Steps towards food web management on farms

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Frans W. Smeding

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Stellingen

1. Biologische landbouwbedrijven hebben voor organismen, hoger in de voedselketen, een grotere draagkracht voor instandhouding van de biodiversiteit dan conventionele landbouwbedrijven. *Dit proefschrift.*

2. Vergroting van het voedselaanbod aan de basis van het voedselweb, is een voorwaarde om de top daarvan te vergroten, hoewel terugkoppelingen, die dit effect tegenwerken ook te verwachten zijn. *Dit proefschrift.*

3. Extra zorg van boeren voor de ecologische infrastructuur, onder meer door gericht beheer van sloten en slootkanten, heeft een sterk positief effect op de biodiversiteit van het platteland. *Dit proefschrift.*

4. De ontrafeling van het menselijk genoom is belangrijk, omdat dit onderzoek de veronderstelde bepalende rol van genen in levende systemen relativeert. *Stephan Jay Gould in NRC Handelsblad d.d. 20 maart 2001.*

5. De oorspronkelijke ideeën van de biologische landbouw zijn door wetenschappers eerst als 'subjectief' afgedaan, maar worden gestaag ontdekt als bruikbaar en 'objectief'.

6. Ecologisch onderzoek moet uitgaan van niet-begrepen waarnemingen in het veld en moet de uitbreiding van de theorie daaraan dienstbaar maken, in plaats van deze voorop te stellen.

7. Wageningen Universiteit stoot studenten af door retorische vragen en technisch vernuft, en zou studenten aantrekken door het tonen van twijfel en zorg over actuele problemen in de landbouw.

8. Het op steeds jongere leeftijd aanspreken van rationele vermogens van kinderen leidt tot vervreemding van de levende omgeving en asociaal gedrag.

Stellingen bij het proefschrift van Frans W. Smeding, *Steps towards food web management on farms*, 6 juni 2000

To my father and mother
who nurtured my interest and love
of nature and the countryside

and in memory of
Peter A. van der Werff (1949-1996)
who greatly encouraged me in this work

Preface

"Our attention is drawn by a blackbird screaming. It is January 28th and I am writing this thesis. I look through the bedroom window with my wife and four-year-old son and we watch a sparrow hawk with a blackbird in his claws. And I guess that his victim is "vlek" ("spot" in English), the female blackbird with one white feather on top of each shoulder, that lives around our house. Impulsively I ran downstairs, through the front door in an attempt to rescue the blackbird; but the sparrow hawk flies away carrying, of course, its prey".

That evening I felt a bit confused about this event. How could a biologist studying food webs, interfere with the hunt of an impressive bird of prey? Perhaps it helped me to realise more profoundly that trophic interactions are not figures but have to do with life and death. Then I remembered an intriguing story from the Hindu epic Mahabharata, which tells of a righteous king who protected a frightened dove from a pursuing falcon. The falcon begged the king to let him eat and warned the king that his interference with 'Dharma' (perhaps 'natural order', in this thesis) would create fate. However, the king stuck to his principles and promised the falcon a quantity of his own flesh that equalled the weight of the dove. Eventually the king was eaten to the bones and both the falcon and the dove laughed at the king and flew away.

Although the Mahabharata story is mysterious to me, it raises an association that I have wanted to put into the preface of this thesis. It considers that there is no doubt that man, as part of nature, should interfere in ecosystems to feed himself. However, if his interference goes beyond his proper needs, and are, so to say, 'none of his business', he may not really know what he is doing and may therefore unwittingly disturb the natural order. Thus the work of modern biologists like Rupert Sheldrake convinced me that current biology has a limited comprehension of living systems. A 'righteous ecologist' (who is for example interfering with food webs) should, therefore, remain modest, whilst keeping an open mind and an open eye, both when looking at nature and at his own motives. This might help to prevent his worst errors. Fortunately that afternoon my attempt to interfere with the hunting sparrow hawk failed, because I would not have known how to care for a severely wounded blackbird.

The small maps of the Flevoland polder in this thesis have a special meaning to me, because they echo the large embroidered map of the Noordoostpolder that hung on the wall of the dining room when I was a child. My grandfather devoted his professional life to polder reclamation. His polder service employed outstanding ecologists like W. Feekes and D. Bakker, who were engaged on both applied and fundamental questions, which was much appreciated by my grandfather (so my father told me). However the aims of reclamation concentrated on the material concerns of food and labour, reflecting needs of society at that time and resulting in large scaled rational landscapes. Following this tradition my father contributed to the development of agricultural education. It is my sincere and modest wish that my current work may contribute to the implementation of a wider scope of agricultural production, and address the physical as well as the emotional and spiritual needs.

Without the support of many people, this thesis would never have been accomplished. I am grateful to:
My promoter Eric Goewie who gave me space and confidence to begin the project, and who strengthened my backbone and inspired me in moments of hesitation. My promoter Ariena van Bruggen who, after her arrival in Wageningen, needed only a half word to understand the contents of the work and helped me to process the piled-up field data. My co-promoter Wouter Joenje, with whom I share common interests in ecological theories and field biology, particularly of pioneer successional stages and the polders.

The funding organisation (LNV-DWK) for supporting a small research group so that they could embark upon a project with an uncertain outcome. However this research group was much strengthened thanks to the invaluable co-operation and friendship of the researchers of Plant Research International (formerly IPO-DLO): Kees Booij, Clasien Lock and Loes den Nijs.

The supervision committee of the project 'Food web management on farms', that enthusiastically guided the research by it's reflections on our plans and results. The committee included: Geert de Snoo (CML-Universiteit Leiden), Frank van Belle (Vereniging Natuurmonumenten), Paul Aukes (IKC Natuur), Paul van Ham (IKC Landbouw), Tibbe Breimer (LNV-DWK), as well as Kees Booij, Wouter Joenje (the chairman) and Eric Goewie.

My research assistant, André Maassen, who was a pillar of strength with all our laborious activities, the designer of instruments and forms, companion of the hundreds of kilometres walked while data collecting, and the one who could, if asked, always help me remember the aims of my work.

The MSc students who did reconnaissance work for the thesis: Elke Boesewinkel, Jacinta de Huu, Nathalie Reijers, Julien Cothenet, Edwin Coomans, Hong Nan, and in particular Bart Venhorst who also supported the field work and insect identification.

People with whom I exchanged ideas or who provided valuable information that contributed to this thesis: Gerard Oomen, Willem Beekman, Jan Diek van Mansvelt, Sjaak Wolfert, Dorine Dekker, Derk Jan Stobbelaar, Karina Hendriks, Darko Znaor, Prof. R.A.A. Oldeman, Ruurdtje Boersma, Manolis Kabourakis, Anor Fiorini, Hans Esselink (who named 'Voedselwebbeheer'), Joop Schaminée, John Vandermeer, Yvette Perfecto, Julian Park, Nigel Boatman, Flip van Koesveld, Jan Jaap van Almenkerk, Wolter van der Kooij, Rob Boeringa, Henk Kloen, Yvonne van den Hork, Monique Bulle, members of the PE-Phd discussion group 'Plant and Crop Ecology', Paula Westerman, Eefje den Belder, Walter Rossing.

The farmers who allowed me access to their farms and who gave their time to answer my questions; in particular, especial thanks are due to Maart en Piet van Andel, Carl en Rini Ferket, Jan en Marleen van Woerden-Zeelenberg, Lex en Jannie Kruit, Henk Leenstra, Evert-Jan Rienks, Jansje Timmermans, Douwe Monsma, Hem and Marjon Cuppen, staff and residents of 'Thedinghsweert' for their hospitality and interest.
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And last but not least my dear friends and family who supported and encouraged me, and with some of whom I could share my aspirations: Annelies, Francis, Philip, my brother Guido, my uncle Kees Cleveringa; but most of all, Elise and Timo who gave me warmth at the coldest moments of my personal 'Winterreise'.

Abstract

This paper is the report of four years of research on the functional group composition of the animal community in relation to farm and ecological infrastructure (E.I.) management on organic arable farms. The results are mainly based on abundance data of ground dwelling arthropods obtained by pitfall trapping, density data of vegetation dwelling arthropods by vacuum sampling and density data of insectivorous birds by territory mapping. Arthropods were collected in wheat crops (representing the crop area) and on the adjacent canal bank (representing the E.I.); the bird, farm and E.I. variables were measured at the farm level. Study areas included in total 18 farms with varying extents of organic duration, crop rotation intensity, and quantity and quality of E.I.

The hypothesis of the research was that the food web structure of an organic arable farm with long organic duration as well as with an improved E.I. (*i.e.* enlarged, late mown), would show a higher abundance of meso- and macrofauna of both herbivorous and detritivorous functional groups. These enhanced primary groups were expected to carry a high predator abundance at both secondary (*i.e.* invertebrates) as well as tertiary (*i.e.* birds) levels. With regard to the crop areas it was found, in contradiction to the hypothesis, that herbivores were most abundant in crop areas of recently converted farms and of organic farms with intensive crop rotation; this herbivore abundance was associated with invertebrate predator abundance and species diversity. In accordance with the hypothesis, some evidence was found for increased detritivore and related epigeic predator abundance related to extensive crop management on the farms of long organic duration. Whilst studying the E.I., an increased abundance of vegetation dwelling predators and also detritivores was found in improved E.I. However K-herbivore numbers did not increase in the improved E.I. when they were compared to the traditionally managed E.I. The summer abundance of epigeic predators was also not related to an improved E.I. Field studies provided some evidence for the dispersal of functional groups, abundant in the E.I., towards the crop area. However, the effects of crop conditions on the arthropod abundance in the crop area were observed to offset the influence of the E.I. Bird studies at the farm level revealed positive correlation between bird functional groups and a combination of crop area and E.I. characteristics. Bird density was found to be positively associated with high arthropod abundance in the E.I. vegetation canopy. Observations also suggested positive correlation to an increased herbivory in the crop area of the long duration organic farms that had an intensive crop rotation.

A proposal for a descriptive or topological farm food web is drawn from field observations as well as from references in literature. Predictions are made for four different farm food web structures that express four extremes of two environmental gradients, which correspond to the length of organic duration and the amount/quality of the E.I. With reference to field observations important themes in the food web theory are discussed, including the indirect effects of subsidised detrital food chains on herbivore abundance and consequently on bird abundance, as well as the possible effects of intra guild predation on arthropod functional group composition.

The implications of the study are that organic duration and the amount/quality of the E.I. may contribute to improving ecosystem services and to aims based on nature conservation. However an optimisation of the farm food web with regard to ecosystem services may not necessarily improve nature conservation values. It is argued that increased understanding of the farm food web and its management is likely to support the development of multi-species agroecosystems that integrate improved ecosystem services and nature conservation goals.

Notes

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Chapters 2, 3, 4 and 6 have been submitted for publication in international journals.

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Chapter 1: General introduction

This thesis is motivated by concerns about biodiversity loss, due to agricultural intensification (Altieri, 1994, 1999; Paoletti, 1999; Wood & Lenné, 1999; Vandermeer *et al.*, 1998) and is primarily concerned with plant and animal species indigenous to agricultural landscapes. Biodiversity loss has been thought to result in artificial ecosystems, requiring constant human intervention and costly external inputs. From this perspective biodiversity has economical value, related to its ecological services, *e.g.* pest control and biotic regulation of soil fertility (Altieri, 1994, 1999; Pimentel *et al.*, 1995). Nature conservation worthy species may have no evident significance for the functioning of agroecosystem (Duelli *et al.*, 1999). However it can be argued that agriculture has, to a certain extent, responsibility for all species and communities which co-evolved with farming during around 10,000 years (Wood & Lenné, 1999), irrespective of their utility.

One important solution for the reversal of biodiversity loss in conventional agriculture of industrialised countries is the development of farming systems that are economically based on utilisation of biodiversity and that also harbour conservation worthy species. This idea is compatible with the concept of multi-species agroecosystems (Vandermeer *et al.*, 1998; Altieri, 1994, 1999; Almekinders *et al.*, 1995; Swift & Anderson, 1993). Development of organic farming systems is a possible implementation of this concept (Stobbelaar & Van Mansvelt, 2000; Vandermeer, 1995; Van der Werff, 1991). The adoption of this concept in the crop area may be complemented by an appropriate management of the semi-natural habitat on the farm, which is defined as the ecological infrastructure (E.I.) (Smeding & Booij, 1999).

A food web approach is an appropriate method for investigations into the higher integration levels of ecosystems (Polis & Winemiller, 1996; Pimm, 1991; Gezondheidsraad, 1997). This approach is therefore suitable for farming systems research. Progress in scientific understanding of food webs is currently expanding into agroecology as is demonstrated by articles on interactions between detrital and herbivore subsystems (Brussaard, 1998; Wise *et al.*, 1999) and among predator functional groups (Tscharntke, 1997). These interactions may affect the abundance of functional groups, crop performance as well as decomposition rates. Complementary to functional analysis, a food web approach might also offer a comprehensive framework for the scattered information on farmland species and habitats (De Snoo & Chaney, 1999).

A simplified set of hypotheses with regard to food web structure on organic farms served as the starting point for the field research of this thesis: it was expected that the duration of organic management, extensive crop rotation as well as an improved E.I. (*i.e.* enlarged area and late mowing date), would relate positively to the abundance of non-pest primary arthropod functional groups (Kromp & Meindl, 1997): the detrital web would be enhanced by the increased input of organic matter, consisting of organic manure, compost and crop residues (of cereals, ley pasture); non-pest herbivore numbers would be enhanced by crop diversity as well as weed diversity (Hald & Reddersen, 1990) and in particular would be boosted by the varied plant tissues (Curry, 1994; Tscharntke & Greiler, 1995) which occur in improved E.I. Consequently predator and parasitoid numbers on the farm would be supported. An accumulated high invertebrate density on the farm would support insectivorous vertebrates, particularly birds (*e.g.* Poulsen *et al.*, 1998).

The objectives of this thesis were:

- To analyse and conceptualise food webs on organic arable farms that encompass the important above- and below ground functional groups and that can be related to farmers' decisions about, for example, crop rotation and manure management, farm lay-out and field margin management;
- To link knowledge of the biology of groups of individual species, crop and vegetation management to food web theories, and to identify possible food web mediated factors that might influence the abundance of functional groups on the farm;
- To suggest strategies for development of farming practices that strive to promote ecological services and conservation of species.

To meet the objectives, field research and analysis of literature data were undertaken. The study area involved organic arable farms that were mainly situated in Flevoland. This region was chosen because of its uniformity in topography and history and because of the occurrence of around 75 organic farms including farms with improved ecological infrastructure, resulting from a prototyping research project (Vereijken, 1997, 1998).

Empirical investigations were concentrated on particular sections of the farmland community. Functional group compositions (*e.g.* detritivores, herbivores and predators) within these sections were assessed. All three empirical chapters start from the same initial set of hypotheses explained above, and reflect to a certain extent on each other in their discussions. Observations on vegetation dwelling arthropods on thirteen farms (Chapter 2) are presented first, because this section included large proportions of all three major functional groups, involving especially herbivores and connected predators.
Observations on ground dwellers on eight farms (Chapter 3) included numerous epigeic predators that are supposed to hold a key position in the farm food web. However this group appears to be more strongly related to the detrital subweb than to the herbivore subweb.
Densities of bird territories on ten farms (Chapter 4) are related to variables of both vegetation dwelling and ground dwelling arthropods as well as to farm and ecological infrastructure traits. Birds represent vertebrates, that might be supported by an increased abundance of prey from the herbivore subweb as well as the detrital subweb.

Chapter 5 includes a landscape comparison between a young polder landscape (*i.e.* Flevoland) and a landscape that has been farmed for many centuries (*i.e.* river region). This explorative study places the observations in Flevoland into a broader geographical context.

A proposal for a descriptive or topological farm food web (Chapter 6) is drawn from field observations as well as from references in the literature. Important themes in the food web theory are tentatively applied to this preliminary model, explaining differences between local farm food web structures and how they are related to farm and/or E.I. management. The initial set of hypotheses on which the fieldwork was based, is modified into more elaborate hypotheses.

An additional chapter (Chapter 7) deals with plans for the coexistence of farm and natural life. It presents a pragmatic advisory instrument that structures expert judgement. The instrument is based on a combination of ecological theory and field biology. However results of the food web study are not included since the instrument (Smeding, 1995) was developed earlier and was therefore an incentive to the food web studies of this thesis.

The discussion chapter (Chapter 8) considers briefly the implications of the research for the development of multispecies farming systems.

It must be noted that compared to the chronology of the investigations, chapters 2-5 are in reverse order. The project started with an assessment of farms in different landscapes (1997). However the study area included too much variation and too few sites to be analysed statistically. Therefore investigations in the following year (1998) were confined to a more uniform area in Flevoland. However the relations between ground dwelling functional groups and the farm and E.I. variables were, at first glance, difficult to interpret and showed little coherence with the bird data. The herbivore subweb of the farm food web was expected, and was also found, to give better distinctions, with regard to investigated variables. Consequently vegetation dwelling arthropods were assessed in 1999.

Chapter 2: Functional group compositions of vegetation dwelling arthropods in relation to ecological infrastructure and time since conversion to organic farming

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Abstract

Hypotheses on the relation of farm management and ecological infrastructure (E.I.) characteristics to the functional group composition of vegetation dwelling arthropods in the crop and E.I. were tested on organic arable farms. The study area included 13 farms that varied with regard to the studied traits. Arthropods were collected by vacuum trapping in wheat crops and adjacent boundaries. Observations in the crop area suggested that both organic duration and farm 'intensity' affect the arthropods. In contrast to expectations from the literature, K-herbivores and associated predators were most abundant in the luxurious crops of recently converted farms. Long duration organic farms with an intensive management, seemed to be most prone to r-herbivore outbreaks, associated with species-diverse but not numerous predators. In support of the expectations, some evidence was collected for an increase of detritivores on long duration farms with an extensive crop rotation. Observations in the E.I. showed that, according to the expectations, improved management (*i.e.* large area and late mowing) enhanced predators and also detritivores. However, herbivore abundance was similarly high in traditionally managed E.I. Effects of high abundance of arthropod functional groups in the E.I. on dispersal into the crop, were largely offset by crop conditions. Possible indirect effects of subsidized detrital food chains on herbivore abundance, as well as effects of intraguild predation on arthropod functional group composition, are discussed with reference to field observations.

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1. Introduction

1.1. Agriculture and biodiversity

The biodiversity of farms and agricultural landscapes in industrialised countries has decreased dramatically (*e.g.* Andreassen *et al.*, 1996; Fuller *et al.*, 1995; Aebischer, 1991). This biodiversity-loss is a matter of great concern for ecologists, agriculturists as well as politicians (Paoletti, 1999; Wood & Lenné, 1999). To reverse this trend of biodiversity-loss, farming system innovation is probably needed (Altieri 1994; Vandermeer *et al.*, 1998; Almekinders *et al.*, 1995; Swift & Anderson, 1993). One of the options to enhance biodiversity is to promote on-farm natural areas that could be valuable for both production as well as for nature conservation aims.

The total area of semi-natural habitat on the farm is also called the 'ecological infrastructure' (E.I.). Field margins are a major constituent of the E.I. (Smeding & Booij, 1999). Agricultural production could be enhanced by various ecological functions of this E.I., such as regulation of pests by predators and parasitoids, nutrient cycling by soil organisms, and pollination by various arthropods. For example, biodiversity of arable field margins significantly contributed to densities on the farm of predatory invertebrates, butterflies, birds and mammals (*e.g.* Boatman *et al.*, 1999; Joenje *et al.*, 1997; LaSalle, 1999).

