



### Markus Piha

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

- I Piha, M., Pakkala, T., Tiainen, J. 2003. Habitat preferences of the Skylark *Alauda arvensis* in southern Finland. Ornis Fennica 80:97–110.
- 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.
- IV Piha, M., Lindén, A., Pakkala, T., Tiainen, J. 2007. Linking weather and habitat to population dynamics of a migratory farmland songbird. — Annales Zoologici Fennici 44:20–34.

### Contributions

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

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Original idea	MP, TP, JT	MP	MP, JT	MP, AL
Data collection & preparation	MP, JT	TS, JT, MP	JT, JH	MP, JT, TP
Methods & Analyses	MP, TP	MP	MP, JH	AL, MP
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### Contents

0 SUMMARY	6
1. Introduction	6
1.1. Agriculture and biodiversity in Europe	6
1.2. Farmland birds and agricultural intensification	7
1.3. Finnish agroecosystems as habitats for farmland birds	11
1.3.1. Description of current Finnish agriculture	11
1.3.2. Biodiversity and modernization of Finnish agriculture	12
1.3.3. Farmland birds in Finland and other boreal European agroecosystems	15
2. Aims of the thesis	19
3. Main results and discussion	20
3.1. Landscape structure — a key determinant of boreal farmland bird populations	20
3.2. Finnish agricultural management and farmland birds	22
3.3. Climate and its relation to agroecosystems and farmland birds	24
3.4. Methodological findings	25
4. Conclusions and implications for conservation	27
5. Acknowledgements	29
6. References	31

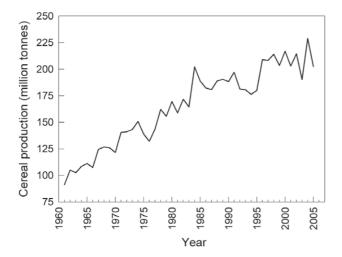
### CHAPTERS

Ι	Habitat preferences of the Skylark Alauda arvensis in southern Finland	.41
Π	Modelling diversity and abundance of Finnish farmland birds —	
	landscape characteristics define diversity and conservation hotspots	.57
III	Effects of land-use and landscape characteristics on avian diversity and	
	abundance in a boreal agricultural landscape with organic and conventional farms	.81
IV	Linking weather and habitat to population dynamics of	
	a migratory farmland songbird	.97

### 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 speciesrich habitats (Wilson et al. 1999, Chamberlain



**Figure 1.** Cereal production in 15 European Union member countries (EU-15) in 1961–2005. Data from FAOSTAT 2007.

*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 km<sup>2</sup>) 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 Hietala-Koivu landscape (*e.g.* 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). То prevent further population declines and the deterioration of

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).

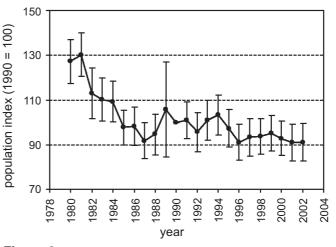
### **1.2. Farmland birds and agricultural intensification**

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 keyfactors 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 (longterm 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 &



**Figure 2.** Pan-European indicator of farmland bird popultions (23 species) in 1980–2002 by Gregory *et al.* 2005. Indices (± 1.96 s.e.) are based on monitoring schemes of 18 countries. Reprinted with the kind permission of the Royal Society of London.

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	agricultural intensification havi	ng largely negative effe	cts on European farmland bi	intensification having largely negative effects on European farmland birds with some study examples.
Process	Consequences on habitats		Consequences on birds	
Increased mechanisation	<ul> <li>- intensified land-use and removal of uncultivated areas (e.g. hedgerows, ditch banks, margins)</li> </ul>	noval of dgerows,	Reduction in suitable nesting	Reduction in suitable nesting and feeding sites (1, 2, 3, 4, 5, 6, 7)
	- mechanised harvesting		Destruction of eggs and chicks in field species (8, 9)	s in field species (8, 9)
Increased fertilizer use	<ul> <li>dense fast growing swards on arable and grass fields</li> </ul>	on arable	Reduction in suitable nesting and feeding sites (10, 11)	and feeding sites (10, 11)
Increased pesticide use	- declined weed and invertebrate	rate	Reduction in food supply (12, 13, 14, 15, 48)	13, 14, 15, 48)
	uiversity & abuilitatioe			
Reduction in spring sowing of cereals	<ul> <li>reduction in over-winter stubbles</li> <li>dense fast growing swards on fields</li> </ul>	obles on fields	Reduction in winter food supply (16, 17, 18, 19, 20, 21) Reduction in suitable nesting and feeding sites (22, 23,	Reduction in winter food supply (16, 17, 18, 19, 20, 21) Reduction in suitable nesting and feeding sites (22, 23, 24, 25, 26, 27)
Farm specialization and	- conversion of semi-natural grasslands to	grasslands to	Reduction in suitable nesting	Reduction in suitable nesting and feeding sites (11, 29, 30, 31, 32, 33)
decreases in mixed farming	improved grassland or arable fields	le fields		
and low-intensity cattle	- loss of habitat heterogeneity		Reduction in suitable nesting	Reduction in suitable nesting and feeding sites (18, 28, 34, 35, 36)
husbandry leading to	- dense fast growing grass swards	vards	Reduction in suitable nesting	Reduction in suitable nesting and feeding sites (32, 34, 37, 38)
simplified crop rotations	- declined invertebrate diversity & abundance	ity & abundance	Reduction in food supply (32, 39, 40, 41)	39, 40, 41)
	associated with decreasing animal husbandry	animal husbandry		
Increased stocking densities	- reduced sward heterogeneity	Ą	Loss of suitable nesting and feeding sites (42)	seding sites (42)
	- increased disturbance		Destruction of eggs and chicks in field species (43)	s in field species (43)
Land drainage	- loss of wet habitats		Reduction in suitable nesting and feeding sites (44, 45)	and feeding sites (44, 45)
	- loss of open ditches and field margins	ld margins	Reduction in suitable nesting	Reduction in suitable nesting and feeding sites (4, 7, 45, 46)
Increased farm and field sizes	- loss of habitat heterogeneity		Reduction in suitable nesting and feeding sites (22, 47)	and feeding sites (22, 47)
<b>References:</b> 1. Gillings & Fuller 1998 2. Stoate <i>et al.</i> 2001b 3. Perkins <i>et al.</i> 2002 4. Bradbury & Bradter 2004 5. Brickle & Peach 2004 6. Fuller <i>et al.</i> 2004 7. Vepsäläinen <i>et al.</i> 2005a 8. Stowe <i>et al.</i> 1997 9. Green <i>et al.</i> 1997	<ol> <li>Atkinson <i>et al.</i> 2005</li> <li>Buckingham <i>et al.</i> 2006</li> <li>Potts 1986</li> <li>Borg &amp; Toft 2000</li> <li>Morris <i>et al.</i> 2005</li> <li>Taylor <i>et al.</i> 2006</li> <li>Taylor <i>et al.</i> 2006</li> <li>Evans &amp; Smith 1994</li> <li>Evans &amp; Smith 1996</li> <li>Siriwardena <i>et al.</i> 2000a</li> </ol>	<ol> <li>20. Donald <i>et al.</i> 2001 a</li> <li>21. Moorcroft <i>et al.</i> 2002</li> <li>22. Schläpfer 1988</li> <li>23. Shrubb 1990</li> <li>24. Wilson <i>et al.</i> 1997</li> <li>25. Chamberlain <i>et al.</i> 1999a</li> <li>26. Chamberlain <i>et al.</i> 2000b</li> <li>27. Brickle &amp; Harper 2002</li> <li>28. Chamberlain &amp; Gregory 1999</li> <li>29. Møller 1983</li> </ol>	30. Bignal & McCracken 1996         31. Söderström & Pärt 2000         32. Vickery et al. 2001         33. Virkkala et al. 2004         34. Perkins et al. 2000         9a       35. Robinson et al. 2001         0b       36. Wilson et al. 2001         37. Milsom et al. 2006         38. Britschgi et al. 1998         39. Tiainen et al. 1989	n 1996 40. Ambrosini <i>et al.</i> 2002 41. Olsson <i>et al.</i> 2002 42. Wakeham-Dawson <i>et al.</i> 1998 43. Hart <i>et al.</i> 2002 44. Wilson <i>et al.</i> 2004 45. Bradbury <i>et al.</i> 2000 47. Benton <i>et al.</i> 2000 48. Brickle <i>et al.</i> 2000

