posterior distributions, which were interpreted as statistically important when zero was excluded.

4. RESULTS AND DISCUSSION

4.1. CURRENT VIEW OF BIODIVERSITY INDICATORS AND RECOMMENDATIONS FOR GOOD PRACTICE

In general terms, recently published academic literature on bird biodiversity indicators was strongly biased towards state indicators measuring species' population trends, whereas pressure indicators covering climate change impacts were much less frequent (**Chapter I**). Both state and pressure indicators also showed spatial, seasonal and methodological biases. Only a few indicators were developed at continental level, and they were almost exclusively focused on Europe. Country-level and sub-continental (i.e. involving more than one country) indicators were mainly published in the UK and in northern European countries, respectively. Further, the breeding season clearly dominated over the non-breeding season. Regarding methodological processes of sampling site and species selection, which were more often applied in state rather than pressure indicators, species selection was more common than site selection procedures. However, there were not that many cases where indicators incorporated both selection procedures at the same time. Some of them used expert opinion as the only mechanism to select species, to assign species to a particular habitat, or to complement species selection procedures. Fortunately, cases in which no site or selection procedures were taken into account were very scarce. Among species selection processes, quantitative methods to associate species with their habitats were fairly commonly used and well-established in the peer-reviewed literature. As for state indicators, the type of habitat represented an additional source of bias, since most indicators were mainly covering either forest or farmland habitats and generally revising or fine-tuning the current versions of wild bird indicators for these habitats. On the other hand, alternative (but complementary) methodologies to the

traditional way of constructing the indicators (i.e. relying on the geometric mean as a measure of biodiversity) included the use of the goodness-of-fit evenness measure (GoF; Studeny et al. 2013, Harrison et al. 2014) to detect patterns of biotic homogenization, or new indicators such as the Biodiversity Change Index (BCI; Normander et al. 2012). Indicators measuring the impact of both climate and land-use change were rare, and more statistically advanced methods are needed in this respect. In addition, correcting for detectability and incorporating spatial patterns in modelling techniques is important to cover a wide range of habitat types or a diverse spread of taxa (Quinn et al. 2011, Johnston et al. 2014). In any case, recently published indicators pointed towards a loss of biodiversity (particularly in farmland habitats), whereas more than half of the pressure indicators measuring climate change impacts showed an increasing trend, indicating that climate change has indeed had an impact on bird communities. This general outcome seems to be in line with other previous reviews on biodiversity indicators (e.g. Butchart et al. 2010, Tittensor et al. 2014). In the light of these results, several recommendations can be made for new bird biodiversity indicators in order to cover the main aforementioned gaps. First, for a sensible assessment of changes in biodiversity, further efforts should be made to **increase the robustness of monitoring schemes** to be able to obtain reliable and quality assured data on biodiversity at acceptable spatial and temporal resolutions (de Heer et al. 2005, Normander et al. 2012). Moreover, common methods to apply and harmonise data from different monitoring schemes should be developed (Normander et al. 2012). This would also allow the inclusion of rare species, which may show more sensitive responses to environmental change (Battisti and Fanelli 2016), in the construction of the indicators. In addition, scarce species, which are not yet in the focus of conservation action, would benefit as well from biodiversity action plans (Studeny et al. 2013). Also, more data

would be readily available to cover other regions that are predicted to be increasingly affected by climate change (e.g. Mediterranean region; EEA 2016). Second, there is also need to **enhance the coverage of indicators in the non-breeding season (Chapter V)** to improve our understanding of bird responses to ecological processes caused by climate and/or land use change. In this sense, migratory behaviour or other species' traits should be more often included in the construction of indicators (**Chapters IV, V**), both during the breeding and the wintering season. Third, although the effect of climate change could equal that of land-use changes (e.g. Clavero et al. 2011, Eglington and Pearce-Higgins 2012), climate change has the potential to dominate over land-use effects on bird abundances (e.g. Ay et al. 2014). In this sense, **establishing a better picture of the effects of climate change** with the development of more pressure indicators (**Chapter IV**) is highly advisable. Fourth, state indicators should **expand the representativeness of understudied habitats** such as urban environments (**Chapter V**), water bodies (**Chapter V**), wetlands (**Chapter III**) and mountain areas (**Chapter II**), some of which may be especially vulnerable to habitat loss and/or climate change. Fifth, this thesis encourages the use of **quantitative methods for species selection procedures (Chapters III – V)**, since this will likely produce more reliable, replicable and accurate indicators than those indicators for which species selection relies exclusively on expert opinion (see **Box 2**). Sixth, **comparing various methodologies during the indicator development stages** (i.e. mainly using different species selection procedures and methods to combine species-specific indices into a single measure) will enhance and ensure the reliability of the results. In this regard, peer review has also a key role in this evaluation process (**Chapters III–V; Box 2**). Seventh and last, although **Chapter I** deals exclusively with

bird indicators, there is a large need of **new comparative studies of responses in multiple taxonomic groups** (including birds) to one particular environmental driver and across different regions. However, this can only be achieved by setting appropriate standards for data quality.

