Spatial and Temporal Determinants of Finnish Farmland Bird Populations
Spatial and temporal determinants of Finnish farmland bird populations

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Academic dissertation

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Spatial and temporal determinants of Finnish farmland bird populations

Markus Piha

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


II Piha, M., Tiainen, J., Seimola, T., Vepsäläinen, V. Modelling diversity and abundance of Finnish farmland birds — landscape characteristics define the diversity and conservation hotspots. — Manuscript.

III Piha, M., Tiainen, J., Holopainen, J., Vepsäläinen, V. Effects of land-use and landscape characteristics on avian diversity and abundance in a boreal agricultural landscape with organic and conventional farms. — Submitted manuscript.


**Contributions**

The following table shows the major contributions of authors to the original articles or manuscripts.

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<tr>
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<td>Methods &amp; Analyses</td>
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<td>MP, JT, TP</td>
<td>MP, JT, VV</td>
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<td>MP, AL, TP, JT</td>
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SUMMARY

1. Introduction

The expansion and intensification of agriculture over the last century are major threats to global biodiversity (Matson et al. 1997, Krebs et al. 1999, Gaston et al. 2003, Green et al. 2005). The rapidly growing human population requires increasingly larger agricultural areas and more efficient agricultural production, which will adversely affect many types of natural ecosystems such as wetlands and tropical rainforests (Tilman et al. 2001). Changes in agricultural ecosystems that have occurred during the past decades due to intensified production have already caused dramatic population declines in a wide range of taxa related to farmland habitats. This has been especially demonstrated in industrialized countries in Europe and in North America (Donald et al. 2002, Stoate et al. 2001a, Robinson & Sutherland 2002, Murphy 2003). Interlinked processes in agricultural intensification are key factors causing biodiversity declines, such as the loss of overall habitat heterogeneity (Benton et al. 2003), the loss and deterioration of species-rich habitats (Wilson et al. 1999, Chamberlain et al. 2000a), and increased agrochemical use (McLaughlin & Mineau 1995). The great challenge for agricultural and environmental policies is to find a balance between agricultural production and conservation actions that are required to halt the ongoing loss of farmland biodiversity (Firbank 2005, Holzkämper & Seppelt 2007).

1.1. Agriculture and biodiversity in Europe

Agricultural and grassland habitats dominate landscapes in large parts of Europe, covering about 50% (5 million km²) of the land surface (Tucker & Dickson 1997). Their origins dating back 10 000 years to the eastern Mediterranean, these human-made agroecosystems now constitute an inseparable and invaluable part of European nature with uniquely adapted and diverse fauna and flora (Stoate et al. 2001a). During the past 60 years, agricultural production has intensified rapidly due to increased mechanization and agrochemical use (Fig. 1; Matson et al. 1997, Krebs et al. 1999, Chamberlain et al. 2000a). Consequent large scale changes in the quality and quantity of farmland habitats have caused dramatic population declines of many taxa and simplification of landscape (e.g. Hietala-Koivu 2002) and biodiversity in agroecosystems (plants: Andreasen et al. 1996, Stevens et al. 2006; invertebrates: Wilson et al. 1999, Sotherton & Self 2000; birds: Donald et al. 2001b, Newton 2004a; mammals: Harris et al. 1995). To prevent further population declines and the deterioration of

![Figure 1. Cereal production in 15 European Union member countries (EU-15) in 1961–2005. Data from FAOSTAT 2007.](image-url)
soil, water, and air quality, agri-environment schemes (AES) were established as a part of European Union’s (EU) Common Agricultural Policy (CAP) in the reform of CAP in 1992. AESs compensate farmers financially for the loss of income associated with measures aiming to benefit the environment or biodiversity. The long-term goal of AESs is to bring the current decline in the biodiversity of agroecosystems to a stop by 2010. The efficacy of AESs in achieving this goal is, however, currently highly debated (Kleijn et al. 2006, Whittingham 2007).

1.2. Farmland birds and agricultural intensification

The breeding farmland bird assemblage is a geographically varying, heterogeneous group of open-country specialists and habitat generalists (Williamson 1967, O’Connor & Shrubb 1986). In my thesis, I focus on bird species predominantly breeding in agricultural habitats, although agricultural habitats are also important wintering and stop-over habitats for migratory birds breeding in other habitats, such as geese breeding in the arctic tundra (e.g. Van Eerden et al. 2005). Breeding farmland birds have declined dramatically in Europe (Fig. 2), and currently 39% of bird species associated with farmland habitats are declining, whereas only 3% are increasing (BirdLife International 2004).

Bird declines have been widely connected to various negative impacts of agricultural intensification (Fuller et al. 1995, Krebs et al. 1999, Chamberlain et al. 2000a, Donald et al. 2001b, Benton et al. 2002, Newton 2004a, Donald et al. 2006). The major processes underlying farmland bird declines are listed in Table 1. These processes are highly linked and have occurred simultaneously making the identification of key-factors difficult (Chamberlain et al. 2000a). In general, large-scale changes in farming practices have resulted in a loss of spatial and temporal habitat heterogeneity and key habitats (Benton et al. 2003) leading to a reduction in summer and winter food resources and nesting sites, all of which can limit bird populations. Additionally, agricultural intensification and changes in landscape structure may have increased the predation risk of birds (Andrén 1992, Grant et al. 1999, Whittingham & Evans 2004). Abandonment of cultivated land occurring particularly in the Mediterranean region, Eastern Europe and in former Soviet areas, poses a further threat to European farmland birds (Suárez-Seoane 2002, Kuemmerle et al. 2006). In Eastern Europe, land abandonment has caused increases in some farmland bird populations (Orłowski 2005). However, these increases are probably temporal, since without regular management, abandoned fields (long-term set-asides) become unsuitable for most farmland birds through natural succession.

Birds are good indicators of environmental change as they are easily monitored, well studied, have long lifespans, and occupy high positions in the food chain (Furness &
Greenwood 1993, Gregory et al. 2005). Many of the main environmental factors behind bird declines are common with other taxa such as weeds and invertebrates, and hence changes in bird populations likely reflect changes occurring at lower trophic levels. Two examples demonstrating the complex causes behind farmland bird population declines and links among ecosystem processes are given in Box 1.

**Farmland bird conservation**

AESs are key means in the attempt to reverse farmland bird declines within the EU. The measures taken and area covered by AESs among EU countries vary greatly and their effects on biodiversity have to a large degree remained unresolved. Hence, the efficacy of AESs on farmland birds as a whole is not clear.

**Box 1.** Two examples of causes underlying farmland bird declines.

**Skylark** *Alauda arvensis*

Although the skylark is still one of the most abundant farmland birds in Europe (breeding population 40–80 million pairs; BirdLife International 2004), it has experienced a dramatic decline across Europe during the last four decades (e.g. Busche 1989, Robertson & Berg 1992, Fuller et al. 1995, Tryjanowski 2000). It has been estimated that the European population has declined more than 40% since 1980 (PECBM 2006). Nowadays the factors behind these population declines are rather well-known, but gathering evidence of the causal processes has required much research on habitat selection, breeding ecology and population trends in relation to agricultural changes (reviewed by Donald 2004). The major causes of the decline in Western and Central Europe include: (1) a shortened breeding season caused by a general switch from spring-sown to autumn-sown cereals, because the sward of autumn-sown cereal fields grows too tall and dense in the spring for multiple nesting attempts (Wilson et al. 1997, Chamberlain & Crick 1999, Chamberlain et al. 1999a, Chamberlain et al. 2000b); (2) diminished winter seed food resources caused by decreased amounts of winter stubbles, a change which is ultimately related to the switch from spring-sown to autumn-sown cereals (Donald et al. 2001a); (3) unfulfilled breeding and feeding preferences due to decreased mixed farming and reduced crop diversity which have caused large monocultures (Schläpfer 1988, Wilson et al. 1997, Chamberlain & Gregory 1999).

**Grey partridge** *Perdix perdix*

The European population of the grey partridge has undergone a large decline during the period of agricultural intensification since the 1950s (Potts 1986), and the current population estimate is 1.6–3.1 million pairs (BirdLife International 2004). The decline of the grey partridge was one of the first incentives leading to a wide concern about farmland birds and yielded a vast research effort on the fate of farmland birds in general. One of the main mechanisms behind the population declines in the UK was recognized already by early studies. Chick survival had declined due to increased herbicide use reducing the abundance of weeds which serve as host plants for the invertebrates eaten by chicks (Green 1984, Potts 1986, Potts & Aebischer 1995). Other factors contributing to the declines are the loss of safe nesting habitats caused by the removal of field boundaries and other non-crop habitats (Potts 1986, Rands 1987), and increased predation risk by corvids and red foxes *Vulpes vulpes* caused by relaxed predator control (Tapper et al. 1996, Potts & Aebischer 1995).
Table 1. Main processes of agricultural intensification having largely negative effects on European farmland birds with some study examples.