#### SUMMARY

(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).

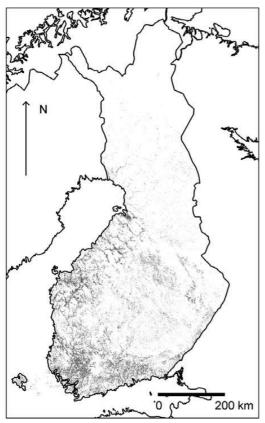
Additionally, migrant farmland birds are influenced by natural and anthropogenic factors operating in their wintering grounds and migration routes (Newton 2004b). Although severe declines in populations of particularly Afro-Palearctic migrants have been reported, underlying factors are relatively poorly 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  $60^{\circ}$  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

#### SUMMARY

Variable	Finland	UK	EU-25
Utilized agricultural area (million ha)	2.3	17.2	164.4
% Agricultural land of total land area	7	70	41
Mean farm size (agricultural ha)	30	61	22
% Permanent grassland	1	66	34
% Arable land	99	34	57
of which:			
% Cereals of which:	55	53	53
% Spring-sown	94	19 <sup>a</sup>	na
% Autumn-sown	6	81ª	na
% Potato and sugar beet	3	5	5
% Rape and turnip rape	4	10	5
% Fallow land (incl. set-aside)	9	9 <sup>b</sup>	na
% Forage plants (mainly fodder grass)	28	21	18
% Arable land under organic management*	7.2	4.4	4.1**
° Dosage of pesticides and other plant protection products (PPI	P)		
used for arable crops in 2003 (kg active ingredient/ha)	0.4	2.5	1.1
° Proportional usage of pesticides and other PPPs:			
% Herbicides	77	60	36
% Fungicides	18	25	46
% Insecticides	2	5	9
% Other PPPs	3	11	9

**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).

Additional data sources:

<sup>a</sup> DEFRA agricultural and food statistics; http://statistics.defra.gov.uk

<sup>b</sup> Eurostat Agricultural statistics; http://epp.eurostat.ec.europa.eu/

<sup>c</sup> The use of plant protection products in the European Union. 2007 edition. Eurostat statistical books.

European Communities 2007. ISBN 92-79-03890-7.

\* 2003 data

\*\* in EU-15 (not EU-25)

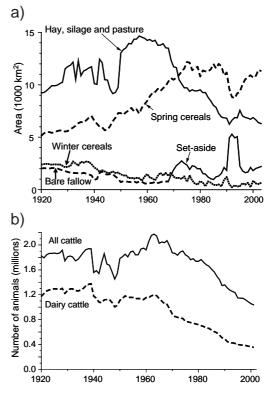
habitat diversity and enabled the occurrence of farmland specialist species. However, agricultural modernization has had multiple, mainly adverse, effects on these habitats and consequently on biodiversity (Hanski & Tiainen 1988, Pitkänen & Tiainen 2001).

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 19<sup>th</sup> century with a rapid decrease in traditional animal husbandry which was based on fodder obtained from seminatural grasslands (Tiainen 2001). Semi-natural grasslands were gradually taken into cultivation, and fodder crops and pastures were included into the crop rotation cycle. Consequently, seminatural 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).

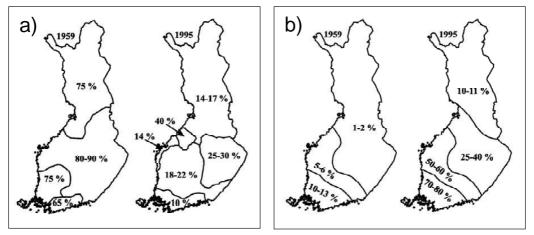
As in many European countries, the period of agricultural intensification introduced by increases in mechanization, artificial fertilizers, pesticides and subsurface drainage began in the 1950s with multiple consequences on farmland habitats and associated wildlife (Tiainen 2001, 2004). The main changes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

- 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. Setaside 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.



**Figure 5.** (a) Proportion of dairy farms of all farms in 1959 and 1995. (b) Proportion of fields with subsurface drainage of all fields in 1959 and 1995. Data compiled by Tiainen (2001) 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. wood pigeon and vellowhammer), 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

#### SUMMARY

**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 1983 and 2004 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.

Species	Main	Pop	oulation	Trer	nd
	nesting	es	timate		
	habitat in	(100	0 pairs)		
	farmland		•		
		Finland	Europe	Finland	Europe
Ortolan bunting Emberiza hortulana	Field	30–50	5 200–16 000	decline (-15.6%)	small decline
Starling Sturnus vulgaris	Farmyard	30-60	23 000–56 000	decline (-4.8%)	moderate decline
House martin Delichon urbicum	Farmyard	80–120	9 900-24 000	decline (-4.0%)	moderate decline
House sparrow Passer domesticus	Farmyard	200-400	63 000-130 000	decline (-3.7%)	moderate decline
Yellow wagtail Motacilla flava	Field	250-400	7 900–14 000	decline (-3.6%)	small decline
Swift Apus apus	Farmyard	30-60	6 900–17 000	decline (-2.8%)	small decline
Whinchat Saxicola rubetra	Edge	300-400	5400-10 000	decline (-2.6%)	small decline
Wheatear Oenanthe oenanthe	Farmyard	150-200	4 600-13 000	decline (-2.1%)	moderate decline
Swallow Hirundo rustica	Farmyard	130–180	16 000-36 000	decline (-1.8%)	small decline
Common snipe Gallinago gallinago	Field	80–120	930-1 900	decline (-1.5%)	moderate decline
Hooded crow Corvus corone	Forest	160–230	7 000–17 000	decline (-1.5%)	stable
Curlew Numenius arquata	Field	35–50	220-360	decline (-1.4%)	moderate decline
Skylark Alauda arvensis	Field	300-400	40 000-80 000	decline (-1.0%)	small decline
Scarlet rosefinch Carpodacus erythr.	Edge	250-350	3 000–6 100	decline (-0.8%)	stable
Yellowhammer Emberiza citrinella	Forest	700-1 100	18 000–31 000	decline (-0.7%)	small decline
Whitethroat Sylvia communis	Edge	250-400	14 000-25 000	stable	small increase
Meadow pipit Anthus pratensis	Field	700-1 200	7 000–16 000	stable	small decline
White wagtail Motacilla alba	Edge	600-900	13 000–26 000	stable	stable
Lapwing Vanellus vanellus	Field	50-80	1 700–2 800	stable	large <b>decline</b>
Magpie Pica pica	Forest	150-200	7 500–19 000	stable	moderate decline
Reed bunting Emberiza schoeniclus	Edge	200-400	4 800-8 800	stable	small decline
Sedge warbler Acrocephalus schoen.	Edge	200-400	4 400-7 400	stable	stable
Red-backed shrike Lanius collurio	Edge	30–60	6 300–13 000	stable	small decline
Wood pigeon Columba palumbus	Forest	150-200	9 000–17 000	increase (+2.2%)	small increase
Pheasant Phasianus colchicus	Edge	10–20	3 400-4 700	increase (+2.6%)	unknown
Fieldfare Turdus pilaris	Forest	1 000–2 000	14 000–24 000	increase (+3.0%)	stable
Jackdaw Corvus monedula	Forest	80–130	5 200–15 000	increase (+6.7%)	stable
Greenfinch Carduelis chloris	Forest	300-400	14 000-32 000	increase(+8.8%)	stable
Tree sparrow Passer montanus	Farmyard	20-40	26 000-48 000	increase(+++)*	moderate decline
Linnet Carduelis cannabina	Farmyard	20-30	10 000-28 000	unknown	moderate decline