1.2. Farm management and on-farm communities

Despite the increasing amount of information on farmland species and vegetation, there is still fragmentary knowledge of the relationships between farm management practices and farm communities (De Snoo & Chaney, 1999). For example, crop rotation, fertility level, weed control, field size, and distribution and management of field margins may all affect farm community composition.

Management practices on organic farms corresponding to production guidelines 2092/91 in the EC countries (Anonymous, 1991) are essentially different from those on conventional farms. In particular, maintenance and promotion of biodiversity is inherent to the philosophy of organic farming. Therefore, organic farms could function as a stepping stone on the road to developing rational, biodiverse farming systems (Stobbelaar & Van Mansvelt, 2000). However, information on the trophic structure of animal communities at the farm level is still scattered and incomplete for conventional as well as organic farming systems (*e.g.* Kromp & Meindl, 1997; Isart & Llerena, 1995). Both empirical and experimental research at the farm level is required to fill the gaps in the knowledge of effects of conversion from conventional to organic farming and of field margin management practices on agroecosystem community composition.

Research addressing the whole 'biocoenosis' is needed to understand the effects of management practices on agroecosystem functioning (Büchs *et al.*, 1997). Recent advances in research of food webs (Polis & Winemiller, 1996), including some studies in agricultural habitats (De Ruiter *et al.*, 1997; Tscharntke, 1997; Wise *et al.*, 1999), are providing inspiring examples of how (agro)ecosystems can be approached at integration levels higher than the species-level. Some of this research indicates that food webs can mediate the effects of environmental stress factors on species (Winemiller & Polis, 1996).

1.3. Hypotheses and objectives

Detritivore numbers are enhanced by the increased organic matter input, involving organic manure, compost and crop residues (of cereals, and ley pasture)(*e.g.* Pfiffner & Mäder, 1997; Weber *et al.*, 1997; Idinger *et al.*, 1996; Heimbach & Garbe, 1996). Non-pest herbivores are enhanced by crop and weed diversity (Hald & Reddersen, 1990; Moreby & Sotherton, 1997; Andow, 1988). Moreover, the effects of organic duration may continue to work cumulatively over years, with regard to both detritivores (Idinger & Kromp, 1997) as well as herbivores (Hald & Redderson, 1990). The abundance of primary functional groups would support predacious functional groups of *e.g.* epigeic predators (Kromp, 1999; Wise *et al.*, 1999), predacious flies and parasitoids (Idinger & Kromp, 1997). The increase of predator abundance may subsequently depress pest-herbivores (Altieri, 1994), provided that crops are not too much affected by herbivores (Van Emden, 1988). Based on these observations, we hypothesise that farms that have been organic for many years, have higher densities of non-pest primary functional groups (both detritivores and non-pest herbivores) and their predators in the crop area than farms that were converted recently.

Additionally we hypothesise that appropriately managed E.I. will support large numbers and diversity of non-pest herbivores, predators and parasitoids both in field margins and crop areas. An increased variety in plant tissue quality and a more varied vegetation structure are assumed to be key factors (Curry, 1994; Feber *et al.*, 1999). Also mown grass strips, less complex than most other boundary habitats, contribute to resources for these groups (Barker *et al.*, 1999; De Snoo & Chaney, 1999). An increased amount and spatial density of E.I.

affects the populations in the adjacent crop area, involving both herbivores (Holland & Fahrig, 2000) and predators (Lys & Nentwig, 1992; Sunderland *et al.*, 1996a). In addition to organic duration, crop rotation intensity and E.I. characteristics (with regard to quantity and diversity), other farm management factors are expected to influence the functional group composition of vegetation dwelling arthropods. For example the effects of the studied factors may be offset or enhanced by crop performance. To take these influences into account some crop variables, indirectly related to variables central in the hypotheses, are also included in the study.

However, the above-stated hypotheses about the effects of organic farming duration and E.I. management on vegetation dwelling arthropod functional groups have not been tested so far. Thus, the objectives of this study were:

1. to determine the density and diversity of vegetation dwelling arthropod functional groups in the crop area and semi-natural field margins on organic farms, and relate the density and diversity of these groups to crop area and ecological infrastructure characteristics;
2. to determine if there are distinct species compositions of vegetation-dwelling arthropod functional groups among farms differing in crop area and ecological infrastructure traits;
3. to relate abundance and diversity of vegetation arthropod functional groups to the distance from the ecological infrastructure.

Our study was focused on vegetation dwelling arthropods because this group comprises both detritivores, herbivores, predators and parasitoids. In many studies the herbivore subweb is not well represented, particularly when pitfalls are used, which primarily collect epigeic predators (Duelli *et al.*, 1999).

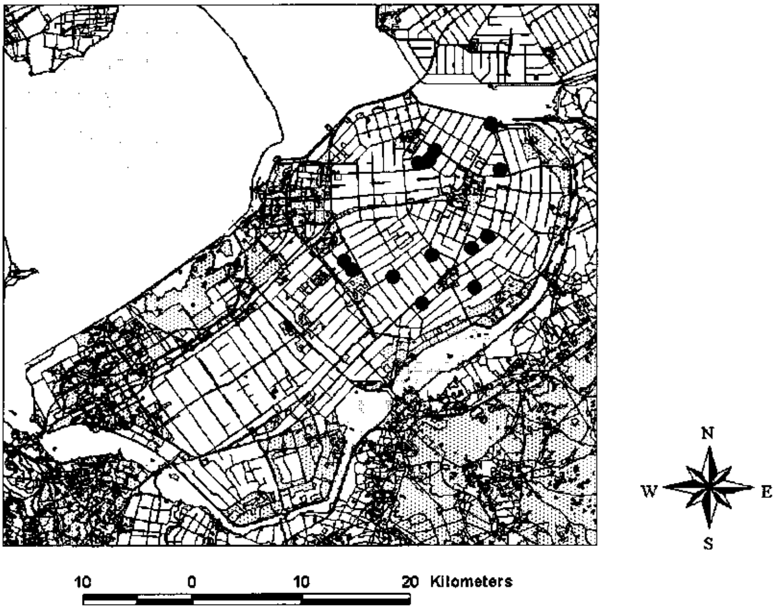

Fig. 1. Study area. The investigated organic arable farms are represented by closed circles.

2. Materials and methods

2.1. Study area

The study was done on organic farms and one integrated farm in the province of Flevoland, The Netherlands. The farms are located within a 280 km^2 area in the polder Oostelijk Flevoland (Fig.1). This polder was reclaimed in 1954 and is dominated by agricultural landuse. The soil is a calcareous clay of marine origin. Flevoland was chosen as a study area because it has a concentration of 75 organic arable farms that are similar with regard to their history and topography.

In the study area 13 farms were selected that differed in various farm structure and ecological infrastructure (E.I.) traits (Table 1). Together the farms comprised 656 ha arable land. The selection included eleven commercial organic farms and two experimental farms. Three of the selected arable commercial farms reared livestock which were fed on home produced fodder in the winter, but were grazed elsewhere during the rest of the year (farms T, K and S). The experimental farms of Wageningen University (farms E and I) are mixed dairy and arable farms; farm E is organic and farm I is integrated. Farm I is divided into two parts by a road and only the northern part was included in the study area. Three commercial farms (T, L and S) were Ecological Arable Farming Systems (EAFS) prototype farms during 1992-1997 (Vereijken, 1997, 1998).

2.1.1. Crop area characteristics

The organic duration of the selected farms ranged from one to sixteen years. Ploughing is generally at 25-30 cm depth. On all the farms a 6-7 year crop rotation is maintained, including per farm 11-41% cereals, 0-18% ley pasture, 12-43% traditional lifted crops (potatoes, sugar beet) and 25-67% vegetable crops. The vegetables grown were mainly onions, peas, sweet corn, various cabbages, and runner beans. The farms with the most intensive crop rotations had up to 60% vegetables and therefore a lower percentage (<20%) of gramineous crops (cereals, and ley pasture). Because the input of nutrients (N,P,K) has to be adjusted to crop requirements, and vegetables need more nutrients than cereals, intensity of crop rotation is assumed to relate to the amount of N application at the farm level. Compared with other crops, gramineous crops provide a large amount of carbon in crop residues and require few soil disturbing operations.

2.1.2. Ecological Infrastructure characteristics

The Ecological Infrastructure (E.I.) of arable farms in Flevoland is mainly determined by canals and banks (together c. 3-4 m width), that are laid out as linear herbaceous boundaries adjacent to the crops. On five farms, boundaries are wider because of adjacent (2-3 m wide) grass strips, often including clovers (*Trifolium* spp.), on one or both sides of the canals. Farm E also has grass strips between crop plots. Percentages of E.I. higher than c. 2% (Table 1) were mainly due to the presence of these grass strips. Only farms L and E possessed a boundary planted with a hedgerow. Spatial density of E.I. is purposefully increased on farm E (Smeding & Joenje, 1999) and farm L. The spatial arrangement of E.I. on the other 6 farms mainly reflects landscape scale.

Extreme types of vegetation management are:

- 'traditional management' involving three or four more cuts per year with a flail mower leaving the shredded cuttings *in situ*;
- 'late mowing management' involving one or two cuts per year after June 21st with a finger-bar mower with hiab grab for removal of cuttings.

The grass strips along the canals in 'late mowing management' are required for transport. The E.I. area is, therefore, related to the mowing date. In this article the E.I. with enlarged area and late mowing is defined as 'improved E.I.'. The improved E.I. on the four farms A, T, L, and D was created during the EAFS-prototyping research program in 1992-1997 (Vereijken, 1997, 1998). The improved E.I. on the experimental farm E started in 1995 simultaneously with conversion of the conventional dairy farm to an organic mixed farm (Smeding & Joenje, 1999).

Table 1
The characteristics of the farm, the wheat crop and the ecological infrastructure (E.I.) on the thirteen selected farms.

		Duration of organic farming	% Semi-natural habitat (E.I.)	% Gramineous crops	Cover of wheat crop	Cover of under story	Species number under story	Date of fisrt mowing E.I.	Cover of vegetation in E.I.	Species number E.I.
	Variable:	**dur**	**area**	**int**	**ccov**	**ucov**	**uspn**	**mow**	**eicov**	**eispn**
	unit:	year	%	%	%	%	n/m^2	month	%	n/m^2
Farm:	level/habitat:	farm	farm	farm	crop	crop	crop	E.I.	E.I.	E.I.
K	organic, arable	16	1.8	30	71	28.6	1.8	5	64	2.1
J	organic, arable	11	4.4	26	64	7.1	4.0	6	92	4.4
S	organic, arable	11	3.2	35	76	7.5	2.7	7	89	5.8
L	organic, arable	11	3.1	18	66	7.8	3.1	7	88	5.1
O	organic, arable	11	1.1	50	73	5.1	4.4	6	89	4.9
T	organic, arable	9	2.3	31	69	9.4	2.7	9	92	4.2
F	organic, arable	8	1.4	35	28	2.3	2.6	5	73	2.7
E	organic, mixed	5	4.5	55	86	16.4	3.6	11	97	5.1
B	organic, arable	2	1.4	17	86	0.3	0.4	5	91	4.4
R	organic, arable	2	1.2	11	63	25.6	3.6	5	76	3.2
H	organic, arable	1	1.5	27	78	5.7	1.3	5	96	4.0
Z	organic, arable	1	1.2	17	79	0.0	0.2	5	90	3.4
M	integrated, mixed	0	2.0	65	87	1.7	1.6	5	68	6.2

Dominant plant species in canal bank swards were: couch (*Elymus repens*), perennial meadow grasses (*Festuca rubra*, *Poa trivilais*, *Lolium perenne*, *Agrostis stolonifera*), common reed (*Phragmitis australis*) and a few perennial herbs: dandelion (*Taraxacum officinale*) and stinging nettle (*Urtica dioica*). Canals with traditional management have a low, relatively open, species poor vegetation (<10 species/4 m^2), dominated by a few grass species. Late mowing particularly related to increased vegetation biomass in June and July as expressed by vegetation height (up to 1-3 m) and cover (up to 90-100%). However late mowing does not necessarily relate to increased higher plant species diversity for two reasons: a) tall grass species may dominate the sward; b) swards of traditional management may locally be cut to ground level and therefore be invaded by ruderals and annuals (increased species number up to 15 species/4 m^2), *e.g.* thistles (*Cirsium arvense*, *Sonchus arvensis*), annual weeds (*e.g. Sonchus asper*, *Polygonum aviculare*) and annuals that are rarely pernicious weeds in Flevoland (*e.g. Myosotis arvensis*, *Veronica persica*, *Cardamine hirsuta*).

High perennial plant diversities found in some locations may relate to various interrelated factors: reduced vegetation productivity, removal of the hay, nutrient buffering by the grass strip, and long organic duration. However, also, artificial species introduction is involved; in the EAFS-project, around 90 different native perennial dicots were artificially seeded in the canal banks to obtain higher plant diversity and flower abundance of plants with limited dispersal capacity (Vereijken, 1998). Although few species were able to settle well (*e.g. Senecio jacobea, Crepis biennis, Heracleum sphondylium*), the introduction clearly affected species diversity: vegetation including sites with >15 species/4 m^2 were confined to prototype farms.

2.2. Sampling and measurements

2.2.1. Arthropods

Sampling of arthropods was done in wheat crops and in adjacent canals banks (E.I.). Spring wheat (*Triticum aestivum* L.) was chosen as a representative crop as this crop is common on organic arable farms in Flevoland and arthropod numbers in cereals are large compared to numbers in other common crops like potatoes and onions (Booij & Noorlander, 1992). Within one wheat field on each of the 13 farms one 50×30 m sampling area was selected; this area was 50 meter long bordering a canal by 30 m perpendicular to that canal. Nine plots of 1 m^2 at distances of 0 m (E.I.), 10 m (wheat) and 30 m (wheat) from the canal bank were selected for measurement of arthropods, crop, weed and E.I.-vegetation variables.

Distance from the top of the canal bank to the crop edge of the wheat could vary between farms, due to the occurrence of grassy strips (farms T, L, S, E, I, J), a sterile strip (H), a recently drilled flower strip (F) or a transport track (O). Sampling was done once, in the period from the 7th of June until the 6th of July, following the methods of Reddersen (1997) and Moreby & Sotherton (1997).
Vegetation dwelling arthropods were collected by means of a vacuum sampler (ES 2100, Echo Lake Zurich, U.S.A.) for 120 s in each 1 m^2 sampling area. The air flow of this sampler was 8.5 m^3 in a sampling area of 0.01 m^2, which corresponds to the air flow of the apparatus recommended by MacLeod *et al.* (1995). A net (pore size: 0.8×0.8 mm^2) was inserted in the suction tube. A square of 1 m^2 area and 0.4 m high, made of four multiplex boards, was placed in the vegetation before switching on the sampler.

The samples were put in a plastic bag, transported in a cool box and stored in a deep freeze (-20 °C). Samples were cleaned in the laboratory. Litter was removed and soil was washed away with water in a sieve (pore size: 1×1 mm^2). Slugs and snails (Gastropoda) and springtails (Collembola) were discarded because vacuum sampling is not effective for quantification of these groups (Potts & Vickermann, 1974). Arthropods were stored in 95% alcohol. Individuals were sorted to taxa at order- or family-level and placed into five different arthropod functional groups:

- Detritivores, including mainly adult diptera that have detritivorous larvae, and woodlice (Isopoda);
- K- or senescense feeding herbivores (White, 1978) that feed on mature plant tissues with high C/N ratios and tend to have a slower development, larger body size (Crawley, 1983) and defensive traits (Power *et al.*, 1996). Herbivores which are an important constituent of 'chickfood' for farmland birds (Moreby *et al.*, 1994), like sawflies, lepidopteran larvae, hoppers, bugs, leaf beetles, weevils and grasshoppers belong to this group;
- r- or flushfeeding herbivores (White, 1978) that feed on young tissues with low C/N ratios and low fibre content (White, 1978). They generally have a small body size, fast development and good dispersal abilities. For reasons of simplicity, r-herbivores were

represented by only *Aphididae*; in few available studies on organic crop communities (Kromp & Meindl, 1997), aphids corresponded most clearly to the definition;

- Predators including both polyphagous and oligophagous species;
- Parasitoids, almost exclusively represented by *Parasitica* (Hymenoptera).

Extra efforts were made to identify Diptera to the family-level (key: Unwin, 1981) because Diptera occurred in large numbers and involved large proportions of all three detritivores, herbivores and predators (Frouz, 1999; Weber *et al.*, 1997).

2.2.2. Crop and E.I.-vegetation

In each 1 m^2 plot in wheat fields, visual estimations were made of crop cover (*i.e.* % cover of soil surface by vertical projection) and under story vegetation cover. The under story included arable weeds and/or undersown grass (*Lolium perenne*) and/or clovers (*Trifolium pratense* or *T. repens*). The species of the under story were listed. In each 1 m^2 plot in the E.I., the vegetation cover was estimated visually and species were listed. Plant species number of under story and E.I. vegetation were calculated for each plot.

2.2.3. Farm management and lay out

A 1:5000 map was made of each farm, depicting the different crops and the ecological infrastructure (E.I.). On these maps the area of semi-natural and crop habitats were measured. The 'E.I.-area' was calculated as the percentage of semi-natural habitat of the farm area (without the farm yard). Farm rotation intensity was defined as the proportion of gramineous crops (cereals and ley pasture) of the total crop area. The spatial arrangement of the E.I. or 'E.I. density', was expressed by the percentage of the farm which lied within 100 m distance of the E.I. In case the canal bank vegetation was cut both after September 15th as well as before May 15th, a distance of 70 m was considered. The influence of field margins on the abundance of large carabid beetles and spiders probably does not exceed 70-100 m (Booij, unpublished data).

Data on the year of conversion of the whole farm to organic husbandry practices in the wheat crop in 1998, and mowing of canal banks and grass strips were obtained using a questionnaire. The mowing management is represented by the month of the first cut, because this cut largely determines the phenological stage of the vegetation in June and July.

2.3. Statistical analyses

All measurements were tested for normality and ^{10}log-transformed. All subsequent analyses were conducted using Statistical Analysis System (SAS Institute, Cary, North Carolina).

2.3.1. Discriminant analyses

Individual farms were classified into one of three groups on the basis of corresponding characteristics (Table 1). For analysis of data from crop area samples (234 m^2), the classifications were based on relevant farm structure characteristics (duration, E.I.-area and rotation intensity) or on crop performance characteristics (crop cover, under story cover and under story species number). For analysis of data from E.I. samples (117 m^2), the classifications were based on relevant farm structure characteristics (E.I.-area and duration) or on vegetation performance characteristics (month of first cut, E.I.-vegetation cover or plant species number per m^2).

Farms were classified according to two splits: the first split based on one of the above mentioned characteristics separated a category of 3-7 farms, and the second split based on another of these characteristics divided the remaining 6-10 farms in a second and a third category. The minimum category size was 3 farms. For all obtained classifications canonical discriminant analyses were performed on the numbers of arthropods in each functional group.

Observations in the wheat and in the E.I. were analysed separately for crop area and E.I. classifications, respectively. Classifications with the highest Wilks' Lambda F-value were selected; this selection yielded the four best classifications.