<table>
<thead>
<tr>
<th>Process</th>
<th>Consequences on habitats</th>
<th>Consequences on birds</th>
</tr>
</thead>
<tbody>
<tr>
<td>Increased mechanisation</td>
<td>- intensified land-use and removal of uncultivated areas (e.g. hedgerows, ditch banks, margins)</td>
<td>Reduction in suitable nesting and feeding sites (1, 2, 3, 4, 5, 6, 7)</td>
</tr>
<tr>
<td></td>
<td>- mechanised harvesting</td>
<td>Destruction of eggs and chicks in field species (8, 9)</td>
</tr>
<tr>
<td>Increased fertilizer use</td>
<td>- dense fast growing swards on arable and grass fields</td>
<td>Reduction in suitable nesting and feeding sites (10, 11)</td>
</tr>
<tr>
<td>Increased pesticide use</td>
<td>- declined weed and invertebrate diversity &amp; abundance</td>
<td>Reduction in food supply (12, 13, 14, 15, 48)</td>
</tr>
<tr>
<td>Reduction in spring sowing of cereals</td>
<td>- reduction in over-winter stubbles</td>
<td>Reduction in winter food supply (16, 17, 18, 19, 20, 21)</td>
</tr>
<tr>
<td></td>
<td>- dense fast growing swards on fields</td>
<td>Reduction in suitable nesting and feeding sites (22, 23, 24, 25, 26, 27)</td>
</tr>
<tr>
<td>Farm specialization and decreases in mixed farming and low-intensity cattle</td>
<td>- conversion of semi-natural grasslands to improved grassland or arable fields</td>
<td>Reduction in suitable nesting and feeding sites (11, 29, 30, 31, 32, 33)</td>
</tr>
<tr>
<td></td>
<td>- loss of habitat heterogeneity</td>
<td>Reduction in suitable nesting and feeding sites (18, 28, 34, 35, 36)</td>
</tr>
<tr>
<td></td>
<td>- dense fast growing grass swards</td>
<td>Reduction in suitable nesting and feeding sites (32, 34, 37, 38)</td>
</tr>
<tr>
<td></td>
<td>- declined invertebrate diversity &amp; abundance associated with decreasing animal husbandry</td>
<td>Reduction in food supply (32, 39, 40, 41)</td>
</tr>
<tr>
<td>Increased stocking densities</td>
<td>- reduced sward heterogeneity</td>
<td>Loss of suitable nesting and feeding sites (42)</td>
</tr>
<tr>
<td></td>
<td>- increased disturbance</td>
<td>Destruction of eggs and chicks in field species (43)</td>
</tr>
<tr>
<td>Land drainage</td>
<td>- loss of wet habitats</td>
<td>Reduction in suitable nesting and feeding sites (44, 45)</td>
</tr>
<tr>
<td></td>
<td>- loss of open ditches and field margins</td>
<td>Reduction in suitable nesting and feeding sites (4, 7, 45, 46)</td>
</tr>
<tr>
<td>Increased farm and field sizes</td>
<td>- loss of habitat heterogeneity</td>
<td>Reduction in suitable nesting and feeding sites (22, 47)</td>
</tr>
</tbody>
</table>

References:
1. Gillings & Fuller 1998
2. Stoate et al. 2001b
3. Perkins et al. 2002
4. Bradbury & Bradter 2004
5. Brickle & Peach 2004
6. Fuller et al. 2004
7. Vepsäläinen et al. 2005a
8. Stowe et al. 1988
10. Atkinson et al. 2005
11. Buckingham et al. 2006
12. Potts 1986
13. Borg & Toft 2000
14. Morris et al. 2005
15. Taylor et al. 2006
16. Donald & Evans 1994
17. Evans & Smith 1994
18. Wilson et al. 1996
19. Sritwardena et al. 2000a
20. Donald et al. 2001a
21. Moorcroft et al. 2002
22. Schläpfer 1988
23. Shrubb 1990
25. Chamberlain et al. 1999a
27. Brickle & Harper 2002
28. Chamberlain & Gregory 1999
29. Möller 1983
30. Bignal & McCracken 1996
31. Söderström & Pärt 2000
32. Vickery et al. 2001
33. Virkkala et al. 2004
34. Perkins et al. 2000
35. Robinson et al. 2001
36. Wilson et al. 2001
37. Milsom et al. 1998
38. Britschgi et al. 2006
39. Tiainen et al. 1989
40. Ambrosini et al. 2002
41. Olsson et al. 2002
42. Wakeham-Dawson et al. 1998
43. Hart et al. 2002
44. Wilson et al. 2004
45. Bradbury & Kirby 2006
46. Bradbury et al. 2000
47. Benton et al. 2003
(Kleijn & Sutherland 2003, Kleijn et al. 2006, Whittingham 2007). However, some AES measures and other recent changes in farmland management have been reported to benefit farmland birds. In the following, I describe the most important in the scope of this thesis.

Set-asides were introduced in the early 1990s as a part of CAP to reduce agricultural surpluses by removing areas of land from production. Later on set-aside measures have been included in many AESs. More widely applied they are likely to benefit bird populations, as many birds prefer set-asides as breeding and foraging areas (Poulsen et al. 1998, Henderson et al. 2000, Orłowski 2005, Bracken & Bolger 2006). Related AES measures include various field margin management actions, such as the establishment of protective margins or shelter belts along waterways, and grass, set-aside, or wildflower margins in cereal fields. The latter are likely to enhance the availability of safe nesting sites and winter and summer food for birds (Vickery et al. 2002).

Organic farming aims to reduce the negative impacts of modern agriculture on the environment by excluding agrochemical use and by generally applying diverse crop rotations. In 2003, organic farming covered ca. 4% of the total arable area in EU-15 (the fifteen EU member states prior to enlargement in 2004; Anon. 2006). Beneficial effects of organic farming have been reported on overall biodiversity (Hole et al. 2005, Bengtsson et al. 2005) and on birds, especially skylark (Christensen et al. 1996, Wilson et al. 1997, Chamberlain et al. 1999b, Genghini et al. 2006). Presumably all AES measures which markedly decrease pesticide and fertilizer applications are beneficial for birds.

Non-inversion tillage (NIT) is a method used to prepare the seedbed for sowing and establishing a crop from the previous year’s stubble without inverting it. The method has the potential to become common in large parts of Europe since it is economically sound. Although its wide impacts on birds have yet remained unstudied, some positive effects on the abundance of seed and invertebrate food resources of birds have been found (Cunningham et al. 2004). However, the downside is that the need for herbicide applications is higher in NIT than in tilled fields (Cunningham et al. 2004).

Some species-specific conservation actions that have been based on ecological research have been successful in Britain (see Aebischer et al. 2000). For example, the dramatically reduced population size of the cirl bunting Emberiza cirlus has increased following the implementation of large areas of overwinter stubble fields and set-asides (Peach et al. 2001). Another example is the corncrake Crex crex that has partially recovered in the UK, especially in areas with conservation management schemes which establish and maintain suitable stands, and uses new methods of grass-mowing (e.g. mowing from the interior parts of the field outwards enabling chicks to escape from mowing machine cutters; Aebischer et al. 2000, O’Brien et al. 2006).

Further threats to farmland birds

Ecological responses to recent climate change are already clearly visible (Walther et al. 2002). Climate change may have multiple influences on farmland birds, but the issue remains largely uninvestigated. Firstly, a rapid response in agricultural practices to changes in temperature and precipitation is predicted to be seen, with shifts in sowing and harvesting times, crop species and varieties, irrigation, drainage, and exploited areas (Olesen & Bindi 2002). These changes are expected to have unprecedented influences on the distribution, availability, and quality of bird habitats. Secondly, changes in the mean values of climatic variables as well as an increase in the frequency of extreme climatic events, such as droughts or heavy storms, are likely to occur (Easterling et al. 2000, IPCC 2007) with probably severe effects on the survival and reproduction of birds (e.g. Baillie & Peach 1992, Bolger et al. 2005). Thirdly, the timing of seasonal activities of
birds have changed as a response to climate warming (e.g. spring migration: Cotton 2003, Jonzén et al. 2006; laying dates: Crick & Sparks 1999; autumn migration: Jenni & Kéry 2003). Recent studies have also related climate change to changes in migration routes (Rivalan et al. 2007). These changes may cause a mistiming in the reproduction of birds, or in their migratory fuelling in relation to e.g. local weather conditions or food resources (Both & Visser 2001, Ahola et al. 2004, Bairlein & Hüppop 2004). Such phenological changes and their consequences in human-managed agroecosystems are highly topical issues for research and conservation, but they are difficult to predict since the timing of farming practices is also prone to change.