4.2. ECOSYSTEMS AT RISK

4.2.1. Sub-Arctic alpine tundra

Despite the fact that no temporal changes in bird population size were detected for any of the study species in an Arctic breeding bird community (**Chapter II**), evidence was provided that both weather and the phase of the rodent cycle had an effect on waterbird populations. However, these effects differed between ducks and wader species. On one hand, the results obtained from waders supported the hypothesis that predators tend to focus on rodents at high densities, which leads to decreased predation pressure on waterbirds (**Fig. 3A**). Wader populations were positively influenced by the abundance of rodents (phases of the rodent population cycles) the same year, with numbers of successful breeding pairs increasing towards the peak phase of the rodent cycle (**Fig. 3B**). This first result had been previously shown indirectly for both ducks and waders using demographic data outside the breeding season (e.g. Pehrsson 1986, Sutherland 1988, Summers et al. 1998, Hario et al. 2009). Whereas no link was detected between waders and weather, ducks were negatively affected by previous years' rainfall, suggesting that an increase in rainfall might have caused nest and brood loss (e.g. due to poor incubation and brood-rearing conditions) and also that drier conditions in the previous breeding season could possibly lead to a breeding population increase.

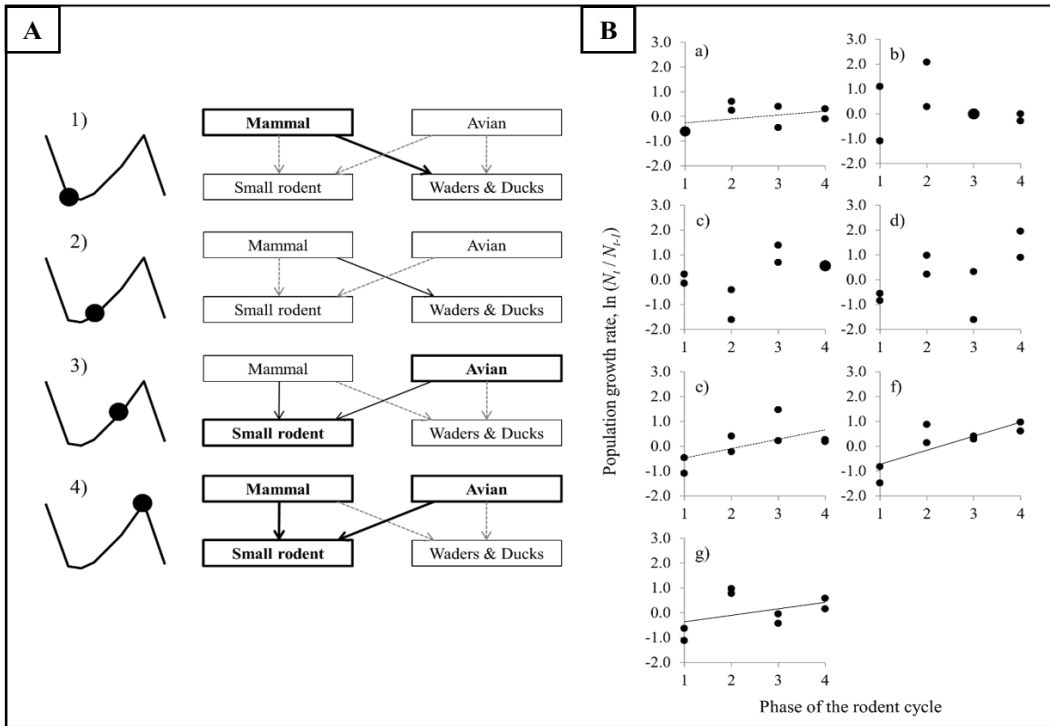


Fig. 3. A) Hypothetical illustration of predator-prey interactions during a four-year rodent cycle in the study area. Years of high mammal or bird abundances are denoted by boxes with thick lines and bolded text. Years of high predation are denoted by thick arrows (three different levels). On the left hand side of the diagram, the different phases of the rodent cycle are presented: 1) decline phase, 2) low phase, 3) increase phase, and 4) peak phase. Low productivity of waders and ducks is expected to occur during the decline phase. Note that some of the interactions are based on observations that have not been tested. This diagram has been adapted from Pearce-Higgins and Green (2014). **B)** Population growth rates of adult wader species in relation to the phase of the rodent cycle the same year (1 = decline phase, 4 = peak phase). The following species are represented: a) Common Ringed Plover (*Charadrius hiaticula*), b) Eurasian Dotterel (*Charadrius morinellus*), c) Wood Sandpiper (*Tringa glareola*), d) Ruff (*Calidris pugnax*), e) Temminck's Stint (*Calidris temminckii*), f) Dunlin (*Calidris alpina*), and g) Red-necked Phalarope (*Phalaropus lobatus*). Solid regression lines represent a significant (p -value ≤ 0.05) and dashed lines a nearly significant (p -value ≤ 0.1) relationship between the variables based on the regression analyses. Large dots in panels a–c represent two data records with the same values. Both figures can be found in **Chapter II**.