Stepwise discriminant analyses were performed on the numbers of arthropods in each functional group to determine the most important groups that could classify the farms into the three categories. Arthropod observations in the crop area and in the E.I. were again analysed separately. Canonical discriminant analysis was used to determine the magnitude and direction of the association of individual variables with indicator variables. Standardised canonical coefficients larger than 0.3 divided by the square root of the eigenvalue of the canonical function (Afifi & Clark, 1984) were considered large enough to contribute significantly to the classification.

2.3.2. Taxa differentiating among farm categories and distance from E.I.

Differences in species composition were expressed by the taxa that had significantly higher or lower numbers in one category as compared to the other categories. Differences in abundance of various taxa between the three categories in the four selected classifications were tested by ANOVA ($P<0.05$), including a Duncan's multiple range test. In this test non-transformed data were used, and taxa that occurred with less than 20 individuals in the whole data-set were omitted. Differences in abundance of taxa among the sampling distances from the E.I. of 0 m (in the E.I.), 10 m (in wheat) and 30 m (in wheat) were also tested with ANOVA ($P<0.05$) including Duncan's multiple range test.

2.3.3. Differences in species diversity

Differences in species diversity were also analysed. Taxa that occurred with less than 20 individuals in the whole data set were omitted. Parasitoids and r-herbivores were not considered because both groups included one taxon. Observations in the crop area (234 m^2; pooled samples of 10 and 30 m from the E.I.) and in the E.I. (117 m^2) were analysed separately. Calculations were made of the number of taxa per arthropod functional group per m^2 (species density: S) and the Margalef diversity index per m^2 ($D_m = (S-1)/\ln N$: S = number of species, and N = number of individuals) (Magurran, 1988). Differences in S and D_m among the three categories in each of the four selected classifications were tested by ANOVA ($P<0.01$), including Duncan's multiple range test. Differences in S and D_m among the sampling distances (0, 10, and 30 m from the E.I.) were also tested by ANOVA ($P<0.01$), including Duncan's multiple range test, using the whole data-set (351 m^2).

2.3.4. Gradient analysis

The pooled data-set of wheat and E.I. samples (351 m^2) was used to analyse the distribution of arthropod functional groups along the gradient from E.I. to crop centre, represented by three sampling distances 0 m (E.I.), 10 m (wheat) en 30 m (wheat), for each farm category. Linear regressions (GLM; $P<0.1$) were performed for the four selected classifications using ^{10}log-transformed data. Effects of distance, category, and distance by category interaction were tested. Crop area observations (234 m^2) and E.I. observations (117 m^2) were also tested separately for differences between categories in the four selected classifications (GLM; $P<0.1$), including Duncan's multiple range test.

3. Results

3.1. Observed numbers of epigeic arthropod functional groups

A total of 26,722 organisms were caught in 351 m^2 sampling area including 12,346 aphids. On average, 63% and 13% of vegetation dwelling arthropod numbers were aphids in the crop area and in the ecological infrastructure, respectively. Average arthropod density in the crop area, excluding aphids, was 28 organisms/m^2 of which the most abundant taxa (>2%) were: herbivores: leaf beetles (Chrysomelidae)(6%) and hoppers (Cicadellidae)(5%); detritivores: chironomid midges (12%) and sciarid midges (4%); predators: spiders (10%), empidid flies (9%), and dolichopid flies (3%); and parasitoids (32%) (Table 2a). The average density in the E.I., excluding aphids, was 67 organisms/m^2 with the most abundant taxa (>2%) being: herbivores: hoppers (36%), chloropid flies (7%), and bugs (3%); detritivores: wood lice (7%) and chironimid midges (5%); predators: spiders (9%) and ants (3%); and parasitoids (7%) (Table 2b).

Table 2a
The total number/18 m^2 per farm of arthropod taxa in the wheat crop captured by vacuum sampling.

Taxa	Funct. group	Farm T	F	K	Z	R	L	H	B	O	S	J	E	M
Isopoda	detr	0	0	0	0	0	0	0	1	0	0	0	0	1
Chironomidae	detr	22	8	34	26	67	92	11	60	20	380	10	52	11
Mycetophilidae	detr	2	0	1	3	9	2	1	20	7	1	2	7	10
Sciaridae	detr	4	12	10	10	18	6	22	65	61	4	23	12	2
Lonchopteridae	detr	1	0	43	2	3	0	1	5	0	3	0	14	0
Phoridae	detr	0	1	0	2	1	0	2	3	0	0	0	1	2
Borboridae	detr	1	1	1	3	0	0	2	7	5	1	3	20	10
Drosophilidae	detr	30	1	20	4	20	1	3	9	3	0	1	18	0
Sepsidae	detr	0	0	1	1	0	0	0	0	1	1	0	8	23
Cicadelidae	K-herb	0	2	18	5	8	5	30	41	11	8	59	30	80
Heteroptera, herbivores	K-herb	2	0	1	0	1	1	0	1	0	0	0	0	0
Chrysomelidae	K-herb	26	6	30	13	29	58	13	62	51	65	8	32	8
Curculionidae	K-herb	0	0	0	0	0	1	0	1	0	0	0	51	4
Tipulidae	K-herb	0	0	6	1	1	0	0	5	0	0	0	0	1
Chloropidae	K-herb	5	1	2	2	23	4	2	14	2	3	0	8	9
Opomyzidae	K-herb	1	0	2	0	0	1	1	0	1	0	0	1	1
Ephidridae	K-herb	6	1	6	6	23	7	1	0	0	0	2	1	0
Symphyta	K-herb	1	0	0	1	4	2	1	0	3	0	0	0	2
Heteroptera, predator	pred	1	0	0	0	1	1	1	1	2	0	0	0	2
Coccinellidae	pred	14	1	7	0	30	8	3	3	11	3	10	1	5
Cantharidae	pred	12	18	12	18	12	10	14	4	5	0	3	4	2
Chrysopidae	pred	2	0	2	0	2	0	0	4	1	6	7	11	6
Syrphidae	pred	20	0	28	3	36	26	1	1	4	3	7	18	8
Empididae	pred	23	7	25	22	27	12	13	68	44	29	17	173	139
Dolochopodidae	pred	1	0	6	7	1	0	3	12	14	5	0	103	30
Aranae	pred	7	10	62	21	72	27	15	189	20	57	42	81	61
Carabidae	pred	0	0	1	0	0	0	1	16	1	3	0	5	10
Staphylinidae	pred	1	2	2	0	3	5	2	6	5	4	3	3	2
Formicidae	pred	0	0	0	2	0	0	0	0	0	1	0	2	0
Parasitica	par	117	68	140	183	311	336	28	118	251	238	67	143	58
Aphididae	r-herb	4693	270	1284	1437	746	701	82	397	290	188	236	367	465

Table 2b
Total number/9 m^2 per farm of arthropod taxa in the ecological infrastructure captured by vacuum sampling.

Taxa	**Funct. group**	**Farm** T	F	K	Z	R	L	H	B	O	S	J	E	M
Isopoda	detr	28	61	12	13	0	364	1	1	0	13	12	26	0
Chironomidae	detr	220	0	2	18	2	32	0	3	3	126	0	14	1
Mycetophilidae	detr	1	0	0	1	0	1	0	1	1	2	0	0	0
Sciaridae	detr	16	0	2	13	5	5	2	18	47	4	1	5	2
Lonchopteridae	detr	16	0	15	1	2	9	1	1	0	6	2	17	0
Phoridae	detr	4	0	0	12	7	0	3	7	6	1	5	1	0
Borboridae	detr	48	3	3	5	16	16	4	4	2	10	1	26	2
Drosophilidae	detr	34	1	6	12	7	8	6	6	10	5	0	1	0
Sepsidae	detr	17	1	2	3	3	2	1	1	3	2	12	4	6
Cicadelidae	K-herb	388	58	8	211	772	190	105	311	496	76	94	66	32
Heteroptera	K-herb	2	2	0	54	1	142	1	0	0	1	7	36	1
Chrysomelidae	K-herb	1	0	3	0	0	1	0	1	0	0	0	0	0
Curculionidae	K-herb	1	0	0	0	0	3	0	0	0	1	2	0	0
Tipulidae	K-herb	6	4	1	3	0	4	0	1	1	1	0	0	0
Chloropidae	K-herb	16	3	2	29	36	12	125	55	104	27	72	35	14
Opomyzidae	K-herb	25	0	2	11	9	5	0	3	1	5	1	1	0
Ephidridae	K-herb	7	0	2	14	7	29	0	1	2	3	1	1	1
Symphyta	K-herb	4	1	0	13	1	6	1	6	1	1	0	2	0
Heteroptera	pred	9	0	2	22	3	91	0	13	0	11	9	5	6
Coccinellidae	pred	4	0	2	0	0	0	0	0	1	0	5	1	6
Cantharidae	pred	17	4	4	26	0	10	0	0	1	0	0	1	0
Chrysopidae	pred	4	1	0	0	0	1	0	0	1	1	0	5	0
Syrphidae	pred	2	0	0	0	0	0	1	0	0	1	0	1	1
Empididae	pred	41	4	21	1	4	9	1	1	1	13	7	21	12
Dolochopodidae	pred	1	0	1	3	6	4	0	11	1	10	2	2	3
Aranae	pred	76	34	31	86	83	116	8	32	31	82	57	43	15
Carabidae	pred	19	6	11	6	4	14	3	1	1	16	4	2	0
Staphylinidae	pred	7	2	6	2	1	29	5	0	0	3	6	1	1
Formicidae	pred	49	49	65	7	19	36	6	0	5	6	5	2	1
Parasitica	par	88	14	27	95	49	47	8	48	59	68	30	35	6
Aphididae	r-herb	488	11	45	106	127	59	4	35	98	10	82	35	90

3.2. Crop area arthropod functional groups and species diversity

3.2.1. Arthropod functional groups affecting distinctions among farm structure categories

The classification 'dur/int' based on organic farming duration (first split) and rotation intensity (second split) gave the best separation of the observations (canonical discriminant analysis, Wilks' Lambda, F-value=18.7, P<0.0001; Table 3). Category 1 included the recently converted organic farms; category 2 included the long duration (>6 years) organic farms with an intensive crop rotation (<33% gramineous crops); category 3 included long duration organic farms with an extensive crop rotation. Classifications based on difference in percentage E.I. ('area') showed less distinction than classifications based on duration and rotation intensity (Table 3).

The separation into duration-intensity categories, based on arthropod functional group numbers in wheat, is illustrated in a plot of canonical variable two versus canonical variable one (Fig. 2). All arthropod functional groups were selected as important factors by stepwise discriminant analysis for discrimination among the three categories (Table 4). The first canonical function containing all arthropod functional groups, separated the organic extensive crop rotation category from both other categories (Fig. 2). r-Herbivores, predators and K-herbivores were positively associated with recent conversion or organic intensive crop rotation, whereas detritivores and parasitoids were positively associated with organic extensive crop rotation (Table 4). The second canonical function, determined mainly by predators and r-herbivores separated long duration intensive farms from recently converted farms; predators were associated with recently converted farms and r-herbivores with intensive farms.

K-herbivores and predators were >25% more abundant on average, in recently converted farms (category 1) than in the other two categories. Detritivores and parasitoids were respectively >40% and >10% more abundant in organic extensive farms (category 3) than in the other the two categories. r-Herbivores were most abundant in intensive organic farms (category 2) and had intermediate numbers in recently converted farms as compared to organic extensive farms (Table 4).

Table 3
Examples of classifications of the crop area and the ecological infrastructure, including the the Wilks' Lambda F-value and the squared canonical correlation obtained by canonical discriminant analysis. Abbreviations of category characteristics are explained in Table 1.

Crop area		**Category 1**	**Category 2**	**Category 3**	F-value	Sq. Can.
Farm structure categories	category	dur<6	dur>6 & int<33	dur>6 & int>33	18.7	0.37
	farms	*HZBREM*	*TKLJ*	*FOS*		
	category	dur<6	dur>6 & area<2.1	dur>6 & area>2.1	8.66	0.23
	farms	*HZBREM*	*FKO*	*TLSJ*		
	category	int>33	int<33 & dur>6	int<33 & dur<6	7.54	0.26
	farms	*FOSEM*	*TKLJ*	*HZBR*		
Crop performance categories	category	ccov>85	ccov<85 & ucov>7.6	ccov<85 & ucov<7.6	38.32	0.56
	farms	*BME*	*TKRL*	*FOHZSJ*		
	category	ccov>85	ccov<85 & usp>3.5	ccov<85 & usp<3.5	25.1	0.54
	farms	*BME*	*ORJ*	*TFKHZLS*		
	category	usp>3.5	usp<3.5 & ucov>7.6	usp<3.5 & ucov<7.6	14.09	0.34
	farms	*OREJ*	*TKL*	*FHZBMS*		
Ecological Infrastructure		**Category 1**	**Category 2**	**Category 3**		
Farm structure categories	category	area>2.1	area<2.1 & dur>6	area<2.1 & dur<6	7.84	0.39
	farms	*TLSEJ*	*FKO*	*HZBRM*		
	category	dur<6	dur>6 & area<2.1	dur>6 & area>2.1	6.53	0.34
	farms	*HBZRME*	*FKO*	*TLSJ*		
E.I. vegetation performance categories	category	mow≥7	mow<7 & eicov>80	mow<7 & eicov<80	15.94	0.48
	farms	*TLSE*	*HZBOJ*	*FKRM*		
	category	mow≥7	mow<7 & eisp>4,3	mow<7 & eisp<4,3	10.53	0.51
	farms	*TLSE*	*BOMJ*	*FKHZR*		
	category	Eicov<80	eicov>80 & eisp<4.3	eicov>80 & eisp>4.3	6.8	0.37
	farms	*FKRM*	*THZ*	*BOLSEJ*		

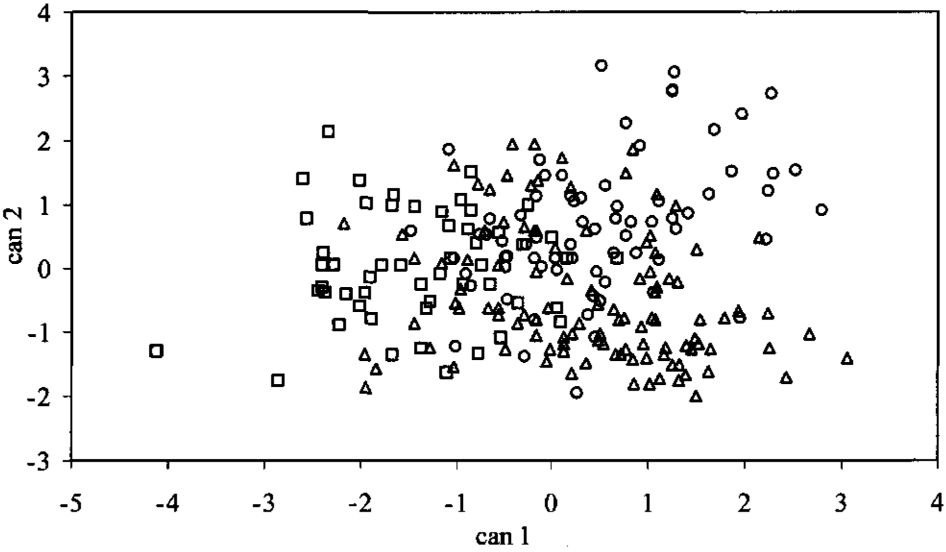

Fig. 2. Plot of the second and first canonical functions discriminating among farm categories of the classification 'int/area'. Squares represent farms with >40% gramineous crops; circles represent farms with < 40% gramineous crops and >2.2% E.I. area; triangles represent farms with >40% gramineous crops and <2.2% E.I.

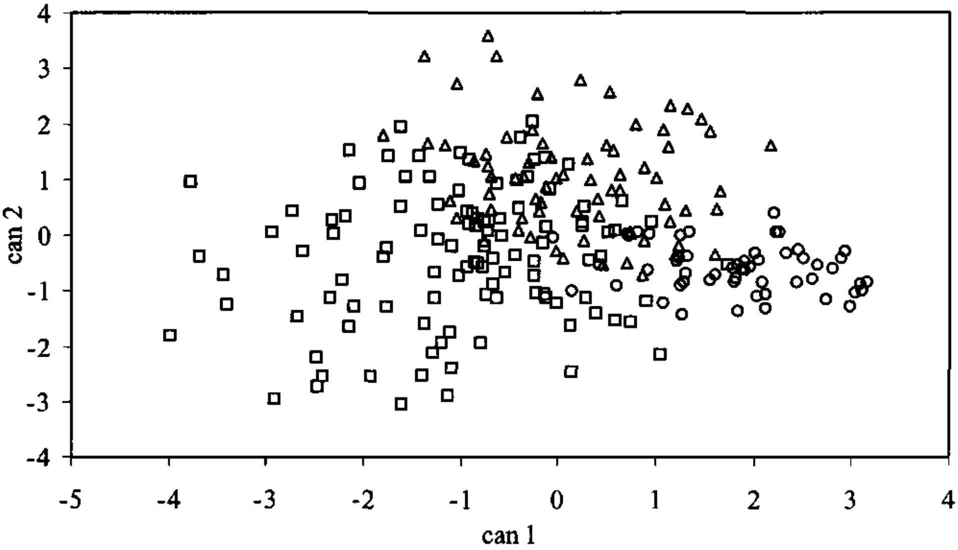

Fig. 3. Plot of the second and first canonical functions discriminating among farm categories of the classification 'int/area'. Circles represent farms with dense crops (>85%); triangles represent farms with sparse crops (<85%) including an under story >7.6%; squares represent farms with a sparse crop including a poor under story (<7.6%).

Table 4

Arthropod variables that contributed significantly to the classification of the crop area observations in the three farm categories by stepwise and canonical discriminant analyses, standardised canonical coefficients, and mean values per crop area category. Classification in 'dur/int'-categories is based on farm structure characteristics and the classification 'ccov/ucov'-categories is based on crop performance characteristics. The abbreviations of the category characteristics are explained in Table 1. Comparison of arthropod mean numbers in the categories according to Duncan's multiple range test.

Farm structure (dur/int)	Can 1[b]	Mean values and multiple range comparison						
Variables[a]	Standardised coefficient	Category 1 *dur<6* mean		Category 2 *dur>6 & int<33* mean		Category 3 *dur>6 & int>33* mean		
r-Herbivores	0.95[c]	32	b	96	a	14	c	(P<0.001)
Predators	0.46	13	a	6	b	5	b	(P<0.001)
Detritivores	-0.62	5	ab	4	b	10	a	(P<0.07)
K-herbivores	0.67	5	a	4	a	3	b	(P<0.001)
Parasitoids	-0.49	8	b	9	ab	10	a	(P<0.05)

Crop performance (ccov/ucov)	Can 1[d]	Mean values and multiple range comparison						
Variables[a]	Standardised coefficient	Category 1 *ccov>85* mean		Category 2 *ccov<85 & ucov>7.6* mean		Category 3 *ccov<85 & ucov<7.6* mean		
Predators	1.15[e]	20	a	7	b	5	c	(P<0.001)
r-Herbivores	0.54	23	b	103	a	23	c	(P<0.001)
Detritivores	-0.15	7	a	5	a	6	b	(P<0.05)
K-herbivores	0.52	7	a	4	b	3	c	(P<0.001)
Parasitoids	-0.44	6	b	13	a	8	b	(P<0.001)

[a] Variables are listed in order of selection by stepwise discriminant analysis.
[b] Canonical function 1; responsible for 71% of the variation.
[c] Standardized coefficients >0.39 were considered large enough for interpretation.
[d] Canonical function 1; responsible for 73% of the variation.
[e] Standardized coefficients >0.26 were considered large enough for interpretation.