Changes in farmland bird populations are expected to occur with the introductions of new crops, such as genetically modified herbicide tolerant crops that would markedly reduce the available seed food of birds (Gibbons et al. 2006). Additionally, the production of bioenergy crops may require massive land areas in the future with largely unstudied effects on birds (but see Roth et al. 2005).

Additionally, migrant farmland birds are influenced by natural and anthropogenic factors operating in their wintering grounds and migration routes (Newton 2004b). Although severe declines in populations of particularly Afro-Palearctic migrants have been reported, underlying factors are relatively poorly known (Sanderson et al. 2006). The illegal hunting of migrants in the Mediterranean region is also a threat to farmland birds (McCulloch et al. 1992). However, the knowledge of its consequences on European bird populations is scarce.

1.3. Finnish agroecosystems as habitats for farmland birds

As in temperate Europe, farmland birds have declined dramatically in boreal agroecosystems (Finland: Tiainen & Pakkala 2000, Väisänen 2005; Sweden: Wretenberg et al. 2006). However, boreal agroecosystems differ in many ways from those of more temperate regions where the majority of farmland bird studies have been conducted (particularly in the UK). Hence, different factors may be responsible for boreal farmland bird declines. In the following, I describe (1) the major characteristics of current Finnish agriculture and its main differences compared to agriculture in the UK and EU as a whole, (2) essential aspects of agricultural modernization in Finland and their effects on biodiversity, and (3) the major characteristics of the Finnish farmland bird assemblage, with a special focus on the role of landscape structure and agricultural intensification.

1.3.1. Description of current Finnish agriculture

Finnish agroecosystems are to a large degree characterized by climatic, geographic, and edaphic (soil) conditions. Forest is the predominant habitat type in Finland (more than 70% of the total land area), whereas the proportion of farmland is only ca. 7%. The largest agricultural plains are located within a ca. 100 km belt along the southern and western coastline, where soil, topography and climatic conditions are most favourable for crop production (Fig. 3). Finland lies almost
Figure 3. Arable land (gray areas) in Finland according to CORINE land cover data (European Commission 1994, Härmä et al. 2004).

exclusively north of latitude 60° N, where low temperatures during the winter and transition seasons limit the growing season to a maximum of six months in the south, and to only three months in the northernmost parts (Kettunen et al. 1988). The predominantly boreal climate shows both oceanic and continental characteristics, with degree of continentality growing inland and eastwards (Tuhkanen 1984). Temperatures and rainfall decrease from the south-western hemiboreal zone to the subarctic region in the northernmost Finland.

The agricultural landscapes of Fennoscandia are often considered as mosaics of forest and farmland (Berg 2002, Heikkinen et al. 2004, Luoto et al. 2004, Bennett et al. 2006) as the landscape consists of scattered patches of farmland that are surrounded by forests. The main characteristics of and differences among agriculture in Finland, the UK and twenty-five EU member states (EU-25) are shown in Table 2. In Finland, agricultural production is based on arable crops and permanent grasslands are rare, whereas in the UK over half of agricultural land is grasslands (Table 2). In sharp contrast to more temperate European agricultural areas, winter cereal production is not common in Finland, and spring cereals (of which 49% barley, 33% oats and 16% wheat) represent the main land use in arable fields along with fodder grass (of which 67% silage, 15% hay, and 14% rotational pasture; Table 2). Fallow and set-aside cover 9% of arable fields. Unlike in the UK and many EU member states, there are no hedgerows in Finland, however, main drains in the fields often grow willows (Salix spp.) or other bushy or shrubby vegetation.

CAP (Common Agricultural Policy of EU) has been applied in Finland since 1995 when Finland joined the EU. Virtually all agricultural land (98%) is under AESs (agri-environment schemes), whereas the total coverage of AES in EU-15 is ca. 25% (Kleijn et al. 2006). The latest Finnish AES (2000–2006) included some compulsory measures, for example the establishment of protective margins along water systems and some reductions in pesticide use, and optional measures such as organic farming, which is more common in Finland than the average in EU-15. Pesticides, especially insecticides, are applied less than the average in EU-15 (Table 2).

1.3.2. Biodiversity and modernization of Finnish agriculture

Although agricultural areas comprise only a relatively small proportion of the total land area in Finland, the agroecosystems hold a rich flora and fauna. Agricultural areas have introduced variation and new habitats into the landscape, such as fields, meadows, farmhouses, farmyards, and villages, which have increased
Table 2. Summary of the agricultural characteristics of Finland, the United Kingdom and the 25 EU member countries (EU-25) in 2004. Data obtained from the official statistics of Finland (Anon. 2006).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Finland</th>
<th>UK</th>
<th>EU-25</th>
</tr>
</thead>
<tbody>
<tr>
<td>Utilized agricultural area (million ha)</td>
<td>2.3</td>
<td>17.2</td>
<td>164.4</td>
</tr>
<tr>
<td>% Agricultural land of total land area</td>
<td>7</td>
<td>70</td>
<td>1</td>
</tr>
<tr>
<td>Mean farm size (agricultural ha)</td>
<td>30</td>
<td>61</td>
<td>22</td>
</tr>
<tr>
<td>% Permanent grassland</td>
<td>1</td>
<td>66</td>
<td>34</td>
</tr>
<tr>
<td>% Arable land</td>
<td>99</td>
<td>34</td>
<td>57</td>
</tr>
<tr>
<td>of which:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Cereals of which:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Spring-sown</td>
<td>55</td>
<td>53</td>
<td>53</td>
</tr>
<tr>
<td>% Autumn-sown</td>
<td>94</td>
<td>19</td>
<td>na</td>
</tr>
<tr>
<td>% Potato and sugar beet</td>
<td>6</td>
<td>81</td>
<td>na</td>
</tr>
<tr>
<td>% Rape and turnip rape</td>
<td>4</td>
<td>10</td>
<td>5</td>
</tr>
<tr>
<td>% Fallow land (incl. set-aside)</td>
<td>28</td>
<td>21</td>
<td>18</td>
</tr>
<tr>
<td>% Forage plants (mainly fodder grass)</td>
<td>28</td>
<td>21</td>
<td>18</td>
</tr>
<tr>
<td>% Arable land under organic management*</td>
<td>7.2</td>
<td>4.4</td>
<td>4.1**</td>
</tr>
<tr>
<td>Dosage of pesticides and other plant protection products (PPP) used for arable crops in 2003 (kg active ingredient/ha)</td>
<td>0.4</td>
<td>2.5</td>
<td>1.1</td>
</tr>
<tr>
<td>Proportional usage of pesticides and other PPPs:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Herbicides</td>
<td>77</td>
<td>60</td>
<td>36</td>
</tr>
<tr>
<td>% Fungicides</td>
<td>18</td>
<td>25</td>
<td>46</td>
</tr>
<tr>
<td>% Insecticides</td>
<td>2</td>
<td>5</td>
<td>9</td>
</tr>
<tr>
<td>% Other PPPs</td>
<td>3</td>
<td>11</td>
<td>9</td>
</tr>
</tbody>
</table>

Additional data sources:

- a DEFRA agricultural and food statistics; http://statistics.defra.gov.uk
- b Eurostat Agricultural statistics; http://epp.eurostat.ec.europa.eu/
- * 2003 data
- ** in EU-15 (not EU-25)

Habitat diversity and enabled the occurrence of farmland specialist species. However, agricultural modernization has had multiple, mainly adverse, effects on these habitats and consequently on biodiversity (Hanski & Tiainen 1988, Pitkänen & Tiainen 2001).

The loss of semi-natural grasslands (meadows and natural pastures) has been one of the first and greatest structural changes in Finnish agricultural habitats to impact biodiversity negatively. This process, driven by great famine years, began in the late 19th century with a rapid decrease in traditional animal husbandry which was based on fodder obtained from semi-natural grasslands (Tiainen 2001). Semi-natural grasslands were gradually taken into cultivation, and fodder crops and pastures were included into the crop rotation cycle. Consequently, semi-natural grasslands that in the 1880s represented two thirds of agricultural areas had virtually
disappeared by the early 1970s (current coverage approximately 1%). The loss of these habitats in Finland and Sweden has had a drastic effect on biodiversity as a whole (Pykälä 2000, Pykälä et al. 2004, Pärt & Söderström 1999), and currently the remaining semi-natural grasslands host many rare specialist plant and invertebrate species (Ryttäri & Kettunen 1997, Pitkänen & Tiainen 2001).