Although negative impacts of rainfall on breeding success had been identified earlier in other systems (e.g. Rodríguez and Bustamante 2003, Lehikoinen et al. 2009), the impacts of rainfall on population dynamics have rarely been observed (e.g. Iles et al. 2013).

The study, however, had some limitations. First of all, the impossibility of evaluating the effect of rainfall and the phase of the rodent cycle in the same model does not allow for a comprehensive assessment on whether rainfall plays a more important role than the phase of the rodent cycle for ducks. Although the time series analysed is longer than other time spans used in

similar works (e.g. Pehrsson 1986, Syroechovski et al. 1991, Underhill et al. 1993, Robinson et al. 2014), it is still too short to detect the impact of extreme weather events upon bird populations such as very cold summers. This could also explain why there was no effect of weather on waders. Similarly, only the four more abundant wader species (Common Ringed Plover *Charadrius hiaticula*, Temminck's Stint *Calidris temminckii*, Dunlin *Calidris alpina* and Red-necked Phalarope *Phalaropus lobatus*) were positively affected by the phase of the rodent cycle (**Fig. 3B**), suggesting that sample sizes were too small to detect effects on less common species.

Given the effects of weather and predator-prey dynamics, and considering the climate predictions for this region with faster-than-average rising air and sea temperatures, climate change is expected to impact severely on this unique ecosystem (EEA 2016). As such, bird populations will be progressively threatened by climate change. Climate-driven dampening of the amplitude of rodent cycles (Gilg et al. 2009, Cornulier et al. 2013, Korpela et al. 2013), and the ever-increasing frequency of extreme weather events will likely affect birds' productivity and population size also during the non-breeding season (e.g. Nolet et al. 2013, Aharon-Rotman et al. 2015, Fox et al. 2016). Importantly, changes in rodent cycles may not only influence predator populations (Schmidt et al. 2012, Millon et al. 2014) but also alternative prey species, such as waders and ducks (Zydelis et al. 2006, Hario et al. 2009, Guillemain et al. 2013, Fox et al. 2015, but see Korpela et al. 2014). In order to obtain further scientific evidence to support such results (e.g. spread of generalist predators, or shifts in wintering distributions along waterbird migration flyways; **Chapter V**), and following the first recommendation of the previous section, there is an urgent need to improve the monitoring of waterbird populations both during the breeding and wintering seasons to better assess annual

survival and reproductive success of e.g. species wintering in pelagic ecosystems. Although increasing sample size and time series may reveal new patterns in bird population dynamics in the Arctic, it will be difficult to separate the effects of rainfall from vole cycles, since dynamic effects of predation are dependent on climate-linked processes (Kausrud et al. 2008). This may be especially true for wader species.

4.2.2. Peatlands

Contrary to **Chapter II**, the population sizes of peatland species (**Chapter III**) decreased by 40% in Northern Europe (see **Fig. 4A**). Although the annual rate of decline in the whole study area (i.e. Finland, Sweden, Norway, Estonia and Latvia) did not differ much from that of Finland only (approximately -2% / year), differences were found among the three regions analysed (i.e. Finland, Scandinavia and the Baltic). Whereas Finland's populations experienced the strongest decline (almost 50%) during the study period, the Baltic populations (Estonia and Latvia) increased by 40% for the same period but showed considerable variation over time. The Scandinavian indicator (Sweden and Norway) showed a 20% decline for a shorter study period, but the annual rate of decline of the Scandinavian populations was less pronounced (-1% / year). As such, almost all peatland state indicators showed negative population trends, with the only exception being the Baltic region.

Although no evidence is provided of a direct relationship between the outcome of the peatland indicators and the history of peatland management in the studied regions, both literature and data support the fact that Finland has suffered the most from drainage (**Box 1, Fig. 5**). In addition, drainage continues to be the most important threat to peatland biodiversity in Finland, not least because of drainage associated with historical ditching, which slowly degrades the habitat (**Box 1**). Unlike Finland, more than

half of the original peatlands are in a natural or nearly natural state in Scandinavia. Despite substantial drainage also occurring in this region especially between the 1930s and 1970s, it has apparently affected a lower proportion of peatland area as compared to Finland (less than 20%; Joosten and Clarke 2002, Vasander et al. 2003, Joosten 2015).