3.2.2. Differences in species diversity among farm structure categories

Recently converted and intensive long duration farms had similar species richness in all functional groups considered (detritivores, K-herbivores, and predators). The species diversities were only similar for K-herbivores and total taxa (Table 5). Detritivores were most diverse in recently converted farms. There were two differentiating taxa: *Phoridae* (detritivorous flies) preferred recently converted farms and herbivorous bugs (*Heteroptera*) preferred long duration intensive farms.

3.2.3. Arthropod functional groups affecting distinctions among crop performance categories

It was envisaged that crop performance factors could offset farm structure factors in determining arthropod functional group assemblages. This proved to be correct: the classification 'ccov/ucov' based on crop cover (first split) and weed cover (second split) provided the best separation of observations (Wilks' Lambda, F-value=38.3, P<0.0001; Table 3). Crop performance category 1 included dense crop stands (cover >85%); crop performance category 2 included relatively sparse crop stands (cover <85%), accompanied by an under story vegetation (>7.6% cover); crop performance category 3 included relatively sparse crop stands which had a poor under story vegetation.

The separation of crop-weed cover categories, based on arthropod functional group numbers in wheat, is illustrated in a plot of canonical variable two versus canonical variable one (Fig. 3). All arthropod functional groups were selected as important factors by stepwise discriminant analysis for discrimination among the three categories (Table 4). Extremes were dense crops and sparse crops with poor under story (Fig. 3). Significant contributions to the first canonical function were the positive associations of predators, r- and K-herbivores with dense crops, and the negative association of parasitoids with dense crops (Table 4). The relation between under story vegetation and arthropod groups was not as pronounced: the category of sparse crops with under story was separated from both other categories by the second canonical function, determined significantly by predators (negative association) and r-herbivores (positive association).

K-herbivores and predators in dense crops (category 1) were respectively >65% and >40% more abundant on average, than in the other categories. r-Herbivores and parasitoids in sparse crops with under story were respectively >75% and >40% more abundant than in the two other categories (Table 4).

3.2.4. Differences in species diversity among crop performance categories

Species richness was generally highest when crop cover was more than 85%. Diversity of senescense-feeding herbivores, predators and detritivores was lowest in the category of sparse crops with poor under story as compared to the other categories. Dense crops had the highest diversity of detritivores. Dense crops and sparse crops with under story had a similar diversity of K-herbivores. Sparse crops with under story had the highest diversity of predators (Table 5).

Thirteen taxa had significantly higher densities in one or two of the crop performance categories (ANOVA Duncan, $P<0.05$): in dense crops the highest densities were observed for woodlice (Isopoda, detritivore), Phoridae, Borboridae, Sepsidae (all detritivorous diptera), Cicadellidae (herbivore), Aranae, Carabidae (polyphagous predators), and Dolichopodidae, Empididae (predacious flies); in sparse crops with under story the highest densities occurred among Drosophilidae (detritivorous fly), herbivorous bugs (Heteroptera), Ephydridae (herbivorous fly), and hooverfly larvae (Syrphidae; predacious fly).

3.3. Ecological Infrastructure arthropod functional groups and species diversity

3.3.1. Arthropod functional groups affecting distinctions among farm structure categories

Of two considered possibilities the classification area/dur, based on E.I. area as first split and farm organic duration as second split gave the best separation of observations (canonical discriminant analysis, Wilks' Lambda, F-value=7.84, $P<0.0001$; Table 3). Farm structure category 1 included farms with an enlarged E.I. (>2.1% of the farm arable area) and corresponded to 'improved E.I.'; the other two categories are farms with a small E.I. which could be long duration organic farms that did not enlarge the E.I. area (category 2) or recently converted organic farms (category 3).

The separation into area-duration categories, based on arthropod functional group numbers in the E.I., is illustrated in a plot of canonical variable two versus canonical variable one (Fig. 4). Detritivores and K-herbivores were selected as important factors by stepwise discriminant

Table 5
*Comparison between the three categories in all four selected classifications, with regard to their species richness (S) and Margalef diversity index (D_m) (GLM; significance level * =P<0.1; ** P<0.01; *** P<0.001); detr = detritivores; K-herb= senescense feeding folivores; pred = predators; total = detritivores, K-herbivores and predators. Abbreviations of category characteristics are explained in Table 1.*

Crop area

	Categories	S detr		D_m detr		S K-herb		D_m K-herb		S pred		D_m pred		S Total		D_m Total	
Farm structure categories	dur<6	2.3	a	1.0	a	2.1	a	0.8	a	3.4	a	1.2	b	7.8	a	2.3	a
	dur>6 & int<33	1.9	a	0.7	b	1.8	a	0.8	a	3.1	a	1.3	a	6.8	b	2.3	a
	dur>6 & int>33	1.5	b	0.6	b	1.1	b	0.4	b	2.4	b	1.1	b	5.0	c	1.7	b
	Significance	***		***		***		***		***		*		***		***	
Crop performance	ccov>85	2.7	a	1.0	a	2.4	a	0.8	a	7.0	a	1.2	b	9.1	a	2.4	a
	ccov<85&ucov>7.6	2.1	b	0.7	b	2.0	b	0.8	a	3.4	b	1.4	a	7.5	b	2.4	a
	ccov<85&ucov<7.6	1.5	c	0.7	b	1.2	c	0.5	b	2.4	c	1.1	b	5.0	c	1.8	b
	Significance	***		**		***		***		***		***		***		***	

Ecological Infrastructure

	Categories	S detr		D_m detr		S K-herb		D_m K-herb		S pred		D_m pred		S Total		D_m Total	
Farm structure	area>2.1	4.1	a	1.2		3.8	a	0.9	a	4.8	a	1.4	a	12.8	a	2.9	a
	area<2.1 & dur>6	2.5	b	1.1		2.0	c	0.7	b	3.2	b	1.0	b	7.7	b	2.0	b
	area<2.1 & dur<6	2.4	b	1.3		3.0	b	0.6	ab	2.8	b	1.0	b	8.2	b	2.0	b
	Significance	***		NS		***		*		***		**		***		***	
E.I. vegetation performance	mow≥7	4.7	a	1.2		4.0	a	0.9	a	5.1	a	1.4	a	13.8	a	3.0	a
	mow<7 & eicov>80	2.7	b	1.3		3.2	b	0.6	b	2.6	c	0.9	c	8.5	b	2.0	b
	mow<7 & eicov<80	2.0	b	1.1		2.0	c	0.7	b	3.6	b	1.2	b	7.2	b	2.0	b
	Significance	***		NS		***		**		***		***		***		***	

analysis for discrimination among the three categories (Table 6). The largest differences in arthropod functional group composition were between the enlarged E.I. category and recently converted farm category (Fig. 4). In the first canonical function detritivores were positively associated and K-herbivores negatively associated with enlarged E.I. (Table 6). Although the predator number was significantly higher in the enlarged E.I. category as compared to the other categories (Table 6), it had little canonical power in the first canonical function because of a high correlation (Pearson correlation coefficient = 0.79; P<0.01) between detritivore and predator abundance. The second canonical function, determined by K-herbivores (positive association), separated both extreme categories from the third category of long organic duration farms with small E.I.

Detritivores and predators were >70% and >40% more abundant on average in the enlarged E.I. category (1) as compared to the small E.I. categories. K-herbivores were >20% more abundant on average in recently converted farms (category 3) than in the other categories (Table 6).

3.3.2. Differences in species diversity among farm structure categories

Species richness of K-herbivores and detritivores and diversity of predators and total taxa were significantly higher in the enlarged E.I. category than in other categories (Table 5). The only differentiating taxa were weevils (Curculionidae; K-herbivore) which preferred enlarged E.I.

3.3.3. Arthropod functional groups affecting distinctions among E.I. vegetation performance categories

The classification 'mow/eicov' based on first mowing date (first split) and E.I. vegetation cover (second split) gave the best separation of observations (canonical discriminant analysis, Wilks' Lambda, F-value=15.94, P<0.0001; Table 3). Vegetation performance category 1 included E.I. which was cut late (after July 1st) and included the 'improved E.I.' of the three prototype farms and the organic experimental farm (E). Ecological infrastructure which was cut before July could have a high vegetation cover (>80%)(category 2) or an 'open vegetation' *i.e.* a low cover (<80%) (category 3). We defined category 2 as 'grassy E.I.' because early mowing in May, combined with a higher mowing frequency per year and/or careful mowing resulted in a stable, dense sward dominated by perennial grass species.

Table 6

Arthropod variables that contributed significantly to the classification of the E.I. observations in the three farm categories by stepwise and canonical discriminant analyses, standardised canonical coefficients, and mean values per crop area category. Classification in 'area/dur'-categories is based on farm structure characteristics and the classification 'mow/eicov'-categories is based on vegetation performance characteristics. The abbreviations of the category characteristics are explained in Table 1. Comparison of arthropod mean numbers in the categories according to Duncan's multiple range test.

Farm structure (area/dur)	Can 1 [b]	Mean values and multiple range comparison						
	Standardised coefficient	Category 1 *area>2.1*		Category 2 *rea<2.1 & dur>6*		Category 3 *area<2.1 & dur<6*		
Variables [a]		mean		mean		mean		
Detritivores	1.16[c]	26	a	7	b	4	c	(P<0.001)
K-herbivores	-0.49	32	a	26	b	41	a	(P<0.01)
Predators	*-0.18*	*21*	*a*	*11*	*b*	*9*	*b*	(P<0.001)
Parasitoids	*0.33*	*6*	*a*	*4*	*b*	*5*	*b*	(P<0.05)
r-Herbivores	*0.03*	*13*	*a*	*6*	*a*	*8*	*a*	NS

E.I. vegetation performance (mow/eicov)	Can 1 [d]	Mean values and multiple range comparison						
	Standardised coefficient	Category 1 *mow>7*		Category 2 *mow<7 & eicov>80*		Category 3 *mow<7 & eicov<80*		
Variables [a]		mean		mean		mean		
Detritivores	1.34[e]	31	a	6	b	5	b	(P<0.001)
K-herbivores	-0.26	35	a	40	a	27	b	(P<0.001)
Predators	0.16	23	a	9	c	12	b	(P<0.001)
Parasitoids	0.11	7	a	5	a	3	b	(P<0.001)
r-Herbivores	-0.22	14	a	7	a	8	a	NS

[a] Variables are listed in order of selection by stepwise discriminant analysis. The italicised variables were not selected by stepwise discriminant analysis.

[b] Canonical function 1: responsible for 85% of the variation.

[c] Standardised coefficients >0.37 were considered large enough for interpretation.

[d] Canonical function 1: responsible for 63% of the variation.

[e] Standardised coefficients >0.31 were considered large enough for interpretation.

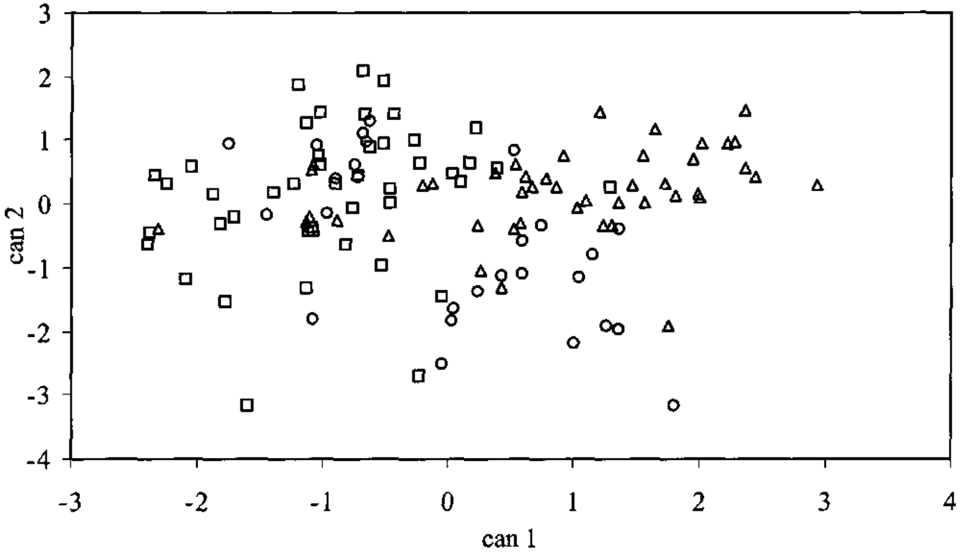

Fig. 4. Plot of the second and first canonical functions discriminating among E.I. categories of the classification 'area/dur'. Triangles represent enlarged E.I. (>2.1%); circles represent small E.I. on farms with a long organic duration; squares represent small E.I. on farms with a short organic duration.

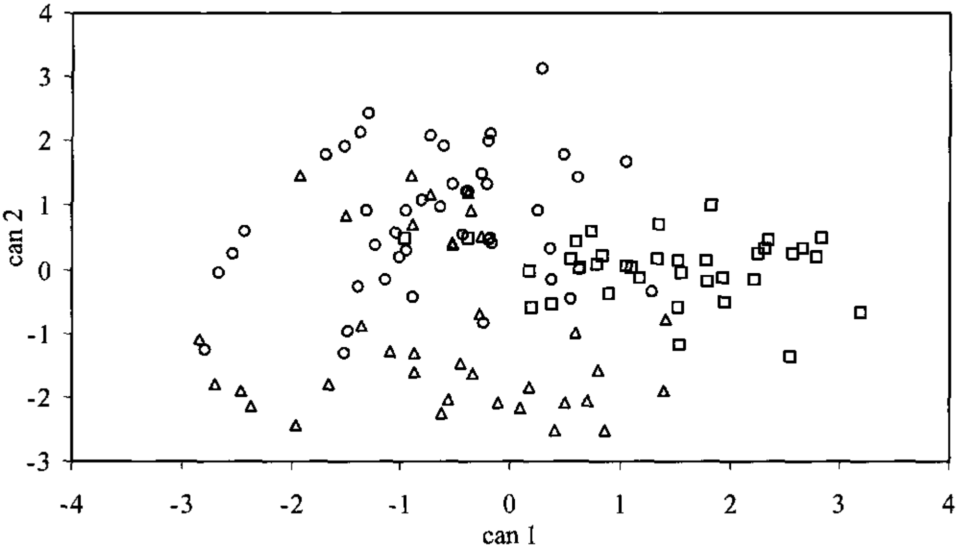

Fig. 5. Plot of the second and first canonical functions discriminating among E.I. categories of the classification 'eispn/eicov'. Squares represent late mown E.I.; circles represent early mown E.I. with dense vegetation; triangles represent early mown E.I. with sparse vegetation.

The separation into 'mow-eicov' categories, based on arthropod functional group numbers in the E.I., is illustrated in a plot of canonical variable two versus canonical variable one (Fig. 5). All arthropod functional groups were selected as important factors by stepwise discriminant analysis for discrimination among the three categories (Table 6). The first canonical function containing only detritivores, separated late mowing category from grassy E.I. and open vegetation categories (Fig. 5). Detritivores are associated positively with late mowing (Table 6). Although the predator number was significantly higher in the late mown E.I. category as compared to the other categories (Table 6), it had little canonical power in the first canonical function because of a high correlation between detritivore and predator abundance in the E.I. The second canonical function, determined mainly by K-herbivores and parasitoids (both positively associated) and predators (negatively associated) showed a separation between grassy E.I. (category 2) and open vegetation (category 3). All functional groups, except the K-herbivores were on average more abundant in the late mown E.I. category (1) as compared to both other categories: detritivores and predators were respectively >80% and >40% more abundant. K-herbivores were >10% more abundant on average in grassy E.I. (category 2) than in both the other categories (Table 6).

3.3.4. Differences in species diversity among E.I. vegetation performance categories

Species richness and diversity of all arthropod functional groups, except diversity of detritivores, were significantly higher in late mown E.I. than in other categories. The category of grassy E.I. had the lowest diversity of predators as compared to the other categories (Table 5). Of the total of eight differentiating species, six preferred late mown E.I.: three detritivorous taxa (Chironomidae, Lonchopteridae, Borboridae) and three predacious taxa (Chrysopidae, Carabidae, and Empididae). The high abundance of chloropid flies (herbivorous) and phorid flies (detritivorous) was typical for the category of grassy E.I. vegetation.

3.4. Arthropod functional groups along the gradient from E.I. to crop

3.4.1. Functional group composition along E.I. – crop gradients

It was expected that the relations between abundance of various functional groups and distance from the E.I. would be similar for different farm categories. However, there were significant interactions between categories in all four selected classifications and distance from the E.I., with regard to abundance of detritivores and predators. There were also significant interactions between categories and distance with regard to K-herbivores for some classifications but not for others. The interactions were strongest for predator distributions, particularly for crop area classifications but also for 'mow/eicov' classifications. These interactions are best illustrated for the E.I. classification 'mow/eicov' (Fig. 6). Although in most farms abundance of predators and detritivores were lowest at 30 m distance from the E.I., farms with an early mowing date and relatively little plant cover in the E.I. (category 3) had more predators and detritivores at 30 m than at 10 m distance from the E.I. (Fig. 6a and c). Thus, high densities in the E.I. do not always go hand-in-hand with high densities in the adjacent crop.

Despite the significant interactions, predators, K-herbivores, and detritivores were generally most abundant in the E.I. and were lower in the wheat field (Fig. 6 a,b,c). Although abundance were generally decreasing or similar with increasing distance from the E.I., in category 3 they were sometimes higher at 30 m than at 10 m inside the wheat field (Fig. 6 a,b,c). On the other hand, abundance of parasitoids and r-herbivores were generally lowest in the E.I. and highest at 30 m inside the wheat field (Fig. 6 d,e), with the exception of the parasitoids in category 2 (grassy E.I.) that were highest at 10 m inside the wheat field and lower in the E.I. and at 30 m inside the wheat field (Fig. 6d).

3.4.2. Differences in diversity between E.I. and crop area

Species richness of detritivores, K-herbivores and predators was significantly higher in the E.I., but diversity (Margalef) was only larger for detritivores. Ten of 30 considered taxa of predators, K-herbivores and detritivores showed a preference for E.I.: Phoridae, Borboridae, Cicadellidae, Chloropidae, Opomyzidae, Symphyta, predacious Heteroptera, Aranae, Carabidae, and Formicidae. Two taxa showed a preference for the crop area: Chrysomelidae (herbivorous) and Syrphidae (predacious). None of the considered taxa had a significantly different abundance between 10 m and 30 m sampling stations.