As in many European countries, the period of agricultural intensification introduced by increases in mechanization, artificial fertilizers, pesticides and subsurface drainage began in the 1950s with multiple consequences on farmland habitats and associated wildlife (Tiainen 2001, 2004). The main changes that have led to the degradation of farmland bird habitat quality and loss of structural heterogeneity include:

1. specialisation of farms in crop production, and the decrease of cattle husbandry (Fig. 4b) which together have simplified the crop rotation and decreased the area of various fodder crops (Fig. 4a). The decrease of cattle husbandry has been especially pronounced in the largest agricultural plains of southern Finland (Fig. 5a; Tiainen 2001)
2. increase in the size of fields and holdings, and decrease in the number of holdings leading to structural homogeneity (Tiainen 1989)
3. increased efficiency of land use, including removal of field verges and other non-crop habitats. For example open ditches and their margins have dramatically decreased due to subsurface drainage (Fig. 5b; Tiainen 2001, Hietala-Koivu 2002)
4. decrease in the farming of autumn-sown cereals, which reduces the over-winter vegetative cover of fields (Tiainen 2001)
5. increased herbicide use, which causes decreases in weed abundance and diversity (Erviö & Salonen 1987, Hyvönen et al. 2003) with potential effects on invertebrates.

The intensified crop production has at times led to problems of cereal overproduction. Set-aside schemes have been applied to overcome these problems, particularly in the 1970s and in the early 1990s (Fig. 4a). Set-asides represent a type of semi-natural habitat that is temporarily unaffected by farming practises and they can be beneficial for various taxa (reviewed in Van Buskirk & Willi 2004).

Figure 4. Changes in (a) arable land use, and (b) cattle farming in Finland during 1920–2003. A decreasing proportion of bare fallow is included in set-asides after 1968, because official statistics do not report bare fallow and vegetated set-asides separately. Data compiled by Tiainen (2004) from the official statistics of Finland.
1.3.3. Farmland birds in Finland and other boreal European agroecosystems

The Finnish farmland bird fauna is a diverse group of species inhabiting various agricultural habitats. The thirty most abundant farmland bird species in Finland and their population estimates in Finland and Europe are shown in Table 3. As forests dominate boreal landscapes, I define farmland birds as species either feeding or breeding predominantly in agricultural areas. This definition leaves out those species that predominantly breed and feed in forests or other habitats, but may occur as breeding in farmland habitats (e.g. very abundant forest species such as dunnock Prunella modularis, song thrush Turdus philomelos, great tit Parus major, and chaffinch Fringilla coelebs). The majority of boreal farmland bird species are migrants, for example the skylark which is mostly sedentary in Western and Central Europe. In Finland, the fields are covered with snow in the winter, and consequently species that are sedentary in Finland (e.g. magpie, house sparrow and tree sparrow) only exceptionally use fields for foraging in the winter, but congregate mostly around human habitations that provide food. In the following, I first describe general characteristics of the boreal farmland bird assemblage, and then give an overview of the changes that have occurred in boreal/Finnish farmland bird populations and potential reasons for these changes.

Structural landscape attributes are important predictors of farmland bird community composition (Fuller et al. 1997, Best et al. 2001). Hence, in the forest-dominated landscapes of Finland, it is justified to classify farmland birds based on their breeding and feeding habits in relation to forests and farmland habitats as following (Tiainen & Pakkala 2001; cf. Table 3): (1) true field species i.e. species breeding and feeding on fields and open verges (e.g. skylark and corncrake), (2) edge species i.e. species breeding in bushy verges and feeding there or in fields (e.g. sedge warbler and reed bunting), (3) farmland’s forest species i.e. species breeding in forest woodlots or edges around fields, but feeding mainly on fields (e.g. sedge warbler and reed bunting), and (4) farmyard species i.e. species mostly nesting in farmyards and farm buildings around or in midst of fields, but feeding on fields as well as in the farmyard (e.g. barn swallow and house sparrow). By considering this ecological classification, it is clear that the mosaic nature of boreal agroecosystems is a principal factor determining the structure of bird
Table 3. Summary of the 30 most abundant farmland bird species and their primary nesting habitats in Finnish agro-ecosystems (according to Tiainen & Pakkala 2001, Tiainen et al. 2004) ranked by their population trends in Finland. The population estimates and European trends are adapted from BirdLife International (2004). The Finnish trends (with the mean population changes per year between 1980 and 2000 in parentheses) are adapted from Väisänen (2005). The Finnish trends and estimates are based on line transect censuses performed in all biotopes in Finland, and therefore some species’ estimates also include shares of populations that breed in other than agricultural habitats (e.g. peatlands). Hence, the trends do not necessarily reflect the changes of the farmland populations in these species. Species with unfavourable conservation status in Europe (SPECs, BirdLife International 2004) are presented in bold.

<table>
<thead>
<tr>
<th>Species</th>
<th>Main nesting habitat in farmland</th>
<th>Population estimate (1000 pairs)</th>
<th>Trend</th>
<th>Finland Trend</th>
<th>Europe Trend</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Ortolan bunting Emberiza hortulana</strong></td>
<td>Field</td>
<td>30–50</td>
<td>5 200–16 000</td>
<td><strong>decline</strong> (–15.6%)</td>
<td>small decline</td>
</tr>
<tr>
<td><strong>Starling Sturnus vulgaris</strong></td>
<td>Farmyard</td>
<td>30–60</td>
<td>23 000–56 000</td>
<td><strong>decline</strong> (–4.8%)</td>
<td>moderate decline</td>
</tr>
<tr>
<td><strong>House martin Delichon urbicum</strong></td>
<td>Farmyard</td>
<td>80–120</td>
<td>9 900–24 000</td>
<td><strong>decline</strong> (–4.0%)</td>
<td>moderate decline</td>
</tr>
<tr>
<td><strong>House sparrow Passer domesticus</strong></td>
<td>Farmyard</td>
<td>200–400</td>
<td>63 000–130 000</td>
<td><strong>decline</strong> (–3.7%)</td>
<td>moderate decline</td>
</tr>
<tr>
<td><strong>Yellow wagtail Motacilla flava</strong></td>
<td>Field</td>
<td>250–400</td>
<td>7 900–14 000</td>
<td><strong>decline</strong> (–3.6%)</td>
<td>small decline</td>
</tr>
<tr>
<td><strong>Swift Apus apus</strong></td>
<td>Farmyard</td>
<td>30–60</td>
<td>6 900–17 000</td>
<td><strong>decline</strong> (–2.8%)</td>
<td>small decline</td>
</tr>
<tr>
<td><strong>Whinchat Saxicola rubetra</strong></td>
<td>Edge</td>
<td>300–400</td>
<td>5 400–10 000</td>
<td><strong>decline</strong> (–2.6%)</td>
<td>small decline</td>
</tr>
<tr>
<td><strong>Wheatear Oenanthe oenanthe</strong></td>
<td>Farmyard</td>
<td>150–200</td>
<td>4 600–13 000</td>
<td><strong>decline</strong> (–2.1%)</td>
<td>moderate decline</td>
</tr>
<tr>
<td><strong>Swallow Hirundo rustica</strong></td>
<td>Farmyard</td>
<td>130–180</td>
<td>16 000–36 000</td>
<td><strong>decline</strong> (–1.8%)</td>
<td>small decline</td>
</tr>
<tr>
<td><strong>Common snipe Gallinago gallinago</strong></td>
<td>Field</td>
<td>80–120</td>
<td>930–1 900</td>
<td><strong>decline</strong> (–1.5%)</td>
<td>moderate decline</td>
</tr>
<tr>
<td><strong>Hooded crow Corvus corone</strong></td>
<td>Forest</td>
<td>160–230</td>
<td>7 000–17 000</td>
<td><strong>decline</strong> (–1.5%)</td>
<td>stable</td>
</tr>
<tr>
<td><strong>Curlew Numenius arquata</strong></td>
<td>Field</td>
<td>35–50</td>
<td>220–360</td>
<td><strong>decline</strong> (–1.4%)</td>
<td>moderate decline</td>
</tr>
<tr>
<td><strong>Skylark Alauda arvensis</strong></td>
<td>Field</td>
<td>300–400</td>
<td>40 000–80 000</td>
<td><strong>decline</strong> (–1.0%)</td>
<td>small decline</td>
</tr>
<tr>
<td><strong>Scarlet rosefinch Carpodacus eryth.</strong></td>
<td>Edge</td>
<td>250–350</td>
<td>3 000–6 100</td>
<td><strong>decline</strong> (–0.8%)</td>
<td>stable</td>
</tr>
<tr>
<td><strong>Yellowhammer Emberiza citrinella</strong></td>
<td>Forest</td>
<td>700–1 100</td>
<td>18 000–31 000</td>
<td><strong>decline</strong> (–0.7%)</td>
<td>small decline</td>
</tr>
<tr>
<td><strong>Whitethroat Sylvia communis</strong></td>
<td>Edge</td>
<td>250–400</td>
<td>14 000–25 000</td>
<td>stable</td>
<td>small increase</td>
</tr>
<tr>
<td><strong>Meadow pipit Anthus pratensis</strong></td>
<td>Field</td>
<td>700–1 200</td>
<td>7 000–16 000</td>
<td>stable</td>
<td>small decline</td>
</tr>
<tr>
<td><strong>White wagtail Motacilla alba</strong></td>
<td>Edge</td>
<td>600–900</td>
<td>13 000–26 000</td>
<td>stable</td>
<td>stable</td>
</tr>
<tr>
<td><strong>Lapwing Vanellus vanellus</strong></td>
<td>Field</td>
<td>50–80</td>
<td>1 700–2 800</td>
<td>stable</td>
<td>large decline</td>
</tr>
<tr>
<td><strong>Magpie Pica pica</strong></td>
<td>Forest</td>
<td>150–200</td>
<td>7 500–19 000</td>
<td>stable</td>
<td>moderate decline</td>
</tr>
<tr>
<td><strong>Reed bunting Emberiza schoeniclus</strong></td>
<td>Edge</td>
<td>200–400</td>
<td>4 800–8 800</td>
<td>stable</td>
<td>small decline</td>
</tr>
<tr>
<td><strong>Sedge warbler Acrocephalus schoen.</strong></td>
<td>Edge</td>
<td>200–400</td>
<td>4 400–7 400</td>
<td>stable</td>
<td>stable</td>
</tr>
<tr>
<td><strong>Red-backed shrike Lanius collurio</strong></td>
<td>Edge</td>
<td>30–60</td>
<td>6 300–13 000</td>
<td>stable</td>
<td>small decline</td>
</tr>
<tr>
<td><strong>Wood pigeon Columba palumbus</strong></td>
<td>Forest</td>
<td>150–200</td>
<td>9 000–17 000</td>
<td><strong>increase</strong> (+2.2%)</td>
<td>small increase</td>
</tr>
<tr>
<td><strong>Pheasant Phasianus colchicus</strong></td>
<td>Edge</td>
<td>10–20</td>
<td>3 400–4 700</td>
<td><strong>increase</strong> (+2.6%)</td>
<td>unknown</td>
</tr>
<tr>
<td><strong>Fieldfare Turdus pilaris</strong></td>
<td>Forest</td>
<td>1 000–2 000</td>
<td>14 000–24 000</td>
<td><strong>increase</strong> (+3.0%)</td>
<td>stable</td>
</tr>
<tr>
<td><strong>Jackdaw Corvus monedula</strong></td>
<td>Forest</td>
<td>80–130</td>
<td>5 200–15 000</td>
<td><strong>increase</strong> (+6.7%)</td>
<td>stable</td>
</tr>
<tr>
<td><strong>Greenfinch Carduelis chloris</strong></td>
<td>Forest</td>
<td>300–400</td>
<td>14 000–32 000</td>
<td><strong>increase</strong> (+8.8%)</td>
<td>stable</td>
</tr>
<tr>
<td><strong>Tree sparrow Passer montanus</strong></td>
<td>Farmyard</td>
<td>20–40</td>
<td>26 000–48 000</td>
<td><strong>increase</strong>(++)</td>
<td>moderate decline</td>
</tr>
<tr>
<td><strong>Linnet Carduelis cannabina</strong></td>
<td>Farmyard</td>
<td>20–30</td>
<td>10 000–28 000</td>
<td>unknown</td>
<td>moderate decline</td>
</tr>
</tbody>
</table>