Apart from management, the level of protection of peatland habitats may also be a plausible explanation for the observed trends. For instance, only 14% of the peatland cover is protected in Finland, whereas in Estonia approximately 75% of the open mires are currently protected and 90% are located within the Estonian Green Network, respectively (Čivić and Jones-Walters 2010, Kimmel et al. 2010). Because of the high protection status in this

country, the majority of the censuses were carried out inside protected areas, which most likely explains the results for the Baltic.

The pattern of decline observed in Finland resembles the general decline observed for Northern Europe, which indicates that Finland may be driving the overall trend. Although drainage has been a common practice in countries other than Finland (e.g. Estonia; Joosten 2015), the long-term protection of peatland ecosystems in the Baltic may be regarded as the main argument to explain the increase in peatland populations. This inevitably raises the question of the extent to which protected areas have the ability to counteract the negative effects of climate change.

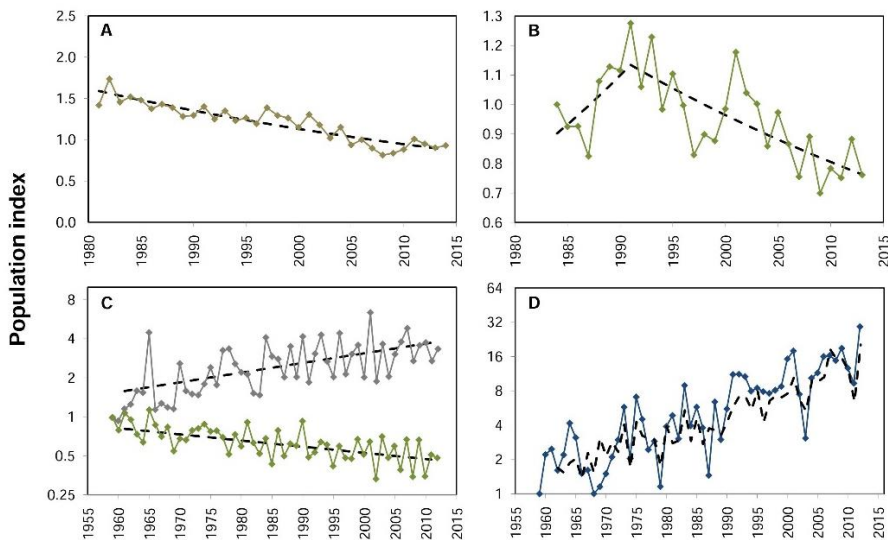


Fig. 4. Main biodiversity indicators produced in this thesis. **A)** Peatland bird status indicator for Northern Europe (15 species included; **Chapter III**). **B)** MF-index for the breeding season ($n = 13$; **Chapter IV**). **C)** Urban indicator (in grey) for the winter season ($n = 19$; **Chapter V**) and forest indicator (in green) for the breeding season ($n = 17$; **Chapter V**). **D)** Southern waterbird indicator for the winter season ($n = 10$; **Chapter V**). In figures **C)** and **D)** the values correspond to the back-transformed \log_2 population indices. In figures **A)**, **B)** and **C)** fitted values include the effect of year only, whereas in figure **D)** fitted values also include the effect of early-winter temperature. Figure adapted from **Chapters III–V**.

For instance, changes in precipitation and run-off regimes, which are expected to be more pronounced in the southern part of the study area, could cause peatlands to become drier, and consequently still cause biotic shifts (Virkkala and Rajasärkkä 2011, Carroll 2012, EEA 2016). Unfortunately, for the time being, this question still remains unanswered.

The decline of Finland's peatland bird populations has accelerated in the last 15 years, which is especially alarming considering that Finland holds the largest peatland bird populations within the EU countries, and so it has the highest responsibility for their conservation. The analyses regarding species-specific habitat preferences for common peatland birds in Finland (passerines and waders) revealed that species prefer habitat characteristics typical for open peatlands – large peatlands, with open areas and low tree heights – with clear avoidance of ditched peatlands and peat extraction areas. In addition, waders were positively associated with wetness. All these results have been previously found to some extent in other studies (Järvinen and Sammalisto 1976, Väisänen and Rauhala 1983, Väisänen et al. 1998), and although they are highly expected, or may seem almost self-evident, results of this kind must be scientifically well-established to form the basis for sound management decisions. Because almost all species' densities were negatively associated with drainage, and considering the fact that drainage in the short (peat extraction) and long term (forest ditching and peat extraction) tends to remove typical peatland properties beneficial for the birds (e.g. due to afforestation), this result supports the earlier view that drainage of peatlands is the driver behind the observed population declines.

Current evidence for the effects of climate change on peatland bird species is not very strong, since northward range shifts were only

detected for a few of the studied species. However, this result is in line with the latest findings and predictions made for the study area (Virkkala and Lehtikoinen 2014, EEA 2016), suggesting that responses of peatland bird populations to climate change will be likely more detectable in the near future (Virkkala et al. 2008). Despite the high conservation value of peatlands, mires and bogs have been recently listed as the most threatened habitat types among terrestrial and freshwater habitats within the EU (Janssen et al. 2016).