\*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 farmyard 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 smallscale 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 setasides (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.

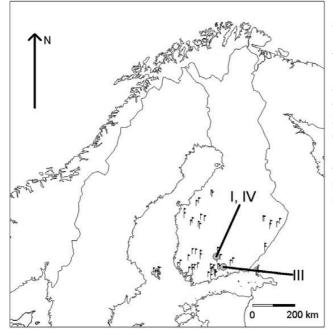
Although domestic changes provide plausible explanations for many of the population changes of Finnish farmland birds, it is likely that the deterioration of wintering and stop-over habitats may provide further explanations, especially for species which predominantly winter in farmland areas. The deterioration 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:  $30 \text{ km}^2$  of arable area in I,  $11 \text{ km}^2$  used in IV), and one in Pukkila, southern Finland (*ca.*  $20 \text{ km}^2$ ) (III). In study II, I used data collected in various parts of Finland (flags) with altogether *ca.* 71 km<sup>2</sup> 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 practises 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

	Main study questions	Main results
_	How do major landscape structures determine skylark occurrence and density in a mosaic farmland landscape?	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.
	Which agricultural land use characteristics are associated with skylark abundance?	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).
_	How do elementary landscape and climatic characteristics determine farmland bird diversity, species richness, and abundance in boreal farmland landscapes?	Local land cover characteristics together with latitudinal and longitudinal climatic gradients set fundamental limits for the distribution of diverse farm-land 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.
	Where do farmland bird diversity and conservation hotspots occur in Finland?	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.
	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.
=	How do landscape structure and agricultural land use affect diversity, species richness, density, and biomass of field-dwelling farmland birds?	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.
	Does organic farming affect the diversity, species richness, density, or biomass of farmland birds?	Organic farming was favourable only to skylark and lapwing, but not to overall bird density, species richness, diversity, or biomass.
$\geq$	How does temporal variation in habitat composition and weather conditions affect population dynamics of a migratory skylark population?	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.
	What is the role of density dependence in skylark population dynamics?	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.

(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).

### **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 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 springsown 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

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 seminatural 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 wintercereals 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  $250 \times 250$  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  $\times$  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 setasides, 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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### 5. References

- Aebischer, N.J., Green, R.E., Evans, A.D. 2000. From science to recovery: four case studies of how research has been translated into conservation action in the UK. In: Aebischer, N.J., Evans A.D., Grice, P.V., Vickery, J.A. (Eds.), The ecology and conservation of lowland farmland birds. British Ornithologists' Union, Tring, UK.
- Ahola, M., Laaksonen, T., Sippola, K., Eeva, T., Rainio, K., Lehikoinen, E. 2004. Variation in climate warming along the migration route uncouples arrival and breeding dates. Global Change Biology 10:1610–1617.
- Ambrosini, R., Bolzern, A.M., Canova, L., Arieni, S., Møller, A.P., Saino, N. 2002. The distribution and colony size of barn swallows in relation to agricultural land use. Journal of Applied Ecology 39:524–534.
- Andreasen, C., Stryhn, H., Streibig, J.C. 1996. Decline of the flora in Danish arable fields. Journal of Applied Ecology 33:619–626.
- Andrén, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. Ecology 73:794–804.
- Anon. 2004. Mid-term evaluation of the Horizontal Rural Development Programme. MMM:n julkaisuja (Publications of the Ministry of Agriculture and Forestry) 1/2004. (in Finnish with English summary)
- Anon. 2006. The yearbook of farm statistics 2005. Official Statistics of Finland. Information Centre of the Ministry of Agriculture and Forestry. Helsinki.
- Arnold, G.W. 1983. The influence of ditch and hedgerow structure, length of hedgerows, and area of woodland and garden on bird numbers on farmland. Journal of Applied Ecology 20:731– 750.
- Atkinson, P.W., Fuller, R.J., Vickery, J.A., Conway, G.J., Tallowin, J.R.B., Smith, R.E.N., Haysom, K.A., Ings, T.C., Asterak, E.J., Brown, V.K. 2005. Influence of agricultural management, sward structure and food resources on grassland field use by birds in lowland England. Journal of Applied Ecology 42:932–942.
- Baillie, S., Peach, W.J. 1992. Population limitation in Palearctic–African migrant passerines. Ibis 134:120–132.
- Bairlein, F., Hüppop, O. 2004. Migratory fuelling and global climate change. Advances in Ecological Research 35:33–47.
- Bengtsson, J., Ahnström, J., Weibull, A.-C. 2005. The effects of organic agriculture on biodiversity and

abundance: a meta-analysis. Journal of Applied Ecology 42:261–269.

- Bennett, A.F., Radford, J.Q., Haslem, A. 2006. Properties of land mosaics: Implications for nature conservation in agricultural environments. Biological Conservation 133:250–264.
- Benton, T.G., Bryant, D.M., Cole, L., Crick, H.Q.P. 2002. Linking agricultural practice to insect and bird populations: a historical study over three decades. Journal of Applied Ecology 39:673– 687.
- Benton, T.G., Vickery, J.A., Wilson, J.D. 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends in Ecology and Evolution 18:182–188.
- Berg, Å. 1991. Ecology of Curlews (*Numenius arquata*) and Lapwings (*Vanellus vanellus*) on farmland. PhD -thesis. Department of Wildlife Ecology, Swedish University of Agricultural Sciences. Uppsala, Sweden.
- Berg, Å. 1993. Food resources and foraging success of Curlews *Numenius arquata* in different farmland habitats. Ornis Fennica 70:22–31.
- Berg, Å. 1994. Maintenance of populations and causes of population changes of curlews *Numenius arquata* breeding on farmland. Biological Conservation 67:233–238.
- Berg, Å. 2002. Composition and diversity of bird communities in Swedish farmland-forest mosaic landscapes. Bird Study 49:153–165.
- Berg, Å., Gustafson, T. 2007. Meadow management and occurrence of corncrake *Crex crex*. Agriculture, Ecosystems and Environment 120:139–144.
- Berg, Å., Pärt, T. 1994. Abundance of breeding farmland birds on arable and set-aside fields at forest edges. Ecography 17:147–152.
- Best, L.B., Bergin, T.M., Freemark, K.E. 2001. Influence of landscape composition on bird use of rowcrop fields. Journal of Wildlife Management 65:442–449.
- Bibby, C.J., Burgess, N.D., Hill, D.A., Mustoe, S.H. 2000. Bird census techniques, 2<sup>nd</sup> edn. Academic Press, London.
- Bignal, E.M., McCracken, D.I. 1996. Low-intensity farming systems in the conservation of the countryside. Journal of Applied Ecology 33:413– 424.
- BirdLife International 2004. Birds in Europe: Population estimates, trends and conservation status. BirdLife Conservation Series No. 12. BirdLife International, Cambridge, UK.
- Bolger, D.T., Patten, M.A., Bostock, D.C. 2005. Avian reproductive failure in response to an extreme climatic event. Oecologia 142:398–406.