*not analyzed in the article by Väisänen (2005), but according to Vepsäläinen et al. 2005b and national winter bird census (Väisänen 2003), population size is well over 10-fold compared to the 1980s’ population, but the causes of the increase are not understood.
communities (see Berg & Pärt 1994, Söderström & Pärt 2000, Berg 2002, Heikkinen et al. 2004, Luoto et al. 2004). For example, it is likely that populations of true field species are concentrated to large and open patches of farmland, whereas for populations of farmland’s forest and edge species these areas are less favourable.

Concern about the declines of Finnish farmland bird populations arose already in the late 1970s – early 1980s (Haila et al. 1979, Linkola 1983, Tiainen & Ylimaunu 1984). Currently, numerous Finnish farmland bird species show decreasing trends as summarized in Table 3 (Tiainen & Pakkala 2000, 2001, Väisänen 2005). Rather similar trends have been observed in Sweden, where the agricultural landscape resembles that of Finland (Wretenberg et al. 2006). The ecological species groups as listed above show notable differences in their general trends: true field species and farmyard species have declined, edge species have remained somewhat stable (or slightly decreasing), and many farmland’s forest species have increased (Tiainen & Pakkala 2001; Table 3). In addition to the thirty most abundant species listed in Table 3, two nowadays rare true field species, the grey partridge and corncrake, have also strongly declined during the agricultural intensification (Tiainen et al. 1985). In general, the Finnish trends of true field species and farmyard species are similar to the European trends, with few exceptions. In strong contrast to the general declining trends in Europe, the tree sparrow has increased very strongly during the last two decades, for yet unknown causes (Väisänen 2003, Vepsäläinen et al. 2005b). The reasons for the increasing population trends of those forest birds that feed in fields (Table 3) are not well-known. However, it has been argued that increased winter feeding has benefited at least the greenfinch (Väisänen & Solonen 1997). On the other hand, increased spring cereal production has probably benefited the wood pigeon, as the species feeds mainly on grains (Saari 1984, Tiainen & Pakkala 2001). Some of the farmland species presented in Table 3 have large populations in habitats other than farmland. For example, the yellow wagtail and meadow pipit breed in open mires as well as in farmland habitats. Hence, the Finnish population trends as presented in Table 3 may not entirely reflect changes in agroecosystems.

Large-scale changes in Finnish agroecosystems (as listed in chapter 1.3.2.) are plausible explanations for many of the observed trends, although direct evidence and detailed understanding of the factors behind the trends are limited to few species. Firstly, the drastic decrease in dairy husbandry has decreased the availability of invertebrate food that is essential for many farmland and field species, such as for the swallow (Møller 1983), starling (Tiainen et al. 1989, Solonen et al. 1991), and curlew (Berg 1993, 1994). Secondly, the removal of small-scale non-crop habitats, such as open ditches, have markedly decreased the small-scale habitat heterogeneity and the amount of suitable nesting and feeding habitats of true field birds with probable impacts on bird populations (Haukioja et al. 1985, Mehtälä et al. 1985, Vepsäläinen et al. 2005a). Thirdly, increased sowing of spring crops and a simultaneous decrease in autumn-sown cereals and fodder crops has probably reduced food resources and lowered the breeding success of birds. This is because an increasing part of the total field area is without vegetative cover in the spring as fields are usually ploughed during the previous autumn (Tiainen & Pakkala 2001). Fourthly, increased herbicide use has likely decreased the availability of important seed and invertebrate food of many birds (Helenius et al. 1995).

Many bird species show a preference to set-asides (Mehtälä et al. 1985, Berg & Pärt 1994), and for example the skylark has increased during set-aside schemes in the 1970s and early 1990s (Tiainen et al. 2001). It is hence conceivable that set-asides which have been implemented in the Finnish and Swedish AESs (or otherwise in the frames of CAP) may prove to be beneficial for birds. However, further evidence of the potential benefits of the Finnish AES on birds has until
now remained scarce. In fact, the Finnish AES has mainly been designed for water protection purposes, biodiversity conservation playing only a minor role.

Although domestic changes provide plausible explanations for many of the population changes of Finnish farmland birds, it is likely that the deterioration of wintering and stop-over habitats may provide further explanations, especially for species which predominantly winter in farmland areas. The deterioration of winter habitats has for example been proposed as one potential reason for the declines of Swedish farmland bird populations (Wretenberg et al. 2006).

In summary, the climate, landscape, and farmland management of Finnish agro-ecosystems differ in many ways from those of Central and Western Europe, and hence the reasons behind the declines in Finnish farmland bird populations may differ from those driving farmland bird population declines in more temperate regions of Europe. For example, one important driver of farmland bird declines in the UK has been the increase of autumn sowing of cereals, a change that has not occurred in Finland. There is a clear need to increase our knowledge of farmland birds’ spatial and temporal habitat associations in modern boreal agroecosystems. This information is essential for the development of actions aiming to prevent the ongoing loss of biodiversity, and also to identify potential future threats posed by likely changes in climate and agricultural practices.
2. Aims of the thesis

The aim of my thesis was to study how characteristics of Finnish farmland landscape and agricultural land use affect farmland birds. Firstly, I studied how the occurrence and density of an abundant farmland bird species, skylark, are affected by landscape structure and agricultural land use (I). Then, in order to identify potential biodiversity and conservation hotspots, I extended the view to the whole farmland bird assemblage by studying how the diversity, species richness, and abundance of a farmland bird assemblage are associated with major landscape features and climatic gradients across Finnish agricultural areas (II). I also examined the effects of organic farming, agricultural land use and landscape structure on diversity, species richness, density, and biomass of a true field bird species assemblage, and additionally the density of five individual bird species (III). Lastly, I focused on how temporal variation in habitat composition and weather conditions in both breeding and wintering grounds affect population dynamics of a migratory skylark population (IV). In conclusion, I aimed to identify essential factors of current boreal agriculture that may limit the diversity and abundance of farmland birds.