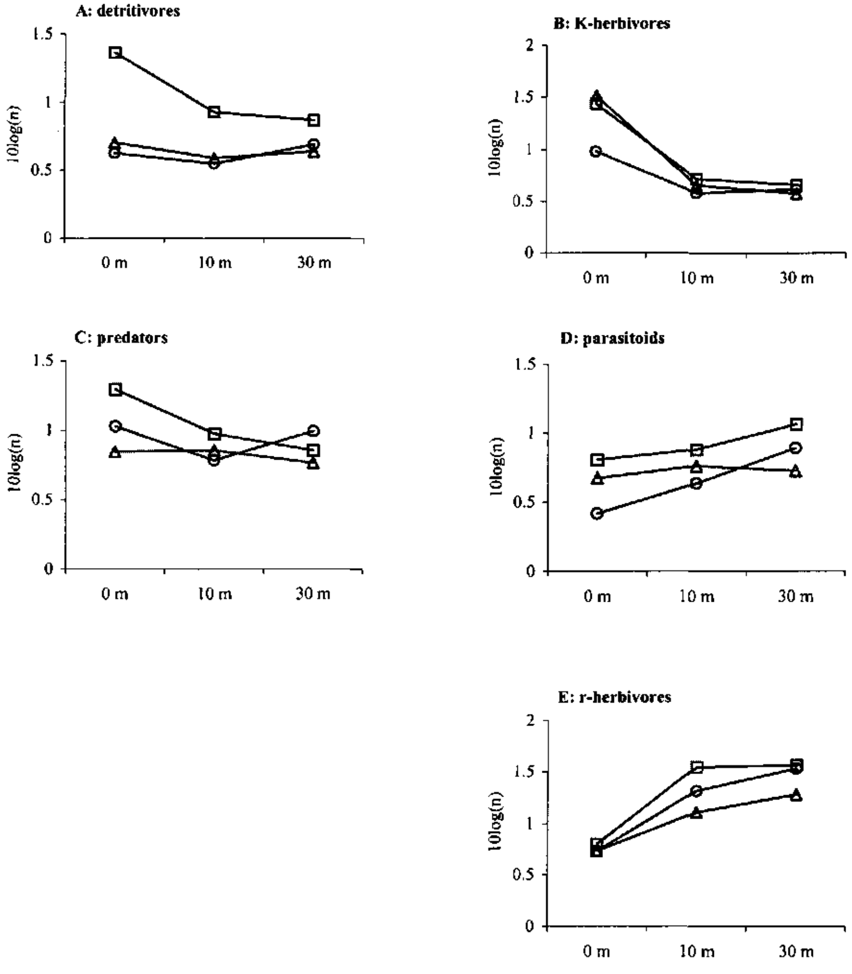

Fig. 6. Abundance of vegetation dwelling arthropod functional groups along the gradient from E.I. (0 m) to the crop area (10 and 30 m). E.I. vegetation performance categories of selected classification 'mow/eicov': category 1 (squares)= late mowing; category 2 (triangles)= early mowing, dense vegetation; category 3 (circles)= early mowing and sparse vegetation. The lines between the averages of arthropod functional group numbers (^{10}log-transformed) are drawn to illustrate different patterns among the three E.I. categories and do not represent estimated points in between the sampling stations. (a) detritivores; (b) K-herbivores; (c) predators; (d) parasitoids; (e) r-herbivores.

4. Discussion

4.1. Observations compared to the hypotheses

It was expected that duration of organic management and extensive crop rotation would relate positively to the abundance of primary arthropod functional groups and that consequently, predator and parasitoid numbers would be supported. It was also expected that improved E.I would promote the abundance of K-herbivores and predators in both E.I. and the adjacent crop area. Observations that may confirm our hypotheses include the relatively high detritivore and parasitoid numbers on farms which had both a long organic duration as well as an extensive crop rotation, and increased densities of predators in improved (*i.e.* late mown) E.I. However, several observations contradicted the hypothesis: dense crops on recently converted farms had the highest densities of K-herbivores and predators; several long duration farms had increased numbers of r-herbivores; K-herbivores and parasitoids were equally abundant in improved E.I. and 'grassy E.I.'; increased densities of predators and K-herbivores in the crops area were, in several cases, not related to increased densities of these groups in improved E.I.

4.2. Vegetation dwelling arthropods community in the crop area

Observations suggest the occurrence of four distinctive arthropod functional group compositions. Outlining these compositions may explain the observed contradictions with the hypotheses and contribute to improved hypotheses. The four functional group compositions represent a shift along the gradient of organic duration (involving *e.g.* carbon flow) and production intensity (involving *e.g.* nitrogen input). They will be discussed in ascending order of intensity: a) short duration with a sparse crop, b) short duration with a dense crop, c) long duration with intensive crop rotation, and d) long duration with extensive crop rotation.

a) Recently converted farms which did not have a luxurious crop growth and which had a poor under story (corresponding to farms H and Z).
Crop areas were characterised by relatively low densities off all functional groups. These low densities are often encoutered in field centres of conventionally managed crop habitats that include almost no arable weeds, particularly when r-herbivores are not considered (Kromp & Meindl, 1997). Establishment of several taxa may require time (Hald & Reddersen, 1990). This 'unsaturated' arthropod community may develop, during at least one crop rotation, towards a community of type d) or c), depending on the farm's (rotation) intensity. However recently converted farms represent relatively unstable farming systems (oral communication G. Oomen) in which still unbalanced N-availability and/or apparent crop susceptibility may rapidly change a community of type a) into a community of type b).

b) Short organic duration with a dense crop represents farms in the conversion process (corresponding to farms B and E), involving the adaptation by soil life to changed manure management, and creating a site-specific balance between N-application and crop requirements.
In this unstable situation luxurious growth may occur and provide a rich food resource for an array of K-herbivorous taxa. In the dense canopy with damp microclimate, several detritivorous diptera taxa are enhanced by decaying leaves (Weber *et al.*, 1997). The large K-herbivore populations in these crops related to high predator densities (Pearson correlation between predators and K-herbivores in crop area: 0.81, $P<0.001$). But also detritivorous flies may have supported predators like, for example, empidid flies. All groups of herbivores, detritivores and predators had high species richness, probably related to the rich food

resource. High predator densities may have affected r-herbivores and parasitoids, which were less abundant than in type c).

c) Long duration farms with an intensive crop rotation (corresponding to farms T, L, K and J) may support the detrital subweb to a much lesser extent than long duration farms with an extensive crop rotation; low densities of detritivores were observed here. Therefore polyphagous predators may be less abundant and therefore have less effect on the herbivore subweb arthropods. Also crops may be more susceptible for herbivory due to the presence of more N, and crops needing more tillage in the crop rotation. Density of (polyphagous) predators and resistant crop physiology are complementary factors controlling r-herbivore outbreaks (Embden, 1988); systems with 'moderate' levels of both factors might already be vulnerable. The long duration farms had a more diverse arthropod community as compared to type d), involving a coexistence of several predacious taxa and K-herbivores in low densities. However the predators could apparently not inhibit outbreaks of r-herbivores. The r-herbivore outbreaks may have supported the observed high parasitoid numbers.

d) Long duration farms with an extensive crop rotation (corresponding to farms O and S) had increased numbers of detritivores which may have related to an increased detrital subweb supported by crop residues and organic manure (*e.g.* Heimbach & Garbe, 1997; Weber *et al.*, 1997). Polyphagous epigeic predators might be supported by an increased quantity of detritivorous prey (Wise *et al.*, 1999) and subsequently depress the herbivore subweb including r- and K-herbivores and oligophagous predators. Also less nutritive and less susceptible crop tissues may explain the low numbers of herbivores in a long duration, with extensive crop rotation (Phelan, 1997; Theunissen, 1994; Van Emden, 1988). Parasitoids were the main predacious functional group in the canopy, possibly due to reduced interference by vegetation dwelling predators (*cf.* Tscharntke, 1997). Hosts of parasitoids might have been r-herbivores occurring in low densities and also detritivorous diptera (Potts & Vickermann, 1974). Parasitoid abundance on all studied farms appeared to be significantly correlated to detritivore abundance (Pearson correlation coefficient=0.52; $P<0.06$) and not to r-herbivore abundance, which may express both direct (*e.g.* food) and indirect (*e.g.* predator release) factors affecting this functional group.

Three of the studied farms corresponded only slightly to the presented typology. Farm F was most similar to type a). However, low arthropod densities on this farm were due to very sparse crop stands near the crop edge and crop centre, related to mechanical weed control. Farm M was similar to type c), but on this integrated farm estimated crop N-requirements were partially supplied by artificial fertilisers. Farm R was recently converted and corresponded therefore to type d); however, due to wet harvest conditions in the pre-crop, the investigated crop had a sparse stand including a relatively dense and diverse weed vegetation which related to increased arthropod abundance.

It must be noted that the extensive organic arable farms in Flevoland are probably more intensive than the organic farms studied by Moreby & Sotherton (1997) and Reddersen (1997). Relatively extensive organic farms in Flevoland have crop rotations including potatoes and vegetables, and are situated in intensively farmed open landscape. This might be illustrated by the total densities of vegetation dwelling arthropods (collected by means of suction sampling); average densities found in organic cereal fields in Flevoland were 9-15% of the average densities found by Moreby & Sotherton (1997), Reddersen (1997) and Potts & Vickermann (1974).

4.3. Vegetation dwelling arthropod community in the ecological infrastructure

Effects of E.I. characteristics and particularly of 'improved E.I.' will be explained by discussing the responses of the different functional groups.

4.3.1. K-herbivores

K-herbivores were equally abundant in improved (*i.e.* enlarged and late mown) and in traditionally managed 'grassy' E.I. However species richness and diversity were greater in improved E.I. Weevils were the only differentiating K-herbivorous species for improved E.I., and may have indicated clovers in the grass strips of enlarged E.I. The arthropod community in 'grassy E.I.' was predominated (55% of individuals) by herbivores: hoppers and chloropid flies. This was probably due to the prolonged vegetative development of frequently mown vegetation. Accordingly, Haugthon *et al.*(1999) observed higher numbers of arthropods (mainly heteroptera) under a field margin management of cutting twice as compared to cutting once. In their experiment, one cut per year was found to be devastating because it inhibited the life cycles of hoppers and bugs. Although this effect could not be assessed in late mown E.I. prior to its mowing date, observations in the 'intermediate' management type seemed to confirm the conclusion of Haugthon *et al.* (1999). This management is often applied by farmers who are convinced that there is no need for frequent mowing, but who are not able to do the extra labour (*e.g.* finger-bar mowing) required for improved management. Vegetation of this kind of boundaries lost its adaptation to frequent mowing and became colonised by ruderal dicots, *e.g.* dandelion; both plant growth and herbivore community seemed to be much more disturbed following a first cut after May 15th with a flail mower set at a low cut level than following traditional management.

4.3.2. Predators and parasitoids

Predators were promoted by 'improved E.I.' with regard to both numbers and diversity. Accordingly, Wakeham-Dawson *et al.* (1999) found a two times increase of spider numbers in long grazed as compared to short grazed vegetation and argued that vegetation structure is a key property (Curry, 1994). The observed predator numbers were particularly correlated to detritivore numbers and not to herbivore numbers. Predators were less abundant in 'grassy E.I.' (with abundant herbivores) as compared to open swards. In open swards, spiders, the generally predominant species in the predator functional group, were accompanied by a high proportion of ants.

High parasitoid numbers were also related to improved E.I., although these numbers were much smaller than numbers in the crop, suggesting that the group is more affected by crop area factors. However the increased proportion of parasitoids in the arthropod community of 'grassy E.I.' may suggest a relation to the abundance of homopteran hosts.

4.3.3. Detritivores and r-herbivores

These groups were not included in the hypotheses because they were expected to have little importance. However the detritivorous component of the E.I. vegetation dwellers showed to be very significant, particularly in improved E.I. Possibly detritivorous diptera and woodlice were favoured by the increased amount of fibrous litter and stalks and a higher humidity in tall vegetation. The earlier mown vegetation of 'grassy E.I.' may provide another litter quality that supports other, not sampled, taxa, *e.g.* fungivorous staphylinids (Smeding *et al.*, 2001a).

r-Herbivores had variable but generally low abundance in E.I. and no significant differences between management types were found. Numbers of aphids in E.I. were highly correlated with numbers in the crop (Pearson correlation coefficient=0.96, $P<0.0001$). However, distinctive crop communities with many or few aphids were more or less evenly distributed over the distinctive E.I. management categories.

4.4. Differences and interactions between crop area and ecological infrastructure

4.4.1. Differences

According to the hypotheses predators, K-herbivores were more abundant and species rich in the E.I. as compared to the crop area. Detritivores were more abundant and both more species rich and diverse in the E.I. The vegetation dwelling arthropod community included several differentiating taxa compared to the crop area. These observations clearly indicate the increased resource of various plant tissues and structures in perennial vegetation as compared to annual crops (Curry, 1994). Parasitoids and r-herbivores were more abundant in the crop area. Only two taxa were significantly more abundant in the crop than in the E.I.; according to observations of Venhorst *et al.* (in prep.), aphidophagous syrphid abundance increased towards the crop centre, probably due to the increase of prey availability.

The ratio between E.I. and crop arthropod numbers (excluding aphids) on the 13 studied farms, was on average 2.8. However, including aphids, seven of 13 studied farms had more arthropod individuals per m^2 in the crop area than in the E.I. Accordingly Remmelzwaal & Voslamber (1996) found in Zuid Flevoland, the highest arthropod numbers in the E.I. in spring and early summer, whereas numbers (of particularly crop herbivores) became higher in the crop area later in the season.

4.4.2. Interactions

Visual assessment of E.I.-crop area gradients suggested that higher average densities in the E.I. of predator, K-herbivore and detritivore functional groups might relate to increased average densities in the adjacent crop area. However crop area conditions could have a much stronger effect on the distribution of these groups. In particular, crop canopy density supporting K-herbivores, and factors supporting detritivorous diptera, may offset potential E.I. influence on the crop community.

Difference between the 10 m and 30 m sampling station with regard to abundance, species richness and diversity of K-herbivores, detritivores and predators were generally insignificant, indicating that the influence of E.I. on the crop community in the summer, may stop before 10 m or might reach further than 30 m.

Aphids in the crop area may be transported and accumulated into emergent structures like ditch slopes and tall vegetation (Hradetzky & Kromp, 1997). This might explain the correlation of E.I. predator abundance to aphid abundance in the crop (Pearson correlation coefficient=0.69, $P<0.01$). Intermediate numbers of parasitoids and aphids at the 10 m sampling station may indicate the effects on these groups of arthropods (*e.g.* predators) in the field margin.
Detritivorous diptera taxa, emerged in the crop area, may also accumulate in the E.I.; however an increased diversity and occurrence of differentiating species in the E.I. suggested that this group is at least partly autochthonous in the field margin habitat.

4.5. Conclusions

Comparison of vegetation dwelling arthropod functional groups in the wheat crops on thirteen organic arable farms suggested that both organic duration and 'intensity' are determining factors. Intensity relates to crop rotation (*i.e.* percentage gramineous crops) but also to soil nutrient level. Observations provided no support for the general hypothesis that organic duration and extensive crop rotation would promote abundance of both primary arthropod functional groups and consequently, support predator and parasitoid numbers.

Results indicated a shift or succession in arthropod functional group compositions from recently converted farms to long duration farms with extensive crop rotation. In recently converted farms pest susceptible crops, *e.g.* due to luxurious growth, may attract various herbivores and therefore support predator abundance. In long duration farms, arthropod communities are not numerous but more diverse. However in these communities, related also to crop condition, particularly r-herbivores (aphids) may not be controlled. However, in extensive crop rotation a 'subsidised increased detrital subweb', related to increased total organic matter input, may support polyphagous predators. These predators possibly depress the herbivore subweb (*i.e.* herbivores and specific predators) by both predation and competition. In this community, as well as in other observed communities, effects of 'predator interference' could play a role, *e.g.* in releasing parasitoids from predation or competition by (oligophagous) vegetation dwelling predators.

According to our hypotheses improved E.I. (*i.e.* large area and late mowing) promoted the predacious functional groups. However herbivore abundance may also be high in the traditional management. The detrital functional group (particularly diptera) contributed strongly to the distinction between improved E.I. and other E.I. types and was therefore a more important component in the E.I. arthropod community than we expected. E.I. had generally much higher densities of non-pest arthropods than the crop area and these arthropods might therefore disperse into the crop area. However it was difficult to detect these E.I. effects because crop conditions were variable between farms and crop area conditions had a strong effect on functional group abundance which may have offset the E.I. effect.

4.6. Recommendations

Further research related to this study may concern the impact of detrital subsidy (Wise *et al.*, 1999; Polis & Hurd, 1996) in arable farming systems, and might specifically address predation pressure in crops where epigeic predators find abundant detritivorous prey. Here the conceptual issue is indirect control of the herbivore subweb, including pests, by management of the detritivore subweb, *i.e.* the soilsystem (De Ruiter *et al.*, 1993; Brussaard, 1998). Connected with the theme of detrital subsidy, are studies on higher trophic levels in the farm food web, which are supported by both detrital and herbivore subwebs. Relations between both primary subwebs may affect food availability for insectivorous birds that have value for nature conservation.

Interference between predators might be another important research topic. Information on intraguild predation and subsequent releases of taxa at lower trophic levels, might explain features that are possibly common in arthropod communities on farms (Tscharntke, 1997).

Appropriate study areas for research with regard to detrital subsidy, predator interference and food web structure should include, preferably, a combination of relatively similar (commercial) farms, and additionally experimental fields for testing extreme management options. Practice farms are important study objects, because effects may only occur in a farming system, and such farm level experiments are very expensive; another reason is that experimental manipulation on farms must necessarily remain within the boundaries of organic agricultural production systems which may safeguard the later applicability of research outcomes.

With regard to functional group assessment, improved definition of the assemblages is needed. In particular, herbivorous taxa might be aggregated in a more sophisticated way. For example Hald & Redderson (1990) distinguished crop-related and non crop-related herbivores, and Tscharntke (1997) distinguished endo- and ectophagous species.

For optimisation of E.I. with regard to arthropod functional groups, further comparative research including experiments of mowing regimes might be required (*e.g.* Boatman *et al.*, 1999; Remmelzwaal & Voslamber, 1996). These studies should also take into account detritivorous and root herbivorous arthropods. Additional attention in arable field margins is required for abundant molluscs and earthworms and the effects of ant nests on the arthropod community.

With regard to practice, results suggest that improving the ecological infrastructure is worthwhile: in particular, late mowing is important to enhance arthropod numbers and diversity. However, frequently mown margins with intact swards can also harbour high insect densities. It might be better to avoid an 'intermediate' type of mowing management, involving few cuts per year and a late (June) first cut to ground level with a flail mower. This management is probably deleterious for arthropod abundance. With regard to the promotion of beneficials in the crops, more research is still needed to find soundly based practical recommendations relating to crop and ecological infrastructure management.

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Chapter 3: Shifts in functional group composition of ground dwelling arthropods in relation to ecological infrastructure and conversion to organic farming

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Abstract

Hypotheses on the relation of farm management and ecological infrastructure (E.I.) characteristics to the functional group composition of ground dwelling arthropods in the crop and E.I. were tested on organic arable farms. The study area included 8 farms that varied with regard to the studied traits. Arthropods were collected by pitfall traps in wheat crops and adjacent canal banks. Observations in the crop area suggested that the arthropods were affected by farm 'intensity', as defined by crop rotation, manuring and soil cultivation. Broadly in accordance with the hypotheses, relatively high abundance of predacious beetles, lycosid spiders, granivorous beetles and folivores were found in crop areas with a comparatively low 'intensity'. In contrast to the hypotheses, small staphylinid beetles, as representing the detritivores, seemed to be associated with a high 'intensity', and the linyphiid spiders suggested an association to large continuous fields. Contrary to improved E.I., traditionally managed E.I. enhanced specific groups like lycosid spiders, small staphylinids as well as ground dwelling herbivores. Improved E.I. did not support a high density of ground dwellers in the summer. Comparison of crop area and E.I. observations suggested that the most numerous epigeic groups (predacious beetles and linyphiid spiders) in both crop area and E.I. were affected by crop area conditions. Possible interactions between epigeic arthropod predators are discussed with reference to field observations.