- Borg, C., Toft, S. 2000. Importance of insect prey quality for grey partridge chicks *Perdix perdix*: a self-selection experiment. Journal of Applied Ecology 37:557–563.
- Both, C., Visser, M.E. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Nature 411:296–298.
- Bracken, F., Bolger, T. 2006. Effects of set-aside management on birds breeding in lowland Ireland. Agriculture, Ecosystems and Environment 117:178–184.
- Bradbury, R.B., Bradter, U. 2004. Habitat associations of Yellow Wagtails *Motacilla flava flavissima* on lowland wet grassland. Ibis 146:241–246.
- Bradbury, R.B., Kirby, W.B. 2006: Farmland birds and resource protection in the UK: Cross-cutting solutions for multi-functional farming? Biological Conservation 129:530–542.
- Bradbury, R.B., Kyrkos, A., Morris, A.J., Clark, S.C., Perkins, A.J., Wilson, J.D. 2000. Habitat associations and breeding success of yellowhammers on lowland farmland. Journal of Applied Ecology 37:789–805.
- Brickle, N.W., Harper, D.G.C. 2002. Agricultural intensification and the timing of breeding of Corn Buntings *Miliaria calandra*. Bird Study 49:219–228.
- Brickle, N.W., Harper, D.G.C., Aebischer, N.J., Cockayne, S.H. 2000. Effects of agricultural intensification on the breeding success of corn buntings *Miliaria calandra*. Journal of Applied Ecology 37:742–755.
- Brickle, N.W., Peach, W.J. 2004. The breeding ecology of Reed Buntings *Emberiza schoeniclus* in farmland and wetland habitats in lowland England. Ibis 146 (Suppl. 2):69–77.
- Britschgi, A., Spaar, R., Arlettaz, R. 2006. Impact of grassland farming on the breeding ecology of an indicator insectivorous passerine, the Whinchat *Saxicola rubetra*: Lessons for overall Alpine meadowland management. Biological Conservation 130:193–205.
- Brommer, J.E., 2004. The range margins of northern birds shift polewards. Annales Zoologici Fennici 41:391–397.
- Buckingham, D.L., Peach, W.J., Fox, D.S. 2006. Effects of agricultural management on the use of lowland grassland by foraging birds. Agriculture, Ecosystems and Environment 112:21–40.
- Busche, G. 1989. Drastische Bestandseinbußen der Feldlerche *Alauda arvensis* auf Grünlandflächen in Schleswig-Holstein. Die Vogelwelt 110:51–59.
- Chamberlain, D.E., Crick, H.Q.P. 1999. Population declines and reproductive performance of Skylarks

*Alauda arvensis* in different regions and habitats of the United Kingdom. Ibis 141:38–51.

- Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C., Shrubb, M. 2000a. Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. Journal of Applied Ecology 37:771– 788.
- Chamberlain, D.E., Gregory, R.D. 1999. Coarse and fine scale habitat associations of breeding Skylarks *Alauda arvensis* in the UK. Bird Study 46:34–47.
- Chamberlain, D.E., Vickery, J.A., Gough, S. 2000b. Spatial and temporal distribution of breeding skylarks *Alauda arvensis* in relation to crop type in periods of population increase and decrease. Ardea 88:61–73.
- Chamberlain, D.E., Wilson, A.M., Browne, S.J., Vickery, J.A. 1999a. Effects of habitat type and management on the abundance of skylarks in the breeding season. Journal of Applied Ecology 36:856–870.
- Chamberlain, D.E., Wilson, J.D., Fuller, R.J., 1999b. A comparison of bird populations on organic and conventional farm systems in southern Britain. Biological Conservation 88:307–320.
- Christensen, K.D., Jacobsen, E.M., Nøhr, H. 1996. A comparative study of bird faunas in conventionally and organically farmed areas. Dansk Ornitologisk Forenings Tidsskrift 90:21–28.
- Cotton, P.A. 2003. Avian migration phenology and global climate change. Proceedings of the National Academy of Sciences of the United States of America 100:12219–12222.
- Crick, H.Q.P., Sparks, T.H. 1999. Climate change related to egg-laying trends. Nature 399:423– 424.
- Cunningham, M.A., Johnson, D.H. 2006. Proximate and landscape factors influence grassland bird distributions. Ecological Applications 16:1062– 1075.
- Cunningham, H.M., Chaney, K., Bradbury, R.B., Wilcox, A. 2004. Non-inversion tillage and farmland birds: a review with special reference to the UK and Europe. Ibis 146:192–202.
- Donald, P.F. 2004. The Skylark. T & AD Poyser, London, UK.
- Donald, P.F., Buckingham, D.L., Moorcroft, D., Muirhead, L.B., Evans, A.D., Kirby, W.B. 2001a. Habitat use and diet of skylarks *Alauda arvensis* wintering on lowland farmland in southern Britain. Journal of Applied Ecology 38:536–547.
- Donald, P.F., Evans, A.D. 1994. Habitat selection by Corn Buntings *Miliaria calandra* in winter. Bird Study 41:199–210.