All the studies were based on extensive field data collected by territory mapping of breeding farmland birds in various parts of Finland. The main study sites are shown in Fig. 6. The mapping method used (see Bibby et al. 2000) provides data with fair estimates of species abundances as well as territory locations allowing many kinds of study approaches. In my thesis, I have analyzed habitat associations of farmland birds in territory (I), population (I, III, IV) and various species assemblage (community) scales (II, III). The temporal data coverage in the studies was one (I, II), two (III), and 20 (IV) years. The various spatial and temporal approaches required the use of geographic information systems (GIS) and several statistical methods, including standard regressions (I), generalized additive modelling (II), spatial autoregressive modelling (III), and temporal autoregressive modelling with Monte Carlo simulations (IV).

Figure 6. The farmland bird census areas in Finland. Two of the papers (I, IV) were conducted in a long-term study site in Lammi, southern Finland (coverage: 30 km² of arable area in I, 11 km² used in IV), and one in Pukkila, southern Finland (ca. 20 km²) (III). In study II, I used data collected in various parts of Finland (flags) with altogether ca. 71 km² of arable area including also small parts from the Lammi and Pukkila study areas.
3. Main results and discussion

The main study questions and results are summarized in Table 4. In the following, I shall begin by discussing these results in the light of two main issues: (1) the importance of general landscape structure in determining the abundance and diversity of farmland birds and (2) the effects of agricultural practices and land use on the abundance and diversity of farmland birds. Then I shall discuss how boreal climate impacts farmland birds with some future prospects of climate change. Lastly, I shall focus on certain methodological findings revealed by my studies.

3.1. Landscape structure — a key determinant of boreal farmland bird populations

In general, species are most abundant in habitats which optimally meet their species-specific requirements and maximize their fitness in terms of survival and/or reproduction (e.g. Rosenzweig 1981). The area and openness of agricultural areas were key determinants of farmland bird abundance and distribution in the studied Finnish farmland landscapes (I, II, III). These findings are in line with the other Fennoscandian studies on the effects of landscape structure on birds (Söderström & Pärt 2000, Berg 2002, Heikkinen et al. 2004, Luoto et al. 2004), and similar findings have been made in North American grassland bird communities (Cunningham & Johnson 2006). Many farmland specialist bird species, such as lapwing and skylark, prefer open and wide agricultural habitats (I, III, Wilson et al. 1997, Chamberlain & Gregory 1999) which may resemble steppe habitats, the likely original habitat of these species (e.g. Pätzold 1983). On the other hand, preference towards landscape openness may be an adaptation to increased nest predation near forest edges, as many nest predators, such as corvids, nest near forest edges (Andrén 1992).

The finding that the area and openness of agricultural areas greatly determine the abundance and distribution of farmland birds has general implications for farmland bird conservation in boreal mosaic landscapes. Combined with the result that many ‘true field species’ (i.e. species that both breed and forage on open fields) have shown severe declines (Tiainen & Pakkala 2001), my results indicate that various conservation actions should be aimed particularly at large patches of farmland, where landscape is suitable for open farmland specialists. Small, isolated farmland patches that are surrounded by forests are very abundant in boreal landscapes, but are clearly unsuitable for skylark (I, III) and diverse farmland bird assemblages (II, III). These habitats are, however, important for other components of biodiversity, such as plants and butterflies (Kivinen et al. 2006).

Although the area and openness of agricultural areas are important for the occurrence of a rich farmland avifauna, many farmland bird species also need other habitats than arable fields for breeding and/or feeding, such as farmyards and wetlands (II, III, Fuller et al. 2004). A basic requirement for a rich farmland avifauna is hence a type of coarse scale type of landscape heterogeneity (cf. Benton et al. 2003). It should be borne in mind that the definition of habitat heterogeneity is entirely dependent of the choice of spatial scale and habitat classification (e.g. Levin 1992, González-Megías et al. 2007).

Identification of important spatial scales for various ecological processes is a central problem in ecological research (Levin 1992). My results provide some useful information on the magnitude of scales that are important for the ecology and conservation of farmland birds in boreal agroecosystems. Firstly, the study on habitat associations of a typical and abundant field bird, the skylark, revealed that skylark occurrence usually requires patches of farmland larger than 11.5 hectares (I). Secondly, in a ‘farm scale’ approach of 25 hectares
Table 4. Summary of the main study questions and results of the articles included in the thesis.

<table>
<thead>
<tr>
<th>Main study questions</th>
<th>Main results</th>
</tr>
</thead>
<tbody>
<tr>
<td>I  How do major landscape structures determine skylark occurrence and density in a</td>
<td>Skylark occurrence was strongly dependent of the size and openness of farmland patches. Skylarks were present in all patches of farmland larger than 11.5 ha.</td>
</tr>
<tr>
<td>mosaic farmland landscape?</td>
<td>The amount of agricultural grasslands and open ditches influenced skylark density positively, whereas it was negatively associated with broad-leaved crops (potato, sugar beet and rape).</td>
</tr>
<tr>
<td>Which agricultural land use characteristics are associated with skylark abundance?</td>
<td>Local land cover characteristics together with latitudinal and longitudinal climatic gradients set fundamental limits for the distribution of diverse farmland bird assemblages. Abundance of mosaic-like farmland habitats (characterized by low-intensity farmland, scattered rural settlements, and habitat heterogeneity) was among the most important positive factors.</td>
</tr>
<tr>
<td>II How do elementary landscape and climatic characteristics determine farmland bird</td>
<td>Hotspots of diversity, species richness, and abundance of farmland birds were associated with the largest cropland areas in southern Finland. However, diversity and species richness of an assemblage consisting of species with unfavourable conservation status in Europe (SPEC-species) showed notable hotspot clusters in northern parts of the country which are characterized by dairy farming.</td>
</tr>
<tr>
<td>diversity, species richness, and abundance in boreal farmland landscapes?</td>
<td>May the conservation of diversity hotspots be cost-effective in Finnish farmland landscapes? According to national-scale predictions, targeting conservation actions at farmland bird diversity hotspots would be an effective conservation approach, since these areas hold higher bird territory densities than expected by their area. For example, by selecting areas based on the prioritisation of bird species diversity, already 31% of the selected area of total farmland area would involve as much as 44% of SPEC-species’ territories.</td>
</tr>
<tr>
<td>Where do farmland bird diversity and conservation hotspots occur in Finland?</td>
<td>Landscape openness and agricultural land use were the principal determinants of the bird assemblage. Agricultural grasslands and the presence of grazing cattle strongly and positively determined the majority of the studied variables describing the bird assemblage.</td>
</tr>
<tr>
<td>Does organic farming affect the diversity, species richness, density, or biomass of</td>
<td>Organic farming was favourable only to skylark and lapwing, but not to overall bird density, species richness, diversity, or biomass.</td>
</tr>
<tr>
<td>farmland birds?</td>
<td></td>
</tr>
<tr>
<td>III How do landscape structure and agricultural land use affect diversity, species</td>
<td>The amount of grassland habitats explained the general trends in skylark population development well. Rainfall had a negative effect on population growth in breeding areas, but a positive effect in wintering areas.</td>
</tr>
<tr>
<td>richness, density, and biomass of field-dwelling farmland birds?</td>
<td></td>
</tr>
<tr>
<td>Does organic farming affect the diversity, species richness, density, or biomass of</td>
<td></td>
</tr>
<tr>
<td>farmland birds?</td>
<td></td>
</tr>
<tr>
<td>IV How does temporal variation in habitat composition and weather conditions affect</td>
<td>Skylark population fluctuations showed first order negative density dependence. Simultaneous inclusion of intrinsic and extrinsic factors in the population dynamical model improved statistical visibility of both factors.</td>
</tr>
<tr>
<td>population dynamics of a migratory skylark population?</td>
<td></td>
</tr>
<tr>
<td>What is the role of density dependence in skylark population dynamics?</td>
<td></td>
</tr>
</tbody>
</table>
Summary

reported as an important factor behind farmland bird declines (Wilson et al. 1997, Chamberlain et al. 1999a, Donald et al. 2001a). Interestingly, for climatic reasons such a switch towards autumn sowing has not occurred in Fennoscandia (Wretenberg et al. 2006, Tiainen 2001).