1. Introduction

1.1. Biodiversity-loss in agriculture

Populations of various animal and plant species on farmlands in industrialised countries are seriously declining due to agricultural intensification (*e.g.* Paoletti, 1999; Fuller *et al.*, 1995; Andreasen *et al.*, 1996). This biodiversity-loss is a matter of great concern for ecologists, agriculturists as well as the general public (Paoletti, 1999; Wood & Lenné, 1999), who are increasingly aware of both the intrinsic as well as the economic value of biodiversity.
To reverse this trend of biodiversity-loss, development of multi-species or sustainable farming systems is probably needed (Vandermeer *et al.*, 1998; Altieri, 1994, 1999; Almekinders *et al.*, 1995). These farming systems utilise ecosystem services provided by biodiversity (*e.g.* pest control, soil fertility) and may also give room for nature conservation-worthy biodiversity of which the utility is not clear (Duelli *et al.*, 1999). Several examples of multi-species farming system practices are elaborated by Altieri (1994), Wood & Lenné (1999), and other authors.

Development of multi-species farming-systems may require specific research approaches, particularly with regard to the study area and studied variables. First the research should take site-specificity of biodiversity into account (Vandermeer *et al.*, 1998), and should preferably start from 'nearly natural systems' which exhibit the processes on which ecosystem services are based (Brown, 1999a). Second the variables, should specifically address the farm-, or higher levels of aggregation (Almekinders *et al.*, 1995), and therefore address the whole biocoenosis (Büchs *et al.*, 1997). This may involve recognition of the holistic concept that not all structures at the system level could be predicted by component knowledge (Stobbelaar & Van Mansvelt, 2000; Bockemühl, 1986; Sheldrake, 1988, 1991). Third the predictor variables should remain clearly related to decisions in the farm management, so outcomes can be translated to farming practice and policy, including management of semi-natural habitats on the farm (Vereijken, 1998; Smeding & Joenje, 1999; Park & Cousins, 1995).

1.2. Organic farms and ecological infrastructure

Among appropriate objects in Europe for empirical system-oriented research on farm biodiversity are probably organic farms, corresponding to production guidelines 2092/91 in the EC countries (Anonymous, 1991); the maintenance and utilisation of biodiversity is inherent to the philosophy of organic farming. Research provides evidence that organic farming as compared to conventional farming involves increased numbers and species diversity of birds (Chamberlain *et al.*, 1999; Braae *et al.*, 1988), vegetation dwelling arthropods (*e.g.* Moreby & Sotherton, 1997; Hald & Reddersen, 1990), epigeic arthropods (reviewed by Kromp, 1999), earthworms (Pfiffner & Mäder, 1997), arable weeds (*e.g.* Van Elsen, 2000; Smeding, 1993) and habitats (*e.g.* Stobbelaar & Van Mansvelt, 2000; Chamberlain *et al.*, 1999).

Of particular interest, because of their increased similarity to 'nearly natural systems' (Brown, 1999a), might be farms that combine organic cropping with a purposefully enlarged, spatially distributed and diversified ecological infrastructure. In this article ecological infrastructure (E.I.) is defined as the total of semi-natural (aquatic, woody, tall herb and grassy) habitats on the farm including its spatial arrangement (Smeding & Booij, 1999). In various farming systems, enlarged and diversified E.I. enhances the numbers and diversity of indigenous plants and animals at the farm level, including the crop area (*e.g.* Joenje *et al.*, 1997; LaSalle, 1999; Boatman *et al.*, 1999). In organic farms this may contribute to pest control (Kromp & Meindl, 1997; Theunissen & Köhl, 1999) and to soil fertility (Brown, 1999b).

1.3. Food web approach

An appropriate methodology for biodiversity research, addressing variables at higher levels of aggregation, is offered by recent advances in research of food webs (Polis & Winemiller, 1996; Pimm, 1991). These advances, including some studies in agricultural habitats (*e.g.* De Ruiter *et al.*, 1995; Tscharntke, 1997), are providing inspiring examples of how (agro) ecosystems can be approached at higher integration levels than the species-level. Some of this research indicates that farm food webs can mediate the effects of environmental factors on species (Wise *et al.*, 1999; Tscharntke, 1997).

Our general hypothesis about the farm food web on organic arable farms with improved E.I. is based on three sub-hypotheses:
First that the detrital web is enhanced by the increased organic matter input, involving organic manure, compost and crop residues (of cereals and ley pasture), and relates to increased numbers of invertebrate meso- and macrofauna (*e.g.* Pfiffner & Mäder, 1997; Weber *et al.*, 1997; Idinger *et al.*, 1996; Heimbach & Garbe, 1996). Second that numbers of various non-pest herbivorous functional groups are enhanced by improved E.I. (Holland & Fahrig, 2000; Boatman *et al.*, 1999) but also by organic crop characteristics (Hald & Redderson, 1990; Morbeby & Sotherton, 1997). Third, combined increase of detrital and herbivore invertebrates relates to a cumulative positive effect on the abundance of predators which feed on prey from both detrital and herbivore subsystems (Wise *et al.*, 1999; Idinger *et al.*, 1996; Sunderland *et*

al., 1996a; Kromp, 1999). This effect is accelerated by the frequently occurring food shortage on farms, limiting the abundance of both predacious invertebrates (Booij *et al.*, 1996) as well as vertebrates (Poulsen *et al.*, 1998).

Additionally we expect that succession of food web structure requires time (Idinger & Kromp, 1997; Idinger *et al.*, 1996), possibly up to at least one or two crop rotations. Former application of pesticides and depletion of organic matter and soil compaction due to reliance on artificial fertilizers may negatively influence the rate of this succession (*e.g.* Paoletti, 1999).

1.4. Hypotheses and objectives

Our field study was focussed on functional group composition of ground dwelling arthropods, comprising detritivore, herbivore and predator groups. Particularly the epigeic predators have major quantitative and functional importance in the farm food web, linking the detrital and grazer food chains (*e.g.* Kromp, 1999; Sunderland, 1991). Complementary studies, published elsewhere, were devoted to vegetation dwelling arthropods (Smeding *et al.*, 2001b) and insectivorous birds (Smeding & Booij, 2001).

Applying the farm food web hypotheses to ground dwelling arthropod functional groups we expected to find more epigeic predators, detritivores and herbivores in crops of organic farms with a long duration and/or extensive crop rotation (*i.e.* high proportion of gramineous crops). We also expected to observe positive effects of improved E.I. (*i.e.* large area and appropriate management) on the abundance of predacious and herbivorous functional groups in both crops and E.I. Although parts of this hypotheses are already tested (references mentioned above and *e.g.* Ryszkowski *et al.* (1993) and Ryszkowski & Karg (1991), who compared above-ground insect biomass in various agricultural landscapes), hypotheses integrating the effects of duration of organic management and effects of E.I. management on functional group composition have not been tested so far.

Thus, the objectives of this study were:

1. to determine the abundance of ground dwelling arthropod functional groups in the crop area and in the ecological infrastructure of organic farms, and relate the abundance of these groups to crop area and ecological infrastructure characteristics;
2. to relate the abundance of ground dwelling arthropod functional groups in the crop area to their abundance in the ecological infrastructure.

2. Materials and methods

2.1. Study area

The study was done on organic farms in the province of Flevoland, The Netherlands. The farms are located in the three polders Noordoostpolder, Oostelijk Flevoland and Zuidelijk Flevoland (Fig.1). These three polders were reclaimed around 1940, 1957 and 1968 respectively, and are dominated by agricultural landuse. The soil is a calcareous clay-sandy clay of marine origin. Flevoland was chosen as a study area because it has a concentration of organic farms that are similar with respect to their history and topography. There are currently 75 economically viable organic arable farms in Flevoland, which are generally large (c. 30-70 ha) and intensive relative to other organic arable farms in Europe.

Eight farms were selected based on differences in crop area and E.I. characteristics (Table 1). The selection included seven commercial organic farms and one experimental farm. The selected commercial farms were all arable, although two (farms N and T) possessed a stable with livestock, which received fodder crops from the same farm but grazed elsewhere during the summer. The experimental farm of Wageningen University (farm E) is a mixed dairy and arable farm. Four commercial farms (farms A, T, L, and D) were Ecological Arable Farming Systems (EAFS) prototype farms during 1992-1997 (Vereijken, 1997); among these farms, farm A is different because it is situated in the youngest polder Zuidelijk Flevoland and joined the EAFS-project a few years later than the others. Farms A and N started in 1985 on an experimental reclamation area, which had never received pesticides.

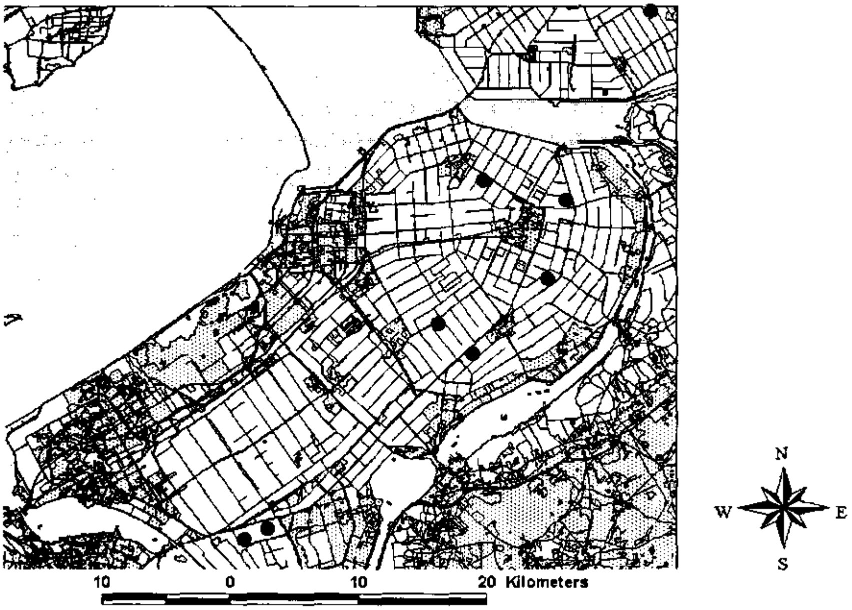

Fig. 1. Study area. The investigated organic arable farms are represented by closed circles.

2.1.1. Crop area characteristics

Organic duration of the selected farms ranged from one to twelve years. Ploughing is done generally at 25-30 cm depth. On all the farms a 6-7 year crop rotation is maintained, with 6-11 different crops per farm. Together the farms comprised 542 ha arable land with per farm 15-33% cereals, 0-36% ley pasture, 10-31% traditional lifted crops (potatoes, sugar beet) and 19-69% vegetable crops. Vegetables involve mainly onions, runner beans, various cabbages, peas, and sweet corn. The farms with most extensive crop rotations had a high percentage (>30%) of gramineous crops (cereals and ley pasture) and therefore a low percentage (<50%) of vegetable crops. As compared to other crops, gramineous crops provide a large amount of carbon in crop residues and require few soil disturbing operations. Because input of nutrients (N, P, K) has to be adjusted to crop requirements, and vegetables need more nutrients than cereals, intensity of crop rotation is assumed to relate to both the amount of crop residues and the amount of N-application at the farm level.

Table 1

Characteristics of the farms and ecological infrastructure and total numbers per farm of arthropod functional groups captured in weekly trappings over an eight week period in the wheat crop (30 m from the field margin) and in the ecological infrastructure.

Level	**Variables**		**D**	**T**	**F**	**R**	**L**	**E**	**A**	**N**
Farm	n Year of organic farming (n)	dur	8	8	7	1	10	4	12	12
Farm	Cereals and ley pasture (%)	int	35	38	24	18	11	61	38	59
Farm	Crops within 100 m range of E.I. (%)	ei 100	72	74	74	65	80	90	47	40
Farm	Semi-natural habitat (E.I.) (%)	area	3.5	2.3	1.4	1.6	3.1	4.5	2.1	0.8
E.I.	Mowing date (farm level) (month)	mow	7	9	5	5	6	6	7	5
E.I.	Mowing frequency (n/year)	mowfrq	2	1	2	3	2	2	2	3
E.I.	Height vegetation (m)	eihgt	1.4	2.4	1.1	0.7	0.8	1.5	0.4	0.5
E.I.	Cover vegetation (%)	eicov	95	95	88	77	85	100	98	67
E.I.	Species diversity vegetation (n/4 m^2)	eispn	16.0	12.0	9.5	7.5	13.2	11.8	10.5	9.3
E.I.	Dominant species diversity (n/4 m^2)	eidom	3.8	3.4	3.1	2.3	3.0	3.4	3.4	2.8
	Age polder (year)	lsage	57	41	41	41	41	41	30	30
Crop	Predacious beetles		1731	1333	3765	1011	1035	2889	952	1064
Crop	Lycosid spiders		8	57	38	18	83	35	53	146
Crop	Linyphiid spiders		1944	2979	2622	2515	2055	1687	3061	3311
Crop	Small staphylinid beetles		541	893	425	640	772	205	1308	329
Crop	Granivorous carabids		15	7	4	3	19	504	5	83
Crop	Folivores		5	7	21	13	6	8	4	3
E.I.	Predacious beetles		926	1205	2808	832	1706	2603	1365	1319
E.I.	Lycosid spiders		64	208	302	46	168	226	87	535
E.I.	Linyphiid spiders		2554	880	4235	1191	1607	1930	2508	2577
E.I.	Small staphylinid beetles		709	444	334	365	217	411	739	703
E.I.	Granivorous carabids		66	83	79	253	291	279	52	149
E.I.	Folivores		100	150	33	38	61	35	104	275

2.1.2. Ecological infrastructure characteristics

The Ecological Infrastructure (E.I.) of arable farms in Flevoland is mainly determined by canals and banks (together c. 3-4 m width) that are laid out as linear herbaceous boundaries adjacent to the crops. On five farms, boundaries are wider because of adjacent (2-3 m wide) grass strips, often including clovers (*Trifolium* spp.), on one or both sides of the canals. Farm E also has grass strips between crop plots. Percentages of E.I. higher than c. 2% (Table 1) were mainly due to the presence of these grass strips. Only farms L and E possessed a boundary planted with a hedgerow. Spatial density of E.I. is purposefully increased on farm E (Smeding & Joenje, 1999) and farm L. The spatial arrangement of E.I. on the other 6 farms mainly reflect landscape scale.

Extreme types of vegetation management are:

- 'traditional management' involving three or four more cuts per year with a flail mower leaving the shredded cuttings *in situ*;
- 'late mowing management' involving one or two cuts per year after June 21st with a finger-bar mower with a hiab grab for removal of cuttings.

The grass strips along the canals are required for field transport in 'late mowing management'. The E.I. area is, therefore, related to the mowing date. In this article the E.I. with enlarged area and late mowing is defined as 'improved E.I.'. The improved E.I. on the four farms (A, T, L, and D) was created during the EAFS-prototyping research program in 1992-1997

(Vereijken, 1997, 1998). The improved E.I. on the experimental farm E started in 1995 simultaneously with conversion of the conventional dairy farm to an organic mixed farm (Smeding & Joenje, 1999).

Dominant plant species in canal bank swards are: couch (*Elymus repens*), perennial meadow grasses (*Festuca rubra, Poa trivialis, Lolium perenne, Agrostis stolonifera*), common reed (*Phragmitis australis*) and a few perennial herbs: dandelion (*Taraxacum officinale*) and stinging nettle (*Urtica dioica*). Canals with traditional management have a low, relatively open, species poor vegetation (<10 species/4 m^2), dominated by a few grass species. Late mowing particularly relates to increased vegetation biomass in June and July as expressed by vegetation height (up to 1-3 m) and cover (up to 90-100%). However, late mowing does not necessarily relate to increased higher plant species diversity for two reasons: a) tall grass species may dominate the sward; b) swards of traditional management may locally be cut to ground level and therefore be invaded by ruderals and annuals (increased species number up to 15 species/4 m^2), *e.g.* thistles (*Cirsium arvense, Sonchus arvensis*), annual weeds (*e.g. Sonchus asper, Polygonum aviculare*) and annuals that are rarely pernicious weeds in Flevoland (*e.g. Myosotis arvensis, Veronica persica, Cardamine hirsuta*).

High perennial plant diversities found in some locations may relate to various interrelated factors (Kleijn, 1997): reduced vegetation productivity, removal of hay, nutrient buffering by the grass strip, and long organic duration. However, also, artificial species introduction is involved; in the EAFS-project, around 90 different native perennial dicots were artificially seeded in the canal banks to obtain higher plant diversity and flower abundance of plants with limited dispersal capacity (Vereijken, 1998). Although few species were able to settle well (*e.g. Senecio jacobea, Crepis biennis, Heracleum sphondylium*), the introduction clearly affected species diversity: vegetation including sites with >15 species/4 m^2 were confined to prototype farms.

2.2. Sampling and measurements

2.2.1. Arthropod sampling

Sampling was done in wheat crops and in adjacent canals banks (E.I.) which were situated in the interior of the organic farm area. Wheat (*Triticum aestivum* L.) was chosen as a representative crop as this crop is common on organic arable farms in Flevoland and arthropod numbers in cereals are large compared to numbers in other common crops like potatoes and onions (Booij & Noorlander, 1992). Within one wheat field on each of the eight farms one 60×30 m^2 sampling area was selected; this area was 60 m long bordering a canal by 30 m perpendicular to that canal. Six pitfall traps (10 cm diameter) were placed in a row with intervals of 10 m at distances of 0 m (E.I.) and 30 m (wheat) from the field boundary. Traps contained a preservative of 4% formaline plus detergent. Weekly samples were taken during 8 weeks, starting from 6th of June until 28th of July 1998. The observations of the six traps and eight sampling dates were treated separately, giving 48 measurements per habitat (crop or E.I.) per farm. Springtails (Collembola), and ants (Formicidae) were discarded because pitfall traps do not give representative measurements of these groups. Arthropods were stored in 95% alcohol. Individuals were sorted to taxa at order- or family-level and placed into six different arthropod functional groups:

- Predacious polyphagous beetles including carnivorous Carabidae and large (>6 mm) staphylinid beetles;
- Lycosid spiders which are relatively large polyphagous predators and represent diurnal wandering spiders (Marc *et al.*, 1999; Sunderland, 1991);

- Linyphiid spiders which are relatively small species and represent highly dispersive sheet-web spiders (Marc *et al.*, 1999; Sunderland, 1991);
- Small staphylinid beetles of the epigeobiontic lifeform (Bohac, 1999) which are mainly fungivorous and represent the detritivore functional group among epigeic arthropods;
- Granivorous carabid beetles (genera *Amara* and *Harpalus*) representing the invertebrate granivore functional group; although these carabids may feed, to some extent, on invertebrates as well (Westerman *et al.*, in prep.);
- Folivorous herbivores represented by weevils (Curculionidae) and leaf hoppers (Cicadellidae).

2.2.2. Vegetation measurements

Vegetation studies included the E.I. where pitfalls were located. The investigation was done from May to August: late mown vegetation was sampled in June-July before the first cut. Early and or frequently mown vegetation was sampled before the first cut (May) or later (until August) when species composition could be identified adequately. The herb layer was sampled in seven plots of 4 m^2 area with intervals of 50 m between samples. Plots included the ditch bank vegetation from the top to the helophytic zone; vegetation affected by flooding was excluded. Parameters were: cover, maximum height, plant species and dominant plant species (totalling 80% cover). Averages were calculated for each farm.