- Donald, P.F., Green, R.E., Heath, M.F. 2001b. Agricultural intensification and the collapse of Europe's farmland bird populations. Proceedings of the Royal Society of London, Series B: Biological Sciences 268:25–29.
- Donald, P.F., Muirhead, L.B., Buckingham, D.L., Evans, A.D., Kirby, W.B., Gruar, D.J. 2001c. Body condition, growth rates and diet of Skylark *Alauda arvensis* on lowland farmland. Ibis 143:658–669.
- Donald, P.F., Pisano, G., Rayment, M.D., Pain, D.J. 2002. The Common Agricultural Policy, EU enlargement and the conservation of Europe's farmland birds. Agriculture, Ecosystems and Environment 89:167–182.
- Donald, P.F., Sanderson, F.J., Burfield, I.J., van Bommel, F.P.J. 2006. Further evidence of continent-wide impacts of agricultural intensification on European farmland birds. Agriculture, Ecosystems and Environment 116:189–196.
- Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R., Mearns, L.O. 2000. Climate extremes: Observations, modelling, and impacts. Science 289:2068–2074.
- Erviö, L.-R., Salonen, J. 1987. Changes in the weed population of spring cereals in Finland. – Annales Agriculturae Fenniae 26:201–226.
- Evans, A.D., Smith, K.W. 1994. Habitat selection of Cirl Buntings *Emberiza cirlus* wintering in Britain. Bird Study 41:81–87.
- FAOSTAT 2007. FAO Statistics Division 2007. http:// faostat.fao.org
- Firbank, L.G. 2005. Striking a new balance between agricultural production and biodiversity. Annals of Applied Ecology 146:163–175.
- Fuller, R.J., Gregory, R.D., Gibbons, D.W., Marchant, J.H., Wilson, J.D., Baillie, S.R., Carter, N. 1995. Population declines and range contractions among lowland farmland birds in Britain. Conservation Biology 9:1425–1441.
- Fuller, R.J., Hinsley, S.A., Swetnam, R.D. 2004. The relevance of non-farmland habitats, uncropped areas and habitat diversity to the conservation of farmland birds. Ibis 146 (Suppl. 2):22–31.
- Fuller, R.J., Trevelyan, R.J., Hudson, R.W. 1997. Landscape composition models for breeding bird populations in lowland English farmland over a 20 year period. Ecography 20:295–307.
- Furness, R.W., Greenwood, J.J.D. 1993. Birds as monitors of environmental change. Chapman & Hall. London, UK.
- Gaston, K.J., Blackburn, T.M., Goldewijk, K.K. 2003. Habitat conversion and global avian biodiversity loss. Proceedings of the Royal Society of London,

Series B: Biological Sciences 270:1293–1300.

- Genghini, M., Gellini, S., Gustin, M. 2006. Organic and integrated agriculture: the effects on bird communities in orchard farms in northern Italy. Biodiversity and Conservation 15:3077–3094.
- Gibbons, D.W., Bohan, D.A., Rothery, P., Stuart, R.C., Haughton, A.J., Scott, R.J., Wilson, J.D., Perry, J.N., Clark, S.J., Dawson, R.J.G., Firbank, L.G. 2006. Weed seed resources for birds in fields with contrasting conventional and genetically modified herbicide-tolerant crops. Proceedings of the Royal Society of London, Series B: Biological Sciences 273:1921–1928.
- Gillings, S., Fuller, R.J. 1998. changes in bird populations on sample lowland English farms in relation to loss of hedgerows and other non-crophabitats. Oecologia 116:120–127.
- González-Megías, A., Gómez, J.M., Sánchez-Piñero, F. 2007. Diversity-habitat heterogeneity relationship at different spatial and temporal scales. Ecography 30:31–41.
- Grant, M.C., Orsman, C., Easton, J., Lodge, C., Smith, M., Thompson, G., Rodwell, S., Moore, N. 1999. Breeding success and causes of breeding failure of curlew *Numenius arquata* in Northern Ireland. Journal of Applied Ecology 36:59–74.
- Green, R.E. 1984. The feeding ecology and survival of partridge chiks *Alectoris rufa* and *Perdix perdix* on arable farmland in East Anglia. Journal of Applied Ecology 21:817–830.
- Green, R.E., Cornell, S.J., Scharlemann, J.P.W., Balmford, A. 2005. Farming and the fate of wild nature. Science 307:550–555.
- Green, R.E., Tyler, G.A., Stowe, T.J., Newton, A.V. 1997. A simulation model of the effect of mowing of agricultural grassland on the breeding success of the corncrake (*Crex crex*). Journal of Zoology 243:81–115.
- Gregory, R.D., van Strien, A., Vorisek, P., Meyling, A.W.G., Noble, D.G., Foppen, R.P.B., Gibbons, D.W. 2005. Developing indicators for European birds. Philosophical Transactions of The Royal Society B 360:269–288.
- Haila, Y., Järvinen, O., Väisänen, R.A. 1979. Longterm changes in the bird community of farmland in Åland, SW Finland. Annales Zoologici Fennici 16:23–27.
- Hanski, I., Tiainen, J. 1988. Populations and communities in changing agro-ecosystems in Finland. Ecological Bulletins 39:159–168.
- Härmä, P., Teiniranta, R., Törmä, M., Repo, R., Järvenpää, E., Kallio, M. 2004. Production of CORINE2000 landcover using calibrated LANDSAT 7 ETM satellite image mosaics and

digital maps in Finland. In: IGRASS 2004, IEEE International Geoscience and Remote sensing Symposium Proceedings, 20–24 September 2004, Anchorage, Alaska, Vol. 4:2703–2706.

- Harris, S., Morris, P., Wray, S., Yalden, D. 1995. A review of British mammals: population estimates and conservation status of British mammals other than Cetaceans. Joint Nature Conservation Committee, Peterborough, UK.
- Hart, J.D., Milsom, T.P., Baxter, A., Kelly, P.F., Parkin, W.K. 2002. The impact of livestock on Lapwing *Vanellus vanellus* breeding densities and performance on coastal grazing marsh. Bird Study 49:67–78.
- Haukioja, M., Kalinainen, P., Nuotio, K. 1985. Maatalouden vaikutus peltolinnustoon. Ympäristöministeriön ympäristön- ja luonnonsuojeluosaston julkaisu A34:1–50. (in Finnish)
- Heikkinen, R.K., Luoto, M., Virkkala, R., Rainio, K. 2004. Effects of habitat cover, landscape structure and spatial variables on the abundance of birds in an agricultural-forest mosaic. Journal of Applied Ecology 41:824–835.
- Helenius, J., Tuomola, S., Nummi, P. 1995. Food availability for the Grey Partridge in relation to changes in the arable environment. Suomen Riista 41:42–52. (in Finnish with English summary)
- Henderson, I.G., Cooper, J., Fuller, R.J., Vickery, J.A. 2000. The relative abundance of birds on set-aside and neighbouring fields in summer. Journal of Applied Ecology 37:335–347.
- Hietala-Koivu, R. 2002. Landscape and modernizing agriculture: a case study of three areas in Finland in 1954–1998. Agriculture, Ecosystems and Environment 91:273–281.
- Hole, D.G., Perkins, A.J., Wilson, J.D., Alexander, I.H., Grice, P.V., Evans, A.D. 2005. Does organic farming benefit biodiversity? Biological Conservation 122:113–130.
- Holzkämper, A., Seppelt, R. 2007. Evaluating costeffectiveness of conservation management actions in an agricultural landscape on a regional scale. Biological Conservation 136:117–127.
- Hyvönen, T., Ketoja, E., Salonen, J. 2003. Changes in the abundance of weeds in spring cereal fields in Finland. Weed Research 43:348–356.
- IPCC (Intergovernmental Panel on Climate Change) 2007. Climate Change 2007: The Physical Science Basis. Summary for Policymakers. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Geneva, Switzerland. http://www.ipcc.ch
- Jenni, L., Kéry, M. 2003. Timing of autumn bird migration under climate change: advances in

long-distance migrants, delays in short-distance migrants. Proceedings of the Royal Society of London, Series B: Biological Sciences 270:1523.