Effects of crop composition

My results clearly indicate that in boreal agroecosystems, farmland birds favour fields with springtime vegetative cover, especially agricultural grasslands including set-asides (I, III, IV). Moreover, the fact that skylark has strongly increased during set-aside schemes (IV, Tiainen et al. 2001) indicates spring-sown arable fields to be suboptimal habitats compared to set-asides. These results are noteworthy, as in contrast to western and central Europe, the majority of arable land in Finland lacks vegetative cover when migratory birds arrive in spring. There are some potential explanations for the observed preferences. Firstly, many birds, especially species that breed in open habitats, require some vegetative cover probably because vegetation offers protection for nests and foraging against predation (Potts 1986, Berg 1991, Stowe et al. 1993, but see Grant et al. 1999). However, the relationships between vegetative cover, foraging efficiency, and predation risk are extremely complex and depend strongly on species-specific foraging habits (Whittingham & Evans 2004). Secondly, invertebrate and seed food is more abundant in various grass crops and set-asides, since herbicides are not applied to these crops in boreal agroecosystems and they are not ploughed in the autumn (Berg 1991, reviewed by Pitkänen & Tiainen 2001, Olsson et al. 2002). Thirdly, regular agricultural practices of spring-sown crops (e.g. tilling and sowing) occur in early May during the early breeding season. These actions cause nest losses of many bird species (Haukioja et al. 1985, Valkama 1999), and may also concentrate territory establishment to grass crops and set-asides that are less intensively

(3.2. Finnish agricultural management and farmland birds

Changes in European farmland habitats caused by agricultural intensification have been extensive (Stoate et al. 2001a), and there is a general agreement that agricultural intensification has been the main driver of the declines of European farmland bird populations (Chamberlain et al. 2000a, Donald et al. 2001b, Donald et al. 2006). As described earlier, the declines in Finnish farmland bird populations show similar patterns with the other European bird populations. However, since agricultural practices and patterns in agricultural intensification differ among European countries (Table 2), it is likely that the factors responsible for farmland bird declines differ among these regions as well. A representational example is the large-scale increase of autumn-sown cereals in Central and Western Europe that have been

(mean farm acreage in Finland is ca. 30 ha), the heterogeneity of the main habitat types (arable fields, low-intensity farming areas, rural settlements, forests, wetlands and water bodies) had a positive relationship with species richness (II). Hence, a landscape composition with enough open farmland combined with key habitats such as farmyards and wetland is likely to provide essential prerequisites for the occurrence of a rich farmland avifauna.

Agricultural areas are unevenly distributed in Finland, with the majority of large areas suitable for open habitat specialists being located in the southern, south-western and western parts of the country (Fig. 3). According to my results, these areas hold the majority of farmland bird diversity and abundance hotspots (II). However, the diversity of the species with an unfavourable conservation status in Europe (SPECs) had notable hotspot areas in northern and north-western agricultural areas, which probably reflects low-intensity land use and frequent cattle farming in these areas (II; discussed in detail in the next chapter).
managed during the early breeding season.

My results lead me to suggest that in the spring cereal dominated Finnish agroecosystems it is rather the absence than the excess of field vegetation that may limit populations of many farmland bird species. Hence, it is likely that the decrease of crops providing vegetative cover in the spring, such as permanent grasslands, cultivated grass, and autumn-sown cereals, has contributed to the declines of Finnish farmland birds. Set-asides may partly have compensated for the effects of the reduction of these crop types (IV, Tiainen et al. 2001).

Crop heterogeneity has been shown to be important for many farmland birds (Chamberlain & Gregory 1999, Robinson et al. 2001, Bradbury & Bradter 2004), and for example bare soil (i.e. fields that are ploughed in autumn and sown in spring) may provide important foraging grounds for some species (Shrubb 1990). Furthermore, species preferences for vegetation height show marked differences. For example, many waders prefer short vegetation (Milsom et al. 1998), whereas corncrake territories occur most frequently in taller vegetation (Berg & Gustafson 2007). Hence, although these studies are mainly from the UK, it is likely that a diverse combination of fields with spring crops and various over-winter crops is necessary for maintaining a diverse farmland bird community in boreal agroecosystems as well. The increase in field parcel sizes and specialization of farms during the last decades have, however, driven the Finnish farmland habitats towards large spring cereal monocultures rather than diverse crop compositions (Pitkänen & Tiainen 2001).

Effects of cattle farming

A drastic decrease in cattle farming has caused the greatest structural change in boreal agricultural ecosystems (Pitkänen & Tiainen, Wretenberg et al. 2006). My results together with other boreal farmland bird studies provide further evidence that cattle farming is a key requirement for a rich farmland avifauna (II, III, Hanski & Tiainen 1988, Söderström & Pärt 2000, Olsson et al. 2002). Cattle farming increases the amount of crops with vegetative cover with potential benefits as discussed above. In addition, many bird species are at least partly dependent on abundant invertebrate fauna related to cattle farming and pastoral habitats (e.g. Tiainen et al. 1989, Ambrosini et al. 2002, Olsson et al. 2002). These species include many species that have undergone declines (e.g. curlew, house martin, swallow, whinchat, wheatear, starling, and house sparrow), but none that would show stable or increasing trends (see Table 3). In addition, my results show that habitat compositions that fit the requirements of a diverse assemblage of farmland bird species with unfavourable conservation status in Finland (SPECs) occur most frequently in the northern parts of Finnish agricultural areas, which are characterized by low-intensity agricultural land use at landscape level and relatively large proportions of cattle husbandry farms (II; Fig. 5a). In the light of these findings, it is most likely that the decrease in cattle farming which has occurred during the past decades has greatly contributed to the declines of farmland birds.

Effects of small-scaled non-crop habitats

The removal of hedgerows and filling of ditches has markedly decreased feeding and nesting sites of farmland birds in Europe (O’Connor & Shrubb 1986, Bradbury et al. 2000, Newton 2004a). There are no hedgerows in Finland, but the number of fields with open ditches has greatly decreased in Finland as a result of subsurface drainage (Fig. 5b; Hietala-Koivu 2002) causing a drastic loss of non-crop habitats and small-scaled habitat heterogeneity (Hanski & Tiainen 1988). Open ditches have been shown to positively affect the overall farmland bird density (Haukioja et al. 1985, Mehtälä et al. 1985), ortolan bunting abundance (Vepsäläinen et al. 2005a), and skylark population density (I). Ditches and their margins are habitats with semi-natural vegetation which likely provide nest
sites and an abundant seed and invertebrate food supply for farmland birds (Arnold 1983, Morris et al. 2001, Perkins et al. 2002). The relative significance of the remaining ditches and main drains has probably increased in Finland after the adoption of the AES in 1995, since one of its obligatory measures was an establishment of 1–3 m broad protective margins along all larger ditches and other waters in farmland. Unfortunately, increase in subsurface drainage is still continuing and even supported by agricultural policy in Finland (Anon. 2004).

Effects of organic farming

Organic farming aims to reduce the negative impact of agriculture on the environment by excluding the use of agrochemicals and by generally applying diverse crop rotations. In a recent Danish study, it was shown that the establishment of organic farming increased land use diversity and decreased mean field sizes (Levin 2007). Effects of organic farming on farmland birds are mainly positive (Christensen et al. 1996, Chamberlain et al. 1999b, reviewed by Hole et al. 2005). In my study, two open field specialist species, the skylark and lapwing, showed positive relationships with organic farming (III), indicating that organic management may enhance food availability and/or the abundance of preferred nest sites. There were, however, no significant relationships between organic farming and overall diversity or species richness of field birds (III). This result is in line with an argument that effects of organic management are not expected to be pronounced in mosaic landscapes comprising of many habitats other than arable fields (Bengtsson et al. 2005). Nevertheless, I propose that organic farming is not insignificant, but its effect may be difficult to detect in boreal agroecosystems where factors other than farming regime, such as crop species and landscape structure, may control a large part of variation in the composition of bird assemblages.

3.3. Climate and its relation to agroecosystems and farmland birds

My results on a 20-year time series of a migratory skylark population revealed that climatic conditions in both breeding and wintering areas are important predictors of population change (IV). Rainfall had a negative effect on population growth in the breeding grounds (IV), probably because it is one of the most important factors of partial brood losses and chick development of skylark (Donald et al. 2001c). However, rainfall in the main wintering areas in France correlated positively with population change. The reasons for this positive relationship are unclear, but it is possible that rainfall increases winter food availability, or that rainfall in some other manner is associated with winter mildness benefiting wintering skylarks. In study II, species richness and abundance of farmland birds decreased with latitudinal gradient (II), i.e. showed a general pattern of decrease in species richness towards the poles (see Rohde 1992). These results provide examples on how temporal and spatial variation in climatic conditions may affect boreal farmland birds.