Further research is needed to increase the ecological knowledge on peatland bird populations beyond the statuses and ecological requirements of species. For instance, it would be essential from a conservation point of view to understand the mechanisms causing the observed declines (e.g. lagged effects on weather variables upon populations; Pearce-Higgins et al. 2015) as well as potential ways to restore already degraded habitats (Kotiaho et al. 2015).

Although the coverage of peatland territory was good enough for the purpose of this study, the monitoring network should be improved in some regions (e.g. in Latvia), as already stressed in the previous chapters (**Chapters I, II**). In addition, the present findings call for more effective conservation actions in Northern European peatland habitats, especially in Finland where peatland management greatly differs from e.g. Estonia. Given that climate change and the continuing anthropogenic degradation of habitats (peat extraction, forest ditching and drainage associated with past management actions) threaten peatland ecosystem functions and its biodiversity, there is urgent need to protect and restore the most biodiversity-rich peatlands (i.e. large open wet peatland areas).

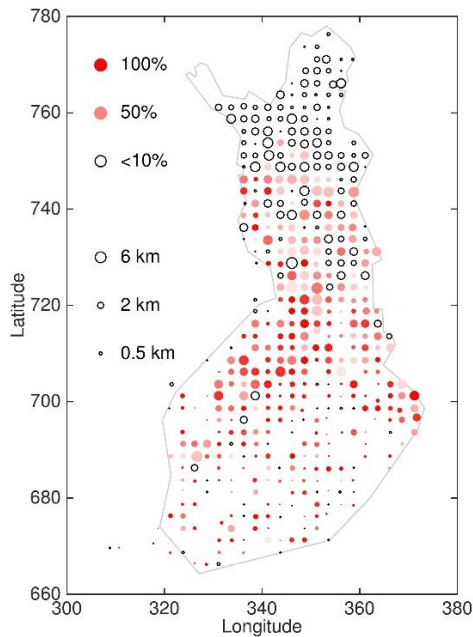


Fig. 5. Map showing the percentage of degradation in peatland habitats along each Finnish fixed route (see section 3.2.) due to ditching and peat extraction based on the main belt habitat type classifications done by the observers. This percentage is calculated as follows: (ditched peatlands + peat extraction areas) / (all peatland habitats) * 100. The size of dots denotes the amount of peatland habitat along the census route (from 0 to 6 km), and the different colours refer to the proportion of peatland habitat that has been degraded, with open dots with black edges representing those transects where less than 10% of peatland habitat has been degraded. Note that many peatlands have been historically turned into either farmlands or forests as a result of e.g. ecological succession after ditching, and so this illustration likely gives an underestimate of peatland habitat degradation (i.e. habitats classified in other categories than peatland). This figure can be found in the supplementary material for **Chapter III**.

4.2.3. Forests

Forest was the most studied environment in this thesis, with population analyses comprising both the breeding and the wintering period (**Chapters IV, V**, respectively). Finland's forest bird populations declined all-year round and at a similar pace in the breeding and the wintering season, in line with the results from **Chapters I and III**. Wintering populations decreased linearly by 60% in just over 50 years (**Fig. 4C**), coinciding with the huge decline in the amount of old-growth forest at the beginning of the study period (1950s–1970s; Järvinen et al. 1977, Virkkala et al. 1993). On the other hand, the general decline of breeding bird species preferring late successional stages (illustrated by the community-level LSH-index) has accelerated in the last c. 20 years (30% decline) in the southern half of Finland. As such, the MF-index including only species relying on old-growth stands showed a 35% decline for the same period (**Fig. 4B**), therefore indicating that late successional species were driving the trend observed in the LSH-index. This result also corroborated the fact that species with a preference for late successional habitats showed more negative population trends in the main analyses. However, the between-species variation in the change of trend, which turned more negative in the second half of the study period (bivariate response; **Chapter IV**), was not explained by any of the predictors. Although not significant, the recovery of the forest bird population shown by the MF-index in the first place could be indirectly caused by four consecutive harsh winters from 1984/1985 to 1987/1988, which may have influenced the populations of many short-distance migrants and residents (Pearce-Higgins et al. 2015). Nevertheless, no indications of temperature effects on the forest indicator were found in winter, despite the increase in the average early-winter temperature by 2.5°C during the study period (**Chapter V**).