- Jonzén, N., Lindén, A., Ergon, T., Knudsen, E., Vik, J.O., Rubolini, D., Piacentini, D., Brinch, C., Spina, F., Karlsson, L., Stervander, M., Andersson, A., Waldenström, J., Lehikoinen, A., Edvardsen, E., Solvang, R., Stenseth, N.C. 2006. Rapid advance of spring arrival dates in long-distance migrants. Science 312:1959–1961.
- Jonzén, N., Lundberg, P., Ranta, E., Kaitala, V. 2002. The irreducible uncertainty of the demographyenvironment interaction in ecology. Proceedings of the Royal Society of London, Series B: Biological Sciences 269:221–225.
- Kettunen, L., Mukula, J., Pohjonen, V., Rantanen, O., Varjo, U. 1988. The effects of climatic variations on agriculture in Finland. In: Parry, M.L., Carter, T.R., Konijn, N.T. (Eds.), The impact of climatic variations on agriculture, Vol. 1. Assessment in Cool Temperate and Cold Regions, Kluwer, Dordrecht, pp. 511–614.
- Kleijn, D., Baquero, R.A., Clough, Y., Díaz, M., De Esteban, J., Fernández, F., Gabriel, D., Herzog, F., Holzscuch, A., Jöhl, R., Knop, E., Kruess, A., Marshall, E.J.P., Steffan-Dewenter, I., Tscharntke, T., Verhulst, J., West, T.M., Yela, J.L. 2006. Mixed biodiversity benefits of agri-environment schemes in five European countries. Ecology Letters 9:243–254.
- Kleijn, D., Sutherland, W.J. 2003. How effective are European agri-environment schemes in conserving and promoting biodiversity. Journal of Applied Ecology 40:947–969.
- Krebs, J.R., Wilson, J.D., Bradbury, R.B., Siriwardena, G.M. 1999. The second Silent Spring? Nature 400:611–612.
- Kuemmerle, T., Radeloff, V.C., Perzanowski, K., Hostert, P. 2006. Cross-border comparison of land cover and landscape pattern in Eastern Europe using a hybrid classification technique. Remote Sensing of Environment 103:449–464.
- Legendre, P. 1993. Spatial autocorrelation: Trouble or new paradigm? Ecology 74:1659–1673.
- Lehtonen, H., Pyykkönen, P. 2005. Structural change in Finnish agriculture up to 2013. MTT:n selvityksiä 100. Agrifood Research Finland, Helsinki. (in Finnish with English summary)
- Linkola, P. 1983. Hiljainen syksy. Suomen Kuvalehti no. 34 (26.8.1983):10–15.
- Levin, G. 2007. Relationships between Danish organic farming and landscape composition. Agriculture, Ecosystems and Environment 120:330–344.
- Levin, S.A. 1992. The problem of pattern and scale in

Ecology. Ecology 73:1943-1967.

- Lichstein, J.W., Simons, T.R., Shriner, S.A., Franzreb, K.E. 2002. Spatial autocorrelation and autoregressive models in ecology. Ecological Monographs 72:445–463.
- Lundberg, P., Ripa, J., Kaitala, V., Ranta, E. 2002. Visibility of demography-modulating noise in population dynamics. Oikos 96:379–382.
- Luoto, M., Virkkala, R., Heikkinen, R.K., Rainio, K. 2004. Predicting bird species richness using remote sensing in boreal agricultural-forest mosaics. Ecological Applications 14:1946–1962.
- Matson, P.A., Parton, W.J., Power, A.G, Swift, M.J. 1997. Agricultural intensification and ecosystem properties. Science 277:504–509.
- McCulloch, M.N., Tucker, G.M., Baillie, S.R. 1992. Hunting of migratory birds in Europe: a ringing recovery analysis. Ibis 134 (Suppl. 1):55–65.
- McLaughlin, A., Mineau, P. 1995. The impact of agricultural practices on biodiversity. Agriculture, Ecosystems and Environment 55:201–212.
- Mehtälä, J., Pakkala, T., Halenius, P. 1985. Peltolinnut Vantaan Keimolassa ja Seutulassa vuosina 1973 ja 1984. Lintumies 20:182–186. (in Finnish with English summary)
- Milsom, T.P., Ennis, D.C., Haskell, D.J., Langton, S.D., McKay, H.V. 1998. Design of grassland feeding areas for waders during winter: the relative importance of sward, landscape factors and human disturbance. Biological Conservation 84:119–129.
- Møller, A.P. 1983. Changes in Danish farmland habitats and their populations of breeding birds. Holarctic Ecology 6:95–100.
- Moorcroft, D., Whittingham, M.J., Bradbury, R.B., Wilson, J.D. 2002. The selection of stubble fields by wintering granivorous birds reflects vefetation cover and food abundance. Journal of Applied Ecology 39:535–547.
- Morris, A.J., Whittingham, M.J., Bradbury, R.B., Wilson, J.D., Kyrkos, A., Buckingham, D.L., Evans, A.D. 2001. Foraging habitat selection by yellowhammers (*Emberiza citrinella*) nesting in agriculturally contrasting regions in lowland England. Biological Conservation 101:197–210.
- Morris, A.J., Wilson, J.D., Whittingham, M.J., Bradbury, R.B. 2005. Indirect effects of pesticides on breeding yellowhammer (*Emberiza citrinella*). Agriculture, Ecosystems and Environment 106:1– 16.
- Murphy, M.T. 2003. Avian population trends within the evolving agricultural landscape of eastern and central United States. Auk 120: 20–34.

- Myers, N., Mittermeier, R.A., daFonseca, G.A.B., Kent, J. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853–858.
- Newton, I. 2004a. The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. Ibis 146:579– 600.
- Newton, I. 2004b. Population limitation in migrants. Ibis 146:197–226.
- O'Brien, M., Green, R.E., Wilson, J.D. 2006. Partial recovery of the population of Corncrakes *Crex crex* in Britain, 1993–2004. Bird Study 53:213– 224.
- O'Connor, R.J., Shrubb, M. 1986. Farming and birds. Cambridge University Press, Cambridge, UK.
- Olesen, J.E., Bindi, M. 2002. Consequences of climate change for European agricultural productivity, land use and policy. European Journal of Agronomy 16:239–262.
- Olsson, O., Bruun, M., Smith, H.G. 2002. Starling foraging success in relation to agricultural landuse. Ecography 25:363–371.
- Orłowski, G. 2005. Endangered and declining bird species of abandoned farmland in south-western Poland. Agriculture, Ecosystems and Environment 111:231–236.
- Pärt, T., Söderström, B. 1999. Conservation values of semi-natural pastures in Sweden: contrasting botanical and avian measures. Conservation Biology 13:755–765.
- Pätzold, R. 1983. Die Feldlerche. Die Neue Brehm-Bücherei 323. A. Ziemsen Verlag, Wittenberg Lutherstadt, Germany. (in German)
- Peach, W.J., Lovett, L.J., Wotton, S.R., Jeffs, C. 2001. Countryside stewardship delivers cirl bunting (*Emberiza cirlus*) in Devon, UK. Biological Conservation 101:361–373.
- PECBM (Pan-European Common Bird Monitoring scheme) 2006. State of Europe's Common Birds 2005. CSO/RSPB, Prague, Czech Republic.
- Perkins, A.J., Whittingham, M.J., Bradbury, R.B., Wilson, J.D., Morris, A.J., Barnett, P.R. 2000. Habitat characteristics affecting use of lowland agricultural grassland by birds in winter. Biological Conservation 95:279–294.
- Perkins, A.J., Whittingham, M.J., Morris, A.J., Bradbury, R.B. 2002. Use of field margins by foraging yellowhammers *Emberiza citrinella*. Agriculture Ecosystems and Environment 93:413–420.
- Pitkänen, M., Tiainen, J. (Eds.) 2001. Biodiversity of agricultural landscapes in Finland. BirdLife Finland Conservation Series No. 3. Yliopistopaino,

Helsinki.