2.2.3. Farm management and lay out

A 1:5000 map was made of each farm, depicting the different crops and the ecological infrastructure (E.I.). On these maps the area of semi-natural and crop habitats were measured. The 'E.I.-area' is calculated as the percentage of semi-natural habitat of the farm area (without the farm yard). Farm rotation intensity is defined as the proportion of gramineous crops (cereals and ley pasture) of the total crop area. The spatial arrangement of the E.I. or 'E.I. density', was expressed as the percentage of the farm within a 100 m distance of the E.I. In case the canal bank vegetation was cut both after September 15th and before May 15th, a distance of 70 m was considered. The influence of field margins on the abundance of large carabid beetles and spiders probably does not exceed 70-100 m (Booij, unpublished data).

Data on the year of conversion of all of the farm to organic, husbandry practices in the wheat crop in 1998, and mowing of canals banks and grass strips were obtained using a questionnaire. The mowing management is represented by the month of the first cut, because this cut largely determines the phenological stage of the vegetation in June and July.

2.3. Statistical analyses

Data from all sampling periods were combined, tested for normality and ^{10}log-transformed. All subsequent analyses were conducted using Statistical Analysis System (SAS Institute, Cary, North Carolina).

Individual farms were classified into one of three groups on the basis of corresponding farm and E.I. characteristics (Table 1). With regard to the crop area samples, the classifications were based on relevant farm level characteristics (duration, rotation intensity, area of E.I., and E.I. density). With regard to the E.I. samples, the classifications were based on both farm level characteristics as well as E.I.-vegetation characteristics (duration, E.I.-area, month of first mowing, vegetation cover, vegetation height, plant species number or dominant plant species number per 4 m^2). The classifications were determined by two splits: the first split based on one of the above mentioned characteristics, separated a category of 2-3 farms and the second split based on another of these characteristics, divided the remaining 5-6 farms in a second and a third category. The minimum category size was 2 farms. For all obtained classifications canonical discriminant analyses were performed on the numbers of the arthropod functional groups. Data of the crop area and of the E.I. were analysed separately for crop area and E.I. classifications respectively. The classifications with the highest Wilks' Lambda F-value were selected.

Stepwise and canonical discriminant analyses were performed on the numbers of arthropod functional groups to determine the most important groups that could classify the farms into three categories. Arthropod observations in the wheat and in the E.I. were again analysed separately. Stepwise discriminant analysis was also used to identify variables that contributed most to the selected classification. Canonical discriminant analysis was used to determine the magnitude and direction of the association of individual variables with indicator variables. Standardised canonical coefficients larger than 0.3 divided by the square root of the eigenvalue of the canonical function (Afifi & Clark, 1984) were considered large enough to contribute significantly to the classification.

Differences in the abundance of arthropod functional groups between the three categories were tested by linear regression (GLM) using the ^{10}log-transformed measurements and including a Duncan's multiple range test.

The combined data-set of wheat and E.I. samples was used to analyse the abundance of arthropod functional groups along the gradient from E.I. to crop centre, represented by two sampling distances 0 m (E.I.) and 30 m (wheat) from the field margin. ANOVA was performed on the two selected classifications to determine interactions between distance and category.

3. Results

3.1. Observed numbers of epigeic arthropod functional groups

During eight weeks 77,784 organisms were caught in 96 pitfall traps including 40,233 organisms in the crop area and 37,551 organisms in the Ecological Infrastructure. Crop area samples comprised 33% predacious carabid beetles, 1% large (>6 mm) predacious staphylinid beetles, 1% lycosid spiders, 50% linyphiid spiders, 13% small (<6 mm) detritivorous staphylinid beetles, 0% folivores and 2% granivorous carabid beetles. E.I. samples comprised 33% predacious carabid beetles, 1% large predacious staphylinid beetles, 4% lycosid spiders, 10% small detritivorous staphylinid beetles, 47% linyphiid spiders, 2% folivores (Curculionide and Cicadellidae) and 2% granivorous carabid beetles.

3.2. Arthropod functional groups in the crop area, affecting distinctions among farm categories

The classification 'int/area' based on crop rotation intensity (first split) and area of the ecological infrastructure (second split) gave the best separation of crop area arthropod observations (canonical discriminant analysis, Wilks' Lambda, F-value=30.1, P<0.0001; Table 2). The second best classification 'ei100/dur' (Wilks' Lambda, F-value=28.1, P<0.0001) was interesting because the distinction was affected by the the most abundant group predacious beetles, whereas the distinction of the best classification was only affected by less abundant groups. Therefore both classifications are presented below.

Table 2

Examples of classifications of the crop area and the ecological infrastructure, including the the Wilks' Lambda F-value and the squared canonical correlation obtained by canonical discriminant analysis. The abbreviations of category characteristics are explained in Table 1.

Crop area:

	Category 1	**Category 2**	**Category 3**	F-value	Sq. Can.
Category	int>40	int<40 & area >2.2	int<40 & area <2.2	30.1	0.52
Farms	*NE*	*TLD*	*AFR*		
Category	ei100<70	ei100>70 & dur<8	ei100>70 & dur>8	28.5	0.46
Farms	*ANR*	*FE*	*TLD*		
Category	int<20	int>20 & ei100<50	int>20 & ei100<50	22.8	0.34
Farms	*RL*	*AN*	*TFED*		
Category	int<30	int>30 & area<2.2	int>30 & area>2.2	19.7	0.32
Farms	*ARL*	*FN*	*TED*		
Category	dur<6	dur>6 & area<2.2	dur>6 & area>2.2	12.0	0.19
Farms	*RE*	*ANF*	*TLD*		

Ecological infrastructure:

	Category 1	**Category 2**	**Category 3**	F-value	Sq. Can.
Category	eispn≥12	eispn<12 & eicov>80	eispn<12 & eicov<80	15.9	0.32
Farms	*TLD*	*AFE*	*NR*		
Category	eispn≥12	eispn<12 & eihgt>1	eispn<12 & eihgt<1	15.7	0.33
Farms	*TLD*	*FE*	*ANR*		
Category	eihgt≤0.5	eihgt>0.5 & mow<7	eihgt>0.5 & mow≥7	14.2	0.27
Farms	*AN*	*FRL*	*TED*		
Category	mow≥7	mow<7 & eidom>3	mow<7 & eidom<3	12.7	0.25
Farms	*TED*	*FL*	*ANR*		
Category	eicov<80	eicov>80 & mow<7	eicov>80 & mow≥7	11.9	0.23
Farms	*NR*	*AFL*	*TED*		

Table 3

Arthropod variables that contributed significantly to classification of the crop area observations in 'int/area' farm categories by stepwise and canonical discriminant analyses, standardised canonical coefficients, and mean values per crop area category. Comparison of arthropod numbers in the categories by Duncan's multiple range test.

	Can 1[b]	Mean values and multiple range comparison						
Variables[a]	Standardised coefficient	Category 1: *int>40* mean		Category 2: *int<40 & area>2.2* mean		Category 3: *int<40 & area<2.2* mean		
Granivorous carabids	0.89[c]	6.1	a	0.3	b	0.1	b	(P<0.0001)
Lycosid spiders	0.43	1.9	a	1.0	b	0.8	b	(P<0.0001)
Small staphylinids	-0.39	5.6	b	15.3	a	16.5	a	(P<0.0001)
Linyphiid spiders	0.15	52.1	b	48.5	b	56.9	a	(P<0.01)
Folivorous insects	-0.05	0.1	b	0.1	b	0.3	a	(P<0.05)
Predacious beetles	-0.04	41.3	a	28.5	b	39.8	b	(P<0.05)

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[a] Variables are listed in order of selection by stepwise discriminant analysis. Italicised variable was not selected by stepwise discriminant analysis.

[b] Canonical function 1; responsible for 95% of the variation.

[c] Standardised coefficients >0.29 were considered large enough for interpretation.

3.2.1. Classification 'int/area'

Category 1 included farms with an extensive crop rotation (>40% cereals and ley pasture); category 2 included farms with an intensive crop rotation and a large E.I. area (which were the three former prototype farms in Oostelijk Flevoland); category 3 included farms with an intensive crop rotation and a small E.I. area.

All arthropod functional groups except predacious beetles, were selected as important factors by stepwise discriminant analysis for discrimination among the three categories (Table 3). The first canonical function containing granivorous carabid beetles, lycosid spiders, and small staphylinid beetles separated category 1 (extensive crop rotation) farms from both other categories with intensive crop rotation (Fig. 2); granivorous carabids and lycosid spiders were positively associated, and small staphylinid beetles were negatively associated with this first axis (Table 3). In the second canonical function none of the arthropod groups had sufficient canonical loading; however, linyphiid spiders contributed most to the separation of categories 2 and 3, and were positively associated with the small E.I. area of category 3.

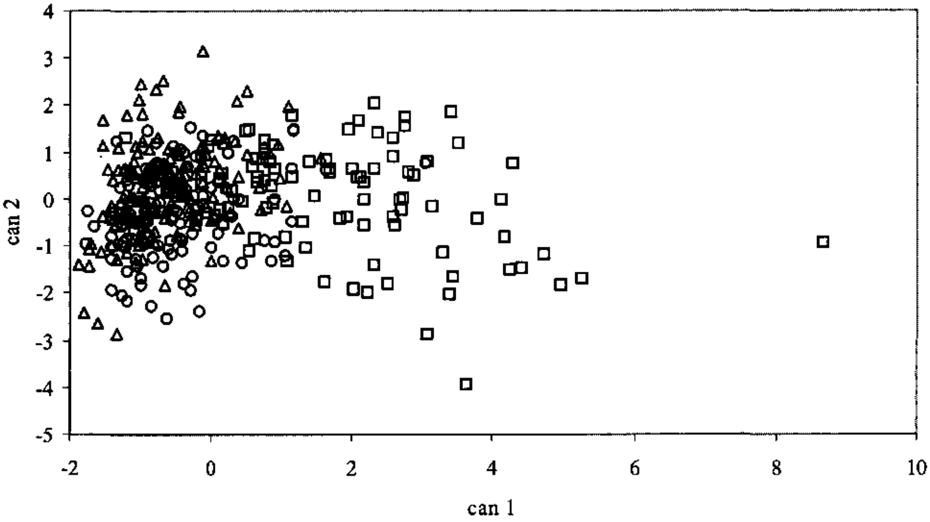

Fig. 2. Plot of the second and first canonical functions discriminating among farm categories of the classification 'int/area'. Squares represent farms with >40% gramineous crops; circles represent farms with <40% gramineous crops and >2.2% E.I. area; triangles represent farms with >40% gramineous crops and <2.2% E.I.

On farms with extensive crop rotation (category 1), granivorous carabid beetles were >20 times more abundant on average, lycosid spiders were >90% more abundant on average and small staphylinid beetles were >60% less abundant on average, than on the other two categories. Linyphiid spiders were 15% more abundant on average in category 3 (intensive crop rotation with small E.I.) than in category 2 (intensive crop rotation with large E.I.) (Table 3).

3.2.2. Classification 'ei100/dur'

Category 1 included farms with large scale E.I./landscape; category 2 included farms with a spatially dense E.I. and moderately long (4-7 years) organic duration; category 3 farms had a spatially dense E.I. and a long organic duration (8-10 years) (these were the three former prototype farms in Oostelijk Flevoland).

The separation into 'ei100/dur' categories, based on arthropod functional group numbers in wheat, is illustrated in a plot of canonical variable two versus canonical variable one (Fig. 2). All arthropod functional groups were selected as important factors by stepwise discriminant analysis for discrimination among the three categories (Table 4). The first canonical function containing predacious beetles, small staphylinid beetles and granivorous carabids separated the farms with dense E.I. and moderate duration (category 2) from both other categories (Fig. 2). Predacious beetles and granivorous carabids were positively associated and small staphylinid beetles were negatively associated with the first axis (Table 4). In the second canonical function none of the arthropod groups had sufficient canonical loading; however, linyphiid spiders contributed most the separation of category 3 and 1, and were positively associated with a large scale landscape (category 1).

In extensive farms (category 1), predacious beetles were >2 times more abundant on average, granivorous beetles >8 times more abundant and small staphylinid beetles were >2 times less abundant on average, than in the other two categories. Linyphiid spiders were >20% more abundant on average in category 3 (large scale landscape farms) than in both other categories (Table 4).

Table 4
Arthropod variables that contributed significantly to classification of the crop area observations in 'ei100/dur' farm categories by stepwise and canonical discriminant analyses, standardised canonical coefficients, and mean values per crop area category. Comparison of arthropod numbers in the categories by Duncan's multiple range test.

	Can 1[b]	Mean values and multiple range comparison						
Variables[a]	Standardised coefficient	Category 1: *ei100<70* mean		Category 2: *ei100>70 & dur<8* mean		Category 3: *ei100>70 & dur>8* mean		
Predacious beetles	0.86[c]	21.1	c	69.3	a	28.5	b	($P<0.0001$)
Small staphylinid beetles	-0.42	15.8	a	6.6	b	15.3	a	($P<0.0001$)
Lycosid spiders	-0.26	1.5	a	0.8	b	1.0	b	($P<0.0001$)
Granivorous carabid beetles	0.28	0.6	b	5.3	a	0.3	b	($P<0.0001$)
Linyphiid spiders	-0.06	61.7	a	44.9	b	48.5	b	($P<0.0001$)
Folivorous insects	0.16	0.1	b	0.3	a	0.1	b	($P<0.05$)

[a] Variables are listed in order of selection by stepwise discriminant analysis.
[b] Canonical function 1; responsible for 86% of the variation.
[c] Standardised coefficients >0.32 were considered large enough for interpretation.

3.3. Arthropod functional groups in the Ecological Infrastructure affecting distinctions among E.I. categories

The classification 'eispn/eicov', based on E.I.-species number (first split) and E.I.-vegetation cover as second split gave the best separation of observations (canonical discriminant analysis, Wilks' Lambda, F-value=15.9 ($P<0.0001$); Table 2). Classifications based on organic duration, E.I. area, date of first mowing, E.I.-vegetation height and dominant species number showed less distinction than the classification 'eispn/eicov' (Table 2). Category 1 included species rich E.I. on prototype farms in Oost Flevoland; category 2 included a less species rich E.I. with a dense vegetation; category 3 included a species poor E.I. with open vegetation related to traditional mowing management.

The separation into 'eispn/eicov' categories, based on arthropod functional group numbers in the E.I., is illustrated in a plot of canonical variable two versus canonical variable one (Fig.3). All arthropod functional groups were selected as important factors by stepwise discriminant analysis for discrimination among the three categories (Table 5). The first canonical function separated the species poor categories 2 and 3 from each other (Fig. 3); predacious beetles and linyphiid spiders were positively associated with dense vegetation and granivorous carabid beetles were negatively associated with dense vegetation (Table 5). In the second canonical function none of the arthropod groups had sufficient canonical loading; however, linyphiid spiders contributed most to the separation of category 1 from both categories 2 and 3, and were negatively associated with species rich vegetation.

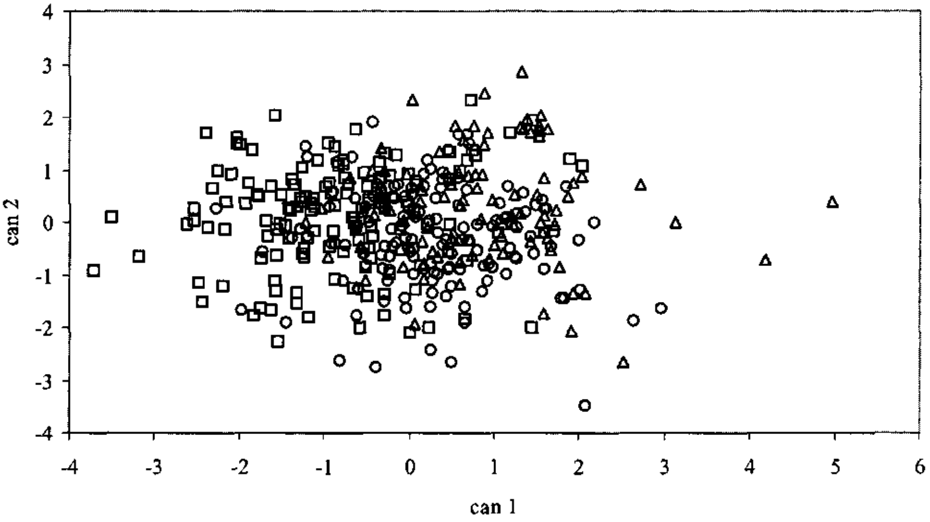

Fig. 3. Plot of the second and first canonical functions discriminating among E.I. categories of the classification 'eispn/eicov'. Circles represent the E.I. with plant species number >12; squares represent E.I. with plant species number <12 and vegetation cover >80%; triangles represent E.I. with plant species number <12 and eicov<80.

Predacious carabid beetles and linyphiid spiders were >70% and >50% respectively more abundant in the E.I. with few plant species and dense vegetation (category 2) as compared to other catagories. Granivorous carabids were >30% more abundant in E.I. with species poor and open vegetation (category 3; 'traditional management'); also folivores were more abundant here but did not contribute to the distinctions between the categories because of their low numbers (Table 5).

Table 5
Arthropod variables that contributed significantly to classification of E.I. observations in 'eispn/eicov' categories by stepwise and canonical discriminant analyses, standardised canonical coefficients, and mean values per crop area category. Comparison of arthropod numbers in the categories by Duncan's multiple range test.

	Can 1[b]	Mean values and multiple range comparison						
	Standardised coefficient	Category 1: *eispn>12*		Category 2: *eispn<12 & eicov>80*		Category 3: *eispn<12 & eicov<80*		
Variables[a]		mean		mean		mean		
Predacious beetles	-0.92[c]	26.7	b	47.2	a	22.6	b	($P<0.001$)
Granivorous carabids	0.52	3.1	b	2.9	b	4.2	a	($P<0.001$)
Linyphiid spiders	-0.51	35.0	b	60.2	a	39.3	b	($P<0.001$)
Small staphylinids	0.43	9.5	b	10.3	b	11.1	a	($P<0.1$)
Folivorous insects	0.32	1.1	b	0.8	b	1.7	a	($P<0.001$)
Lycosid spiders	0.27	3.1	b	4.3	b	6.1	a	($P<0.05$)

[a] Variables are listed in order of selection by stepwise discriminant analysis.
[b] Canonical function 1; responsible for 89% of the variation.
[c] Standardised coefficients >0.43 were considered large enough for interpretation.

3.4. Interactions between distance to E.I. and farm category

Abundance of lycosid spiders, granivorous carabid beetles and folivores were significantly higher in the E.I. than in the wheat (Table 6). The distribution of linyphiid spiders showed a preference for the crop area. Abundance of predacious beetles and small staphylinid beetles did not significantly differ between crop area and E.I. (Table 6).

Table 6
Average numbers of arthropod functional groups in the E.I. and in the wheat crop (30 m from the field margin). Comparison of ^{10}log-transformed values by Duncan's multiple range test.