The Community Latitude Index (CLI) indicated that the average latitude of the community was shifting almost significantly around 30 km southwards in the last 30 years, suggesting increasing representation of southern species compared to northern species in the breeding bird assemblage. Although temperature for the breeding season did not show any trend for this period, it had a significant negative effect on CLI, meaning that temperature may partly explain the increased dominance of southern species in the whole bird community. The change in CLI (~1.0 km / year) was very similar to what has been found in previous Finnish studies of distribution (0.7–1.3 km / year) and density shifts (1.3 km / year) (Virkkala and Lehtikoinen 2014, Välimäki et al. 2016). This suggests that species may be expanding or retracting their ranges partly as a consequence of the rise in global temperatures (Brommer et al. 2012, Virkkala and Lehtikoinen 2014). The negative effect of temperature and the decline in CLI can be compared to a positive association between temperature and the Community Temperature Index (CTI), which has also been found for other countries with latitudes comparable with Finland (e.g. Sweden; Lindström et al. 2013). Therefore, in line with the findings of this and other studies (**Chapter I**), the results of CLI hint at an increasing pressure from climate change on forest bird communities during the next decades. Along these lines, the results also indicated that populations of breeding forest birds preferring nutrient-poor, primarily northern coniferous, habitats had more negative trends relative to species associated with nutrient-rich, primarily southern, deciduous habitats (see Merilä et al. 2014). This may be an indication that not only forest communities are being shaped by changes in forest age structure (Ylitalo 2012) but also by climate change, which is predicted to increase the proportion of deciduous forests in southern Finland (Parviainen and Västilä 2012) and can aggravate this situation by causing species to

move northwards (e.g. Virkkala and Lehtikoinen 2014).

Changes in forest age structure probably explain the general decrease of mature forest bird species both during the breeding and wintering seasons. Similar to the MF-index, species included in the forest winter indicator were also strong forest specialists with clearly higher densities in forests, with more than half of the species being residents. Population declines in resident species, which share the same breeding and wintering areas, should be more likely affected by habitat loss (Newton 1998). Conversely, for the more adaptable species, the effects on the resources needs (i.e. habitat preferences) may be more complex. This may explain the lack of effect of e.g. species flexibility on population trends, since some of these species occur in many different forest types.

Over 75% of the forests in southern Finland grow on private lands, and this also plays an important role in biodiversity conservation. Although there are programmes promoted by the Finnish government, such as METSO, which encourages voluntary forest conservation among private forest owners since 2008 (Finnish Government 2008, Syrjänen and Paloniemi 2010, Vihervaara et al. 2011), the proportion of protected forests is much higher in the north compared to southern Finland. The same pattern applies for the conservation status of old-growth forest species (Virkkala and Rajasärkkä 2007). Given the long-term loss of mature forest birds at regional (southern Finland) and national levels, as well as the accelerated decline in forest bird communities during the breeding season, the remaining old-growth forests need complete protection, especially those that provide habitat for endangered species (Virkkala and Rajasärkkä 2007). Conservation areas may also alleviate the effects of climate change on species of conservation concern, particularly in northern

boreal latitudes (Virkkala et al. 2014). Because CLI and similar indicators have the potential to pick range shifts towards the north, the construction of this type of indicator should be enhanced for both breeding and non-breeding seasons (**Chapter I**). In the case of forest species especially, it is also important to investigate how forest indicators are connected with similar indicators of forest specialists among other taxa (e.g. insects, plants, fungi) – another of the recommendations specified in **Chapter I**.

4.3. URBAN ENVIRONMENTS

‘Urbanity’ (relative use of urban habitats) had significant effects on species’ wintering population trends, with exclusive urban species (hypothetical case with urbanity = 1) showing on average ~4.5% larger annual growth rates than exclusive forest species (urbanity = 0). Wintering populations of urban species showed in general a c. threefold increase during a 54-year period (**Fig. 4C**). The outcome of this indicator contrasted with other state indicators produced for different environments (e.g. **Chapters III, IV**). These findings suggest that wintering habitat may have an important role in population dynamics, particularly when talking about the increase in urban species. One of the main drivers of this pattern is most likely the expanding popularity of bird feeding during the last decades (Vepsäläinen et al. 2005), which translates to huge quantities of supplementary food available for birds. Climate change could potentially contribute to ameliorate the situation of urban species with increasing temperatures in urban areas (Smith 2003, Wilby and Perry 2006). The combination of climate change and the provision of supplemental food during winter time (Jokimäki and Kaisanlahti-Jokimäki 2012a,b) may improve both habitat conditions and decrease species mortality of both resident and migratory species, causing populations to stay in winter (Virkkala 2004, Nilsson et al. 2006, Virkkala and Rajasärkkä 2011).

4.4. MIGRATORY GROUPS: FROM WATERBIRDS TO LANDBIRDS

Contrary to **Chapter IV**, migratory strategy did explain variation in population trends for the winter period (**Chapter V**). Wintering populations of short-distance migratory waterbirds were clearly increasing and exhibited noticeably higher trends than other migratory strategies in Finland. In the same way as for the urban indicator, the population index for waterbirds increased c. 11 times during the whole study period (**Fig. 4D**). The increase in this indicator, whose construction was based on migratory strategy, coincided with simultaneous declines detected for a large number of the study species during the breeding season (Pöysä et al. 2012). However, unlike wintering forest and urban populations, temperature had an effect on southern waterbirds, which is likely related to increasing wintering numbers in Northern Europe (new suitable areas available for wintering waterbirds with the decrease in maximum ice cover in the Baltic Sea; Jylhä et al. 2008, Pavón-Jordán et al. 2015).