- Potts, G.R. 1986. The Partridge: Pesticides, Predation and Conservation. Collins, London, UK.
- Potts, G.R., Aebischer, N.J. 1995. Population dynamics of the Grey Partridge *Perdix perdix* 1793–1993: monitoring, modelling and management. Ibis 137 (Suppl. 1):29–37.
- Poulsen, J.G., Sotherton, N.W., Aebischer, N.J. 1998. Comparative nesting and feeding ecology of skylarks *Alauda arvensis* on arable farmland in southern England with special reference to setaside. Journal of Applied Ecology 35:131–147.
- Pykälä, J. 2000. Mitigating human effects on European biodiversity through traditional animal husbandry. Conservation Biology 14:705–712.
- Pykälä, J., Pöyry, J., Kuussaari, M., Heikkinen, R. 2004. Perinnebiotooppien kasvi- ja eläinlajisto. In: Tiainen, J. Kuussaari, M., Laurila, I.P., Toivonen, T. (Eds.), Elämää pellossa: Suomen maatalousympäristön monimuotoisuus. Edita. Helsinki, Finland. pp. 204–219.
- Rands, M.R.W. 1987. Hedgerow management for the conservation of partridges *Perdix perdix* and *Alectoris rufa*. Biological Conservation 40:127– 139.
- Ranta, E., Lundberg, P., Kaitala, V. & Laakso, J. 2000. Visibility of the environmental noise modulating population dynamics. Proceedings of the Royal Society of London, Series B: Biological Sciences 267:1851–1856.
- Rivalan, P., Frederiksen, M., Loïs, G., Julliard, R. 2007. Contrasting responses of migration strategies in two European thrushes to climate change. Global Change Biology 13:275–287.
- Robertson, J., Berg, Å. 1992. Status and population changes of farmland birds in southern Sweden. Ornis Svecica 2:119–130.
- Robinson, R.A., Wilson, J.D., Crick, H.Q.P. 2001. The importance of arable habitat for farmland birds in grassland landscapes. Journal of Applied Ecology 38:1059–1069.
- Robinson, R.A., Sutherland, W.J. 2002. Post-war changes in arable farming and biodiversity in Great Britain. Journal of Applied Ecology 39:157–176.
- Rohde, K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. Oikos 65:514–527.
- Rosenzweig, M.L. 1981. A theory of habitat selection. Ecology 62:327–335.
- Roth, A.M., Sample, D.W., Ribic, C.A., Paine, L., Undersander, D.J., Bartelt, G.A. 2005. Grassland bird response to harvesting switchgrass as a biomass energy crop. Biomass and Bioenergy

28:490-498.

- Rothery, P., Newton, I., Dale, L., Wesolowski, T. 1997. Testing for density dependence allowing for weather effects. Oecologia 112:518–523.
- Ryttäri, T., Kettunen, T. (Eds.) 1997. Uhanalaiset kasvimme. Kirjayhtymä, Helsinki. (In Finnish)
- Saari, L. 1984. The ecology of Wood Pigeon (*Columba palumbus* L.) and Stock dove (*C. oenas* L.) populations in the SW Finnish archipelago. Finnish Game Research 43:13–67.
- Sanderson, F.J., Donald, P.F., Pain, D.J., Burfield, I.J., van Bommel, F.P.J. 2006. Long-term population declines in Afro-Palearctic migrant birds. Biological Conservation 131:93–105.
- Schläpfer, A. 1988: Populationsökologie der Feldlerche Alauda arvensis in der intensiv genutzen Agrarlandschaft. Der Ornithologische Beobachter 85:309–371.
- Shrubb, M. 1990. Effects of agricultural change on nesting Lapwings *Vanellus vanellus* in England and Wales. Bird Study 37:115–127.
- Siriwardena, G.M., Crick, H.Q.P., Baillie, S.R., Wilson, J.D. 2000a. Agricultural habitat-type and the breeding performance of granivorous farmland birds in Britain. Bird Study 47:66–81.
- Siriwardena, G.M., Crick, H.Q.P., Baillie, S.R., Wilson, J.D. 2000b. Agricultural land-use and the spatial distribution of granivorous lowland farmland birds. Ecography 23:702–719.
- Söderström, B., Pärt, T. 2000. Influence of landscape scale on farmland birds breeding in semi-natural pastures. Conservation Biology 14:522–533.
- Solonen, T., Tiainen, J., Korpimäki, E., Saurola, P. 1991. Dynamics of Finnish Starling *Sturnus vulgaris* populations in recent decades. Ornis Fennica 68:158–169.
- Sotherton, N.W., Self, M.J. 2000. Changes in plant and arthropod diversity on lowland farmland: an overview. In: Aebischer, N.J., Evans A.D., Grice, P.V., Vickery, J.A. (Eds.) The ecology and conservation of lowland farmland birds. British Ornithologists' Union, Tring, UK.
- Stevens, C.J., Dise, N.B., Gowing, G., Mountford, J.O. 2006. Loss of forb diversity in relation to nitrogen deposition in the UK: regional trends and potential controls. Global Change Biology 12:1823–1833.
- Stoate, C., Boatman, N.D., Borralho, R.J., Carvalho, C.R., de Snoo G.R., Eden, P. 2001a. Ecological impacts of arable intensification in Europe. Journal of Environmental Management 63:337–365.
- Stoate, C., Morris, R.M., Wilson, J.D. 2001b. Cultural ecology of Whitethroat (*Sylvia communis*)

habitat management by farmers: Field-boundary vegetation in lowland England. Journal of Environmental Management 62:329–341.

- Stowe, T.J., Hudson, A.V. 1988. Corncrake studies in the Western Isles. RSPB Conservation Review 2:38–42.
- Stowe, T.J., Newton, A.V., Green, R.E., Mayes, E. 1993. The decline of the corncrake *Crex crex* in Britain and Ireland in relation to habitat. Journal of Applied Ecology 30:53–62.
- Suárez-Seoane, S., Osborne, P.E., Baudry, J. 2002. Responses of birds of different biogeographic origins and habitat requirements to agricultural land abandonment in northern Spain. Biological Conservation 105:333–344.
- Tapper, S.C., Potts, G.R., Brockless, M.H. 1996. The effect of an experimental reduction in predation pressure on the breeding success and population density of Grey Partridges (*Perdix perdix*). Journal of Applied Ecology 33:965–978.
- Taylor, R.L., Maxwell, B.D., Boik, R.J. 2006. Indirect effects of herbicides on bird food resources and beneficial arthropods. Agriculture, Ecosystems and Environment 116:157–164.
- Tiainen, J. 1989. Temporal changes in and spatial variation of the fauna of Finnish agroecosystems. Lammi Notes 16:1–14.
- Tiainen, J. 2001. The Finnish agricultural environments. In: Pitkänen, M., Tiainen, J. (Eds.), Biodiversity of agricultural landscapes in Finland. BirdLife Finland Conservation Series No. 3. Yliopistopaino, Helsinki, pp. 9–12.
- Tiainen, J. 2004. Maatalousympäristön historia. In: Tiainen, J. Kuussaari, M., Laurila, I.P., Toivonen, T. (Eds.), Elämää pellossa: Suomen maatalousympäristön monimuotoisuus. Edita. Helsinki, Finland. pp. 26–42.
- Tiainen, J., Hanski, I.K., Pakkala, T., Piiroinen, J., Yrjölä, R. 1989. Clutch size, nestling growth and nestling mortality of the Starling *Sturnus vulgaris* in south Finnish agroenvironments. Ornis Fennica 66:41–48.
- Tiainen, J., Pakkala, T. 2000. Population changes and monitoring of farmland birds in Finland. In: Solonen, T., Lammi, E. (Eds.), Linnut-vuosikirja 1999. BirdLife Suomi, Luonnontieteellinen keskusmuseo and Suomen ympäristökeskus, Helsinki, pp. 98–105. (in Finnish with English summary)
- Tiainen, J., Pakkala, T. 2001. Birds. In: Pitkänen, M., Tiainen, J. (Eds.), Biodiversity of agricultural landscapes in Finland. BirdLife Finland Conservation Series No. 3. Yliopistopaino, Helsinki, pp. 33–50.