As described earlier, climatic conditions to a large degree determine agricultural practices, such as the timing of sowing and harvesting, and the geographic distribution of crop species. In current Finnish agroecosystems, efficient crop production is restricted to southern and western parts of the country, and cultivation of winter cereals is rare. Climate also sets basic ecological constraints on wildlife. For example, in boreal agroecosystems the majority of farmland birds are migrants, and the relatively short summer limits the duration of breeding season for many species and consequently the potential number of broods per season (von Haartman 1969). Furthermore, because fields are covered with snow in the winter, they do not provide winter food for most sedentary species.

Hence it is presumable that climate change which has already affected the ecology of birds,
including their distribution, breeding success, winter survival, and migratory behaviour (e.g. Crick & Sparks 1999, Ahola et al. 2004, Brommer 2004, Jonzén et al. 2006), will also alter farmland bird habitats through anthropogenic responses in agricultural practices. As a hypothetical example, it is conceivable that an increase in the mean temperature would extend the range of profitable cultivation of winter cereals in Finland notably modifying habitat composition available for birds. On the other hand, an increased mean temperature would probably enable multiple nesting attempts per breeding season for some bird species, or make wintering in Finland possible for nowadays migrant species. Similar complex outcomes of climate change on agroecosystems are multiple, and undoubtedly important issues of future research.

3.4. Methodological findings

A common property of ecological phenomena is autocorrelation which is often present both in time and space (Box 2). Spatial and temporal autocorrelation leads to problems in statistics by violating the applicability of standard techniques which assume independence among observations. Therefore in the spatial (III) and temporal (IV) investigation on relationships between farmland birds and environmental factors, I applied autoregressive models which incorporate an autocorrelation structure in the analysis.

Variables describing a farmland bird assemblage in a continuous study area using a 250 × 250 metre grid system showed clear positive spatial autocorrelation (III). The autoregressive model worked technically

Box 2. Autocorrelation in ecological data

Spatial autocorrelation means that observations at certain distance apart are more similar (positive autocorrelation) or less similar (negative autocorrelation) than expected for randomly associated observations (see Legendre 1993). Multiple environmental and population/community processes can lead to spatially structured observations. For example in case of farmland birds, spatial dependency in geomorphology, landscape structure, and farming practices together with territorial or social behaviour of birds likely cause spatial dependency of bird observations. Complex interactions between environment and organisms generally make it difficult or impossible to assess the importance of various potential factors causing autocorrelation (Legendre 1993, van Teeffelen & Ovaskainen 2007).

Ecological time-series are frequently temporally autocorrelated i.e. observations are either negatively or positively correlated at a certain time interval. Temporal patterns can be understood in the light of a synthetic view of population regulation i.e. both endogenous (mostly density-dependent) processes and environmental variability are usually simultaneously important in determining population dynamics (Turchin 1999). As in the case of spatial autocorrelation, the separation of these two processes is often difficult or impossible (Ranta et al. 2000, Jonzén et al. 2002).
well in terms of making the model residuals uncorrelated, but the factors behind the spatial autocorrelation, whether caused by environmental or population/community dynamical processes cannot usually be further identified (cf. Legendre 1993, van Teeffelen & Ovaskainen 2007). The use of autoregressive modelling was not convenient in the predictive modelling study using bird data from various sites of Finland in a 500 × 500 metre grid system, mainly because there were not enough data for estimation of autoregressive terms (II). However, examination of the degree of residual autocorrelation indicated that landscape structure explained a large part of the spatial autocorrelation in the variables describing farmland bird assemblage. Hence as proposed by Heikkinen et al. (2004) and Siriwardena et al. (2000b), it is possible that spatial structure in bird data in the given scale may reflect distributions caused by a clumping of preferred or avoided habitats. However, generalizations should be avoided, since the mechanisms leading to spatial autocorrelation are complex and perception is entirely dependent on the choice of scale, methodology, and variables measured (Levin 1992, Legendre 1993, Lichstein et al. 2002).

The results of the study on temporal changes in a skylark population indicated that population growth was density-dependent (IV), which is a generally accepted demographic process regulating natural populations (Turchin 1999). More interestingly, the results provided further evidence that having intrinsic and extrinsic factors simultaneously in a population dynamical model can improve the statistical visibility of both factors (IV; Rothery et al. 1997, Lundberg et al. 2002).

The studies in my thesis are based on farmland bird monitoring data collected by territory mapping census. These data are useful for many kinds of approaches on habitat associations of birds and allow studies to be conducted at scales that are adequate for farmland bird conservation. The downside is that these studies are correlative by nature rather than factorial experiments. There is hence a clear need for the establishment of novel monitoring schemes providing demographic data on farmland birds’ survival and breeding performance parallel to current monitoring schemes.
4. Conclusions and implications for conservation

According to my results, there are approximately five million farmland bird pairs in Finnish agroecosystems, of which more than a million belong to species with an unfavourable conservation status in Europe (II). The dramatic declines in Finnish farmland bird populations are alarming (Table 3), and there is a clear need for strong policy actions aiming to reverse these declining trends. In agroecosystems, food production is the main land use purpose and resources available for preserving biodiversity tend to be limited. Hence, reversing farmland bird population declines is a challenging task requiring more efficient application and spatial targeting of conservation actions such as AESs. A step towards efficiently targeted actions is to identify hotspots of biodiversity (II, see Myers et al. 2000). My results provide evidence that bird territories are, in a predictable manner, unevenly distributed in agricultural mosaic landscapes, and that conservation actions performed in bird diversity hotspots could be cost-efficient (II). For example, by selecting areas based on the prioritisation of bird species diversity, already 31% of the selected area of total farmland area would involve as much as 44% of SPEC-species’ territories (II).

The mosaic structure of boreal agricultural landscapes sets fundamental restrictions for the occurrence of rich farmland avifauna (I, II, III, Berg 2002, Luoto et al. 2004). Therefore considerable attention needs to be paid to landscape factors when selecting areas for various conservational management actions (see also Milsom et al. 1998). My results indicate that a major problem for farmland bird conservation in Finland is the conflict between landscape structure and agricultural management. Areas with mixed and cattle farming are virtually absent from the large agricultural plains of southern and south-western Finland, where the landscape structure is more likely to be favourable for rich farmland bird assemblages. On the other hand, mixed and cattle farming is still rather frequent in northern and central parts of the country, where the landscape structure is not suitable for many farmland specialist birds requiring open landscapes.

Once landscape prerequisites favour the occurrence of a rich farmland avifauna, the variation in agricultural land-use, farming practices and small-scaled habitat heterogeneity fine-tune the suitability of a given area for various bird species. My results provide evidence that set-asides, rotational grasslands, and pastures are highly important for farmland birds in boreal agroecosystems (I, III, IV). Their significance is probably enhanced since permanent grasslands nowadays nearly lack from Finland and are scarce in Sweden. Grass crops have persistently declined in Finland as a consequence of specialization in crop production and the large-scale decline in cattle husbandry (Figs 4 and 5). In addition, small-scale non-crop habitats, especially ditches and ditch margins, are also important for many bird species in Finnish agroecosystems (I, Haukioja et al. 1985, Vepsäläinen et al. 2005a), but have dramatically declined during the last decades. I propose that actions promoting the abundance of set-asides, grass crops, and ditches would markedly benefit Finnish farmland bird populations. These actions should be targeted at areas with suitable landscape structure for farmland birds. In addition, my results indicate that organic farming may benefit farmland birds, but it is not clear how general its beneficial effect is in boreal agroecosystems.

During the next 10 years, the number of livestock farms has been predicted to halve in Finland (Lehtonen & Pyykkönen 2005). Consequently, livestock farming will continue to be concentrated to a few intensive production areas, while the production and number of farms may decrease in large parts of the country, especially in sparsely populated areas.
in the northern, eastern, and central parts of Finland. Many farms will continue with crop production, but in eastern and northern Finland, the number of crop farms is expected to decline due to unfavourable natural conditions. The likely consequence is land abandonment and a clear decrease in the amount of remaining low-intensity farmland habitats in the region. According to my results, these large scale structural changes may have strikingly negative effects on farmland birds. Therefore I suggest that the most urgent action aiming to preserve farmland biodiversity would be to strongly support re-introducing and sustaining cattle farming by environmental subsidies. This would be especially beneficial in the southern parts of Finland, where the landscape characteristics and abundance of agricultural areas are most suitable for farmland birds and where cattle farming is currently rare.

Many important aspects in the conservation of boreal farmland bird populations differ from those important for the Central and Western European agroecosystems, and the results obtained in my thesis provide useful guidelines for farmland bird conservation in current Finnish agroecosystems. However, more research is needed to gather evidence on causal factors behind the population trends of boreal farmland bird populations, including species-specific studies on breeding biology and survival. Complex interactions among the ongoing climate change, structural changes in agriculture, and agricultural policy provide a huge challenge for future farmland bird research and conservation.
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