With regards to landbirds, no significant trends were found for either nomadic or irruptive species, probably resulting from large between-year fluctuations caused by variation in food availability (e.g. Meller et al. 2016). The nearly significant positive trend for residents could be partly driven by milder winters and winter feeding, with an improvement of habitat conditions and decrease in species mortality (Virkkala 2004, Nilsson et al. 2006, Virkkala and Rajasärkkä 2011). Unlike in **Chapters III, IV**, latitude did not affect population trends of wintering landbirds, contrary to significant changes in wintering ranges observed in large-scale studies (e.g. North American and North European Birds; EPA 2016, Lehtikoinen et al. 2016).

Linking declines to specific causes or threats is especially challenging for migratory birds, since they are difficult to track and face several threats on their breeding and wintering areas, and along their migratory routes (Lebbin et al. 2010). Examining patterns of population change in one particular habitat type may not reflect other potential causes of decline (e.g. in long-distance migrants in **Chapter IV**; Vickery *et al.* 2014) that could actually be more important (Hewson and Noble 2009). Given the increasing trend in the number of waterbirds in northern latitudes, and because migrant birds often cross country boundaries, there is need for more international collaboration between countries in order to protect their populations. This is also linked to the improvement of waterbird monitoring schemes during both breeding and wintering periods to further understand the ongoing and future consequences of climate change on waterbird populations (e.g. range shifts), as already stated in **Chapter II**.

4.5. A CLOSER LOOK AT THE SPECIES LEVEL

A total of 76 species were included in the present work (with species appearing in more than one chapter counted only once). From these, 40% of species are considered to be under threat according to the Red List of Finnish Bird Species (Tiainen et al. 2016). Ruff (*Calidris pugnax*) is listed as critically endangered (CR), and Tufted Duck *Aythya fuligula*, Greater Scaup *Aythya marila*, Temminck's Stint *Calidris temminckii* and Snow Bunting *Plectrophenax nivalis* are listed as endangered (EN). In addition, there are 13 species classified as vulnerable (VU) and 13 as near threatened (NT). Around 30% of these 31 species of special concern relied on peatland habitats (including waders and passerines), 15% on open water environments (mostly ducks), and approximately 15% were forest species. The remaining 40% from the total number of species

of special concern were classified as urban or "intermediate" species (i.e. neither classified as urban nor forest species) during winter, or not associated with any specific habitat. The most threatened species (categories CR and EN) were either short- or long-distance migrants. Ruff showed a steep decline in peatland habitats (the percentage of multiplicative net change was 97%). Almost all species belonging to the VU and NT categories declined during the breeding season.

A total of eight species relied on forest habitats both during the breeding and wintering seasons according to our species selection procedures (species preference ratio in **Chapter IV** and urbanity index in **Chapter V**); Hazel Grouse (*Tetrastes bonasia*), Western Capercaillie (*Tetrao urogallus*), Black Woodpecker (*Dryocopus martius*), Goldcrest (*Regulus regulus*), Willow Tit (*Poecile montanus*), Crested Tit (*Lophophanes cristatus*), Eurasian Treecreeper (*Certhia familiaris*), and Red Crossbill (*Loxia curvirostra*). From these eight species, five declined during the breeding season (Western Capercaillie, Goldcrest, Willow Tit, Crested Tit, and Eurasian Treecreeper), one increased (Red Crossbill) and two did not show any trends (Hazel Grouse and Black Woodpecker). Many of the same species declined during the winter period as well (Hazel Grouse, Western Capercaillie, Goldcrest, Willow Tit, Crested Tit, Red Crossbill), whereas Black Woodpecker increased and no trends were found for Eurasian Treecreeper. Moreover, half of the species found mainly in forest habitats in the breeding season were further classified as mature forest species based on a second preference ratio (Western Capercaillie, Goldcrest, Crested Tit, and Eurasian Treecreeper; **Chapter IV**). All these species declined during the breeding and wintering seasons, with the only exception being Eurasian Treecreeper, which declined only in the breeding season. Four out of nine forest resident species

declined in the breeding season (> 40%), and seven out of ten in the winter season. These results reinforce the idea that the loss of mature forests is more likely the cause driving the decline of species both during the breeding and wintering seasons. Importantly, two forest species that declined both during breeding and winter time were listed as VU (Willow Tit and Crested Tit).