- Tiainen, J., Pakkala, T., Piiroinen, J., Rintala, J., Sirkiä, J. 2001. Long-term population trends of Skylarks *Alauda arvensis* in Finland. In: Donald, P. F. & Vickery, J. A. (Eds.), The ecology and conservation of Skylarks. Royal Society for the Protection of Birds, Sandy, UK. pp. 11–24.
- Tiainen, J., Pakkala, T., Piiroinen, J., Vickholm, M., Virolainen, E. 1985. Changes of the avifauna of farmland at Lammi, southern Finland during the past 50 years. Lintumies 20:32–42. (in Finnish with English summary)
- Tiainen, J., Ylimaunu, J. 1984. Changes and status of avifauna of farmland in Finland. Lintumies 19:26–29. (in Finnish with English summary)
- Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W.H., Simberloff, D., Swackhamer, D. 2001. Forecasting agriculturally driven global environmental change. Science 292:281–284.
- Tryjanowski, P. 2000. Changes in breeding bird populations of some farmland birds in W. Poland in relation to changes in crop structure, weather conditions and number of predators. Folia Zoologica 49:305–315.
- Tucker, G.M., Dixon, J. 1997. Agricultural and grassland habitats. In: Tucker, G.M., Evans, M.I. (Eds.) Habitats for birds in Europe: a conservation strategy for the wider environment. BirdLife International (BirdLife Conservation Series no. 6), Cambridge, UK.
- Tuhkanen, S. 1984. A circumboreal system of climaticphytogeographical regions. Acta Botanica Fennica 127:1–50.
- Turchin, P. 1999. Population regulation: a synthetic view. Oikos 84:153–159.
- Väisänen, R.A. 2003. Regional population trends of 33 common bird species in Finland during 27 winters. Linnut-vuosikirja 2002:41–62. (In Finnish with English summary)
- Väisänen, R.A. 2005. Monitoring population changes of 84 land bird species breeding in Finland in 1983–2004. Linnut-vuosikirja 2004:105–119. (In Finnish with English summary)
- Väisänen, R.A., Solonen, T. 1997. Population trends of 100 winter bird species in Finland in 1957– 1996. Linnut-vuosikirja 1996:70–97. (In Finnish with English summary)
- Valkama, J. 1999. Factors affecting breeding success and behaviour in the curlew on farmland. PhD thesis, Annales Universitatis Turkuensis, Ser AII 119.
- Van Buskirk, J., Willi, Y. 2004. Enhancement of farmland within set-aside land. Conservation Biology 18:987–994.

- Van Eerden, M.R., Drent, R.H., Stahl, J., Bakker, J.P. 2005. Connecting seas: western Palearctic continental flyway for water birds in the perspective of changing land use an climate. Global Change Biology 11:894–908.
- van Teeffelen, A.J.A., Ovaskainen, O. 2007. Can the cause of aggregation be inferred from species distributions? Oikos 116:4–16.
- Vepsäläinen, V., Pakkala, T., Piha, M., Tiainen, J. 2005a. Population crash of the ortolan bunting *Emberiza hortulana* in agricultural landscapes of southern Finland. Annales Zoologici Fennici 42:91–107.
- Vepsäläinen, V., Pakkala, T., Tiainen, J. 2005b. Population increase and aspects of colonization of the Tree Sparrow *Passer montanus*, and its relationships with the House Sparrow *Passer domesticus*, in the agricultural landscapes of Southern Finland. Ornis Fennica 82:117–128.
- Vickery, J.A., Tallowin, J.R., Feber, R.E., Asteraki, E.J., Atkinson, P.W., Fuller, R.J., Brown, V.K. 2001. The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. Journal of Applied Ecology 38:647–664.
- Vickery, J.A., Carter, N., Fuller, R.J. 2002. The potential value of managed cereal field margins as foraging habitats for farmland birds in the UK. Agriculture, Ecosystems and Environment 89:41–52.
- Virkkala, R., Luoto, M., Rainio, K. 2004. Effects of landscape composition on farmland and redlisted birds in boreal agricultural-forest mosaics. Ecography 27:273–284.
- von Haartman, L. 1969. The nesting habits of Finnish birds. I. Passeriformes. Commentationes Biologicae 32:1–187.
- Wakeham-Dawson, A., Szoszkiewicz, K., Stern, K., Aebischer, N.J. 1998. Breeding skylarks *Alauda arvensis* on Environmentally Sensitive Area arable reversion grass in southern England: survey-based and experimental determination of density. Journal of Applied Ecology 35:635–648.
- Walther, G.-R., Post, E., Convey, P., Menzel, A.,

Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O., Bairlein, F. 2002. Ecological responses to recent climate change. Nature 416:389–395.

- Whittingham, M.J., Evans, K.L. 2004. The effects of habitat structure on predation risk of birds in agricultural habitats. Ibis 146 (Suppl. 2):210–220.
- Whittingham, M.J. 2007. Will agri-environment schemes deliver substantial biodiversity gain, and if not why not?. Journal of Applied Ecology 44:1–5.
- Williamson, K. 1967. The bird community of farmland. Bird study 14:210–226.
- Wilson, A.M., Vickery, J.A., Browne, S.J. 2001. Numbers and distribution of Northern Lapwings *Vanellus vanellus* breeding in England and Wales in 1998. Bird Study 48:2–17.
- Wilson, A.M., Ausden, M., Milsom, T.P. 2004. Changes in breeding wader populations on lowland wet grasslands in England and Wales: causes and potential solutions. Ibis 146 (Suppl. 2):32–40.
- Wilson, J.D., Taylor, R., Muirhead, L.B. 1996. Field use by farmland birds in winter: an analysis of field type preferences using resampling methods. Bird Study 43:320–332.
- Wilson, J.D., Evans, J., Browne, S.J., King, J.R. 1997. Territory distribution and breeding success of Skylarks *Alauda arvensis* on organic and intensive farmland in southern England. Journal of Applied Ecology 34:1462–1478.
- Wilson, J.D., Morris, A.J., Arroyo, B.E., Clark, S.C., Bradbury, R.B. 1999. A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. Agriculture, Ecosystems and Environment 75:13–30.
- Wretenberg, J., Lindström, Å., Svensson, S., Thierfelder, T., Pärt, T. 2006. Population trends of farmland birds in Sweden and England: similar trends but different patterns of agricultural intensification. Journal of Applied Ecology 43:1110–1120.