Two of the species classified as forest species in southern Finland (**Chapter IV**) were also classified as peatland species at the national level (**Chapter III**; Rustic Bunting *Emberiza rustica* and Common Greenshank *Tringa nebularia*). Rustic Bunting (NT) has declined similarly in both Finnish forests and peatlands (around 80%) during the breeding season. On the other hand, Common Greenshank has declined in the forests of southern Finland but no trends have been found in peatlands at the national level. Interestingly, both species showed a preference for old stands in the breeding season. Another two species (Eurasian Chaffinch *Fringilla coelebs* and Brambling) classified as forest species during the breeding period (**Chapter IV**) were regarded as urban in winter (**Chapter V**), but only a declining trend was found for Brambling in the breeding season. Seven of the forest species in **Chapter IV** did not show any clear preference either for forest or urban habitats during the wintering season (**Chapter V**); Great Spotted Woodpecker *Dendrocopos major*, Coal Tit *Periparus ater*, Eurasian Jay *Garrulus glandarius*, Common Raven *Corvus corax*, Eurasian Siskin *Carduelis spinus*, Common Redpoll *Carduelis flammea*, and Eurasian Bullfinch *Pyrrhula pyrrhula*. Eurasian Bullfinch (VU) declined both in winter and in the breeding season. Eurasian Jay, Eurasian Siskin, Common Redpoll and Eurasian Bullfinch declined in forests during the breeding season. Lastly, Long-tailed Duck *Clangula hyemalis* (NT) was present in both **Chapter II** and **Chapter V**, but only an increasing trend was

found in the winter period, most likely due to climate-driven shifts in the species' wintering range.

5. CONCLUSIONS

The need to counteract the negative effects of human activities on biodiversity has never been greater, but so are opportunities to deliver effective conservation. Bird indicators are currently one of the finest tools to track changes in biodiversity, helping to identify drivers of community dynamics. Using the best available methodology, this thesis provides a robust and informative assessment of bird population trends in five different environments in northern Europe, taking into account seasonal variations in habitat use and migratory behavior (i.e. breeding and wintering). In an effort to contribute to setting priorities for bird habitats, most urgent conservation actions are identified for northern Europe with a special focus on Finland. In addition, the bird indicators resulting from this work have the potential to communicate bird conservation to decision-makers in a policy-relevant manner.

Rates of decline are accelerating in forests and peatlands during the breeding period, and a continuous decline of forest bird populations have also been detected in winter. Mature forests and large open peatlands are considered to be the most threatened habitats, providing refugia for almost half of the study species of conservation concern. The main causes of decline in peatland and forest populations are attributed on the one hand to drainage, which tends to degrade typical peatland properties beneficial for birds (e.g. afforestation), and on the other hand to changes in forest structure due to the intensification of forest management plans. Although breeding and wintering landbirds may at present be more affected by changes in land use (also including urbanization) rather than climate change,

evidence is provided that waterbird communities are being shaped by weather conditions. Examples of this include the poleward range shifts of species associated with high levels of climate warming, most likely explaining the massive increase in wintering waterbird numbers, or the potential alterations in breeding populations given species' sensitiveness to changes in predator-prey interactions. Therefore, waterbirds seem to be benefiting from increasing favorable weather conditions during winter, but may be suffering in the breeding season (e.g. climate effects on breeding success).

The effects of climate change on the breeding peatland and forest bird communities are still moderate, but given the latest climatic predictions for the study area, these effects may be exacerbated in the near future. Although climate change will probably cause increasing wintering waterbird numbers in Northern Europe, colder-dwelling bird species with more northerly distributions will likely suffer the largest population declines. Because of multiple stressors, more research should focus on the interplay between climate and land-use change impacts on biodiversity in order to improve conservation planning. The combination of climate change and a continuing anthropogenic degradation of habitats may lead to larger rates of population decline than the two processes separately.

With these considerations in mind, there is an urgent need to allocate additional conservation resources for the future conservation of the avifauna in boreal peatlands and forests, particularly those areas that maximize the abundance and diversity of birds. This requires collaboration among landowners and managers in order to protect and restore high priority habitats for birds. Addressing resources to conserve common species can also benefit other species which may co-occur in the same habitats

targeted for conservation. As for climate change, protecting and restoring areas where species might shift could also be an important strategy. In this sense, conservation planning should include climate change considerations. Protected area networks should be positioned according to when and where bird species migrate in response to various climate and land-use drivers. This implies the need for a collaborative effort between different countries to protect populations of migrant species. At the international scale, Finland has a strong responsibility for protecting the growing waterbird populations in northern Europe, but also sustaining the peatland bird populations largely relying on the increasingly threatened Finnish peatlands.

Last but not least, although many of the causes for bird population declines still remain unknown, we must make use of the best information available to guarantee that bird conservation priorities are established based on robust science. Importantly, the impact of conservation actions should be evaluated on a regular basis with tools such as bird indicators to assess our success or failure in conserving bird populations and, consequently, in conserving ecosystem functions and biodiversity as a whole.

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