Arthropod functional group	E.I.		Crop area		Significance
Predacious beetles	12764	a	13780	a	(NS)
Lycosid spiders	1636	a	438	b	($P<0.001$)
Linyphiid spiders	17482	b	20174	a	($P<0.001$)
Small staphylinids	3922	a	5113	a	(NS)
Granivorous carabids	1252	a	640	b	($P<0.001$)
Folivorous insects	446	a	67	b	($P<0.001$)

High numbers of predacious beetles and lycosid spiders in the E.I. coincided with high numbers in the crop area (Fig. 4a and 4b). The differences in linyphiid spiders (Fig. 4c) and granivorous carabid beetles (Fig. 4d) were similar for the E.I. categories 1 ('prototype farms') and 3 ('traditional management'). However, the difference of these species was in the opposite direction in E.I.-category 2 (species poor and dense vegetation): high linyphiid abundance in the E.I. decreased towards the crop area, while it increased in both other categories (Fig. 4c); granivorous carabid beetles in category 2 were most numerous in the crop area and least numerous in the E.I. (Fig. 4e). Increased numbers of small staphylinid beetles and folivores in the E.I. did not always coincide with increased numbers in the crop area (Fig. 4e and 4f): distribution patterns of small staphylinids were very variable; folivore abundance in the E.I. was different between categories but was generally low in the crop area.

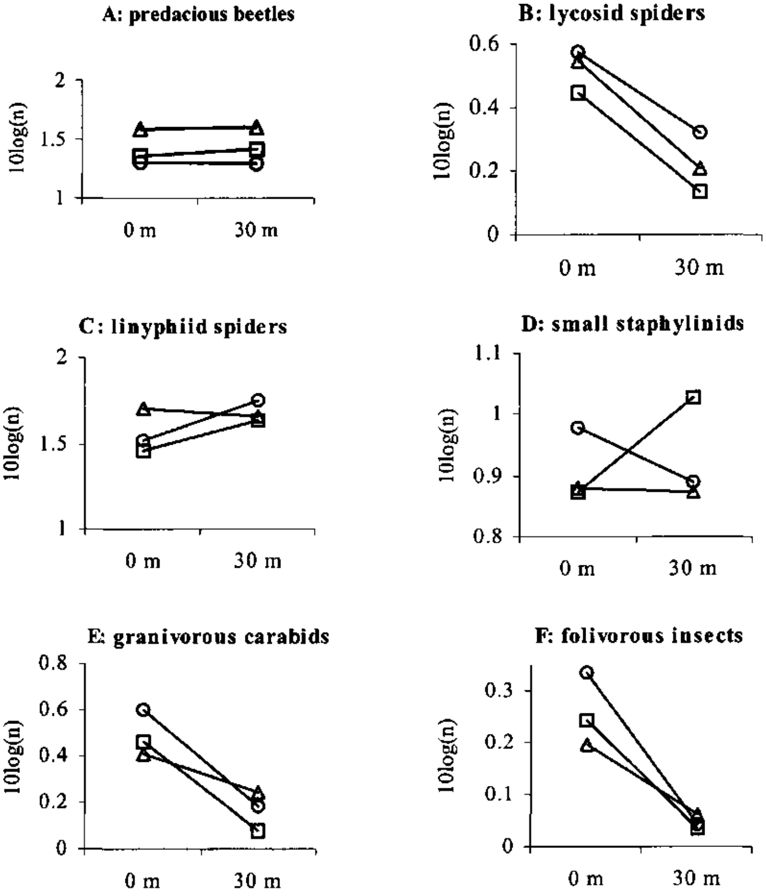

Fig. 4. The abundance of arthropod functional groups in the E.I. (0 m) and in the crop area (30 m). E.I. categories of selected classification 'eispn/eicov': Category 1 (squares)= species rich E.I. vegetation; category 2 (triangles)= species poor and dense vegetation; category 3= (circles) species poor and sparse vegetation. Lines between the averages of arthropod functional group numbers (^{10}log-transformed) are drawn to illustrate the different patterns among the three E.I. categories and do not represent estimated points in between the sampling stations. (a) predacious beetles (b) lycosid spiders; (c) linyphiid spiders; (d) small staphylinid beetles; (e) granivorous carabid beetles; (f) folivorous insects.

4. Discussion

4.1. Epigeic arthropods in the crop area

4.1.1. Observations compared to the hypotheses

It was expected that organic duration, extensive crop rotation, area of E.I., and high spatial density of E.I. would relate positively with the abundance of predacious and herbivorous ground dwelling arthropods. Also, that organic duration and extensive crop rotation would relate positively to the abundance of detritivorous epigeic arthropods. All mentioned factors indeed related to differences in the abundance of the arthropod functional groups involved in the study. However only a few of the observations of the direction of changes of abundance, were in accordance with the hypothesis: lycosid spiders (which were the least abundant predacious functional group) and granivorous carabid beetles showed affinity for extensive crop rotation; predacious beetles were associated with the farms with dense E.I.

Most observations did not correspond with our hypotheses. Extensive crop rotations (farm N and E) had a low abundance of (epigeic) detritivores, represented by small staphylinids. Predacious beetles and linyphiids, representing 84% of all observed epigeic arthropods in the crop area, did not prefer extensive crop rotation, neither a large E.I. area nor a long organic duration. Contrary to expectation, prototype farms which had a long duration, a large E.I. area and a dense spatial arrangement of E.I., harboured comparatively low abundance of all five predacious and herbivorous functional groups.

4.1.2. Small staphylinid beetles

Contrary to our hypothesis, an abundance of detritivorous staphylinids seemed to be associated with 'intensity' including not only percentage gramineous crops but also interrelated management factors like manure application, soil cultivation, weed control and pest control by entomopathogens. Ambiguous behaviour of staphylinids with regard to intensity, as compared to other large epigeic groups, is found in studies which relate to tillage treatment (Heimbach & Garbe, 1996) and farming systems comparisons (Booij & Noorlander, 1992; Reddersen, 1997; Büchs *et al.*, 1997). However, positive effects on staphylinids were reported with regard to manure (Bohac, 1999) and house waste compost (Idinger & Kromp, 1997). In a comparison of four, long-duration organic farms in an old culture landscape and polder landscape, more staphylinids were found in the polder which represents an earlier successional stage of soil community (Smeding & Booij, 1999).

Our observations and data from literature may suggest that small staphylinid abundance is positively related to a certain quantity of organic manure and frequent soil cultivation. Small staphylinids may therefore not be an appropriate indicator for the aggregate functional group of saprovorous arthropods (including also large Collembola and Diptera larvae); low C/N ratio and fiber content of organic matter input could relate to dominance within this functional group by small staphylinids.

4.1.3. Predacious beetles

The observed highest densities of predacious beetles (mainly carabids) were not associated with long organic duration or extensive crop rotation. This observation is contradicted by several field studies in which carabids were found to be associated with less intensive or organic crops (*e.g.* Booij & Noorlander, 1992; Holland *et al.*, 1996; Basedow, 1991). Several authors reported that the underlying factors which positively affected carabids were crop cover and weeds, manure and less frequent soil cultivation (Den Nijs *et al.*, 1996; Holland *et al.*, 1996; Booij & Noorlander, 1992; Idinger *et al.*, 1996). Therefore it could be possible that the farm category 2 with moderately long-duration farms might have had a lower 'intensity' (according to the above given wider definition) than category 3 with long-duration farms; category 3 included former prototype farms which had proceeded further in optimalisation of intensive vegetable production. Wheat crops in 1998 of farm category 2 had relatively high weed densities, including *Capsella bursa-pastoris* on farm E and *Polygonum aviculare* on farm F, and there was an apparent abundance of springtails on farm F, although we did not measure these features. On both farms, the robust carabid species *Pterostichus melanarius* dominated the carabid community, which was also found in the most extensive systems of comparative studies by Booij & Noorlander (1992) and Holland *et al.* (1996).

4.1.4. Spiders

Superior dispersive abitilies of linyphiid spiders are stressed by several literature sources (*e.g.* Sunderland, 1991; Halley *et al.*, 1996). This could explain the observed positive association with farms that have a low E.I. density. Both farms in Zuidelijk Flevoland had a long organic duration but the polder is young (1968) which implies larger fields and also a possibly earlier successional stage of the soil biocoenosis. Farm R is the most recently converted farm in the study area and is situated centrally in a very open landscape part of Oostelijk Flevoland. Abundance of linyphiid spiders might also indicate an earlier successional stage of the epigeic community (that could be sustained in large scale landscape with less reinvasion possibility). Accordingly, Idinger *et al.* (1997) observed most linyphiids in the inorganic as compared to organic treatments.

In all the epigeic arthropod data there was a negative correlation between large organisms (mainly carabids) and small organisms (mainly linyphiids). This suggested that intraguild predation might influence functional group composition of ground dwellers. According to Sunderland *et al.* (1996b) linyphiid abundance might be affected by predation.
Lycosid spiders were positively associated with extensive crop rotation. This was in accordance with other studies which found that lycosids prefer organic above conventional farms (Idinger *et al.*, 1997) and belong to later stages of succession (Büchs *et al.*, 1997). This suggests that lycosids are the most vulnerable functional group among predacious ground dwellers.

4.1.5. Ground dwelling herbivores

With regard to granivorous carabids, extensive crop rotation or lower 'intensity' was probably correlated with (weed) seed availability. Several studies reported the relation between mobile granivorous carabids and presence of weeds (De Snoo, 1995; Kromp, 1999). Folivores seemed to be an insignificant group in the crop area and were slightly affected by 'intensity' (*e.g.* weed control). The higher mid-field densities in less intensive systems observed by Hald & Reddersen (1990) and Büchs *et al.* (1997) were collected by vacuum sampling or emergence traps respectively, which might be more appropriate sampling methods for this group.

4.2. Epigeic arthropods in the Ecological Infrastructure

4.2.1. Observations compared to the hypotheses

Our hypothesis was that improved E.I. would promote the densities of predacious and herbivorous epigeic arthropod functional groups. However, observations did not provide evidence for this hypothesis. The E.I. category based on high plant species number, included the most succesful examples of improved E.I. This catogory involved the three former prototype farms in Oostelijk Flevoland. In this E.I. all six investigated functional groups had decreased densities as compared to other categories. Highest densities of ground dwelling detritivore and herbivore functional groups were found in the E.I. category with presumed adverse management ('traditional management' including a damaged sward).

4.2.2. Small staphylinid beetles

Although detritivores were not considered in our hypothesis with regard to the E.I., observations suggested that small staphylinids might be an important functional group in field margins. Small staphylinid numbers were positively associated with 'traditional management'. This observation suggests that staphylinids could be supported by the shredded and easily decomposable litter of frequent cuts. In a field margin study in Zuidelijk Flevoland, staphylinid density increased in the grass margins with 4 cuts per year as compared to crop edges (Remmelzwaal & Voslamber, 1996). Accordingly, Canters *et al.* (1997) found that staphylinids related positively to mowing frequency. Preference of small staphylinids to crop as compared to E.I., observed in the 'prototypes' category (late mowing) was in accordance with observations of Holland & Thomas (1996).

4.2.3. Predacious beetles

In improved E.I. in early summer, predacious beetles may be a relatively small component of the arthropod community, because potential prey is foraging or resting higher in the vegetation canopy. High densities of vegetation dwelling arthropods were found in improved E.I. by means of vacuum sampling (Smeding *et al.*, 2001b). Similar observations with regard to predacious beetles were done by Haysom *et al.* (1999) in grassed headland; lowest densities of carabids were observed in the uncut and 1 cut per year sites as compared to 3 cuts per year, field centre and unmanaged boundary sites. However, the highest predacious beetles abundance were observed in tall and species poor vegetation. Interpretation of this abundance may require a consideration of crop area influence.

4.2.4. Spiders

Linyphiid spider abundance in E.I. was difficult to interpret in relation to E.I. characteristics and probably requires consideration of interaction with the crop area density. Lycosid spiders prefer sites with a warm microclimate (Remmelzwaal & Voslamber, 1996); this may explain the observed positive relation to 'traditional management'.

4.2.5. Ground dwelling herbivores

Granivorous carabids and folivores showed positive association with the 'traditional management' of frequent mowing without litter removal. With regard to the carabids this might be explained by the occurence of annual species in open locally disturbed swards; these plants have short life cycles, may have ascendant phenotypes and can provide seeds early in the summer.

With regard to folivores more frequent cutting may improve the food availability near the soil surface, because the vegetative stage of the vegetation is sustained by the inhibition of flowering. Observations by Haughton *et al.* (1999), involving around 85% bugs and hoppers (Hemiptera), showed a devastating effect on arthropod numbers by 1 cut per year in the summer as compared to 2 cuts per year in spring and late summer. In our study such a devastating effect was not found, however folivore numbers captured by pitfalls indeed showed a positive association with frequent mowing.

4.3. Comparison of Ecological Infrastructure and the crop area

4.3.1. Differences between E.I. and crop area

According to the hypothesis, lycosid spiders, granivorous carabids and folivorous insects showed a higher abundance in the E.I. than in the crop area. However, abundance of the most numerous functional groups (predacious beetles, linyphiid spiders and small staphylinids) did not significantly decrease towards the crop. In the case of linyphiid spiders the opposite was found, which corresponds to the observations of Holland & Thomas (1996) and could relate to the dispersive abilities discussed above.

The E.I. crop area distribution pattern of linyphiid spiders, granivorous carabids and folivorous insects on the farm-type with species poor and tall E.I. vegetation was significantly different from distribution patterns found on the farm types with other E.I. traits. Mean linyphiid numbers decreased towards the crop centre on this farm type, and mean numbers of granivorous carabids and folivorous insects decreased less on this farm type than in other

farm types. Another apparent characteristic of farms with species poor and tall E.I. vegetation was the low abundance of small staphylinids in both E.I. and crop area.
A possible explanation of these observations on linyphiid spiders, granivorous carabids, folivorous insects and small staphylinid beetles may involve the abundance of predacious beetles. Predacious beetles had the highest abundance in the crop area of farms with species poor and tall E.I. vegetation. This high predacious beetle abundance in the crop area could have interfered with the abundance of small-organism epigeic groups. Accordingly, in the whole data set a marginally significant negative correlation was found in the crop area between total number/farm of carabid beetles and total number/farm of pooled linyphiids and small staphylinids (Pearson correlation coefficient = –0.61, P<0.0105). Interaction between predacious beetles and linyphiid spiders may involve 'intraguild predation' (Sunderland *et al.*, 1996b). The above mentioned increased abundance of herbivores (*i.e.* granivorous carabids and folivorous insects) in crops with abundant predacious beetles, could indicate a cause as well as an effect of predacious beetle abundance:

- herbivorous functional groups indicate the suitability of the crop habitat (weeds) for herbivory which involves increased prey availability for the ground dwelling beetles (Booij & Noorlander, 1992);
- predacious beetles reduce predation pressure on herbivores by interfering with predators that can more effectively hunt in the canopy (*e.g.* spiders) whereas carabids prefer to hunt at the soil surface (Kromp, 1999).

4.3.2. Indications for dispersive movements between E.I. and crop area

Only lycosid spider distribution suggested that the E.I. could be a resource for crop area populations, because E.I. populations were generally much larger than crop area populations and the lycosid abundance in E.I. was correlated to lycosid abundance in the crop area.

High numbers of predacious beetles in the E.I. were also associated with high numbers in the crop area. Accordingly, in the whole data set a significant positive correlation is found between total number per farm of carabid beetles in the crop area and total number per farm in the E.I. (Pearson correlation coefficient = 0.72, P<0.05). However, high numbers of predacious beetles in both E.I. and crop area, could be better explained by crop area traits than by E.I. traits: the group of farms (farms A, F, E) with species poor and tall E.I. vegetation overlapped with the group of farms with a relatively 'extensive production' in the crop area (farms F, E). For this latter category it could be argued that predacious beetles were enhanced in the crop area. Whereas for the former category explanation was difficult because the E.I. represented an intermediate E.I. type possessing a vegetation cover or plant species number similar to other E.I. types. An additional argument for the assertion that crop area traits and not E.I. traits determined the high predacious beetle number, is that crop area size exceeds the E.I. size and may therefore include a larger amount of food for epigeic predators than the E.I. Since predacious beetles are mobile species (Thomas *et al.*, 1997), they may easily dwell from crop area to E.I. and *vice versa*.

Observations of linyphiid spiders, a mobile species, also suggested that abundance in the E.I. might be determined by crop area abundance. High abundance in the crop area was associated with high abundance in the E.I. However, the highest abundance in the E.I. (species poor with tall vegetation) was not related to a high crop area abundance. This divergent situation might have been due to high carabid abundance in the crop area, as explained above.

With regard to the distribution of small staphylinids in E.I. and crop area, observations did not indicate dispersive movement. Apparently high levels in both E.I. and in crop area were associated with low levels in adjacent habitat (crop area or E.I. respectively). High abundance

in each habitat were possibly related to local habitat factors, as suggested earlier in this paper: flail mowing in E.I. and intensive crop management in the crop area.
Since the improved E.I. vegetation did not harbour high abundance of epigeic functional groups, it could not be identified as a resource for epigeic arthropods in the crop area. This observation and also indications of effects on abundance in the E.I. by populations in the crop area (with regard to predacious beetles and linyphiid spiders), are seemingly contradicting reports on enhancing effects on arthropods of (improved) E.I. vegetation. However, these reports are often dealing with winter shelter and subsequent dispersion of arthropods in spring (references reviewed in De Snoo & Chaney, 1999). It might be possible that enhancing effects of E.I. cannot be observed in the summer, because epigeic arthropods have already left their shelter. Subsequently their number at the farm-level might be determined by crop area resources of initially detrital and later mixed detrital/herbivore origin. However availability of shelter provided by E.I. during winter and spring may still affect the total farm-level numbers (Lys, 1994; Lys & Nentwig, 1992). This expectation was supported by observations (in the discriminant analyses above) of the positive effect of spatial density of E.I. on predacious beetles. However, this effect may not be observable in a comparison of E.I. and crop area numbers.

4.4. Conclusions

Comparison of epigeic arthropod functional groups on eight organic arable farms suggests that the 'intensity' of the crop area is a major determining factor. The concept of 'intensity' should not only address percentage gramineous crops but also, for example, manuring and soil cultivation. Length of organic duration by itself may provide no clear basis for distinctions between the farms because of differences in 'intensity' among the long-duration farms. Interpretation of field observations deliniates three more or less distinct functional group compositions in the crop area:

- relatively high abundance of predacious beetles (mainly carabids), lycosid spiders, granivorous beetles and folivores in crop areas with comparatively low 'intensity';
- relatively high abundance of small (fungivorous) staphylinids in crop areas with a comparatively high 'intensity';
- relatively high abundance of linyphiid spiders in crop areas which represent an earlier successional stage due to recent conversion or to landscape factors.

The area and quality of Ecological Infrastructure provided no clear basis for distinctions between the farms. Summer abundance in E.I. of dominant ground dwelling groups, predacious beetles and linyphiids, might be determined by crop area conditions. Traditional management of E.I., that was expected to be adverse, showed to have a qualitatively different epigeic community and may positively support lycosid spiders, small staphylinids and epigeic herbivores as compared to other management. Potential increase of arthropod abundance in late mown E.I. may not involve ground dwelling arthropods but involve vegetation dwelling arthropods that occur in a higher stratum of the vegetation.

Increased abundance of predacious species is not equal to the capacity of the cropping system to control herbivorous pests (*e.g.* Wood & Lenné, 1999). Low epigeic predator abundance (as observed in the 'prototypes') could indicate both a sufficiently balanced system, in which predators inhibit initial pest development, as well as a pest outbreak susceptible system. Conversely high predator abundance may positively correlate with high herbivorous pest densities because these predators might have been supported by abundant prey. High numbers of predators may indeed represent pest control potential if they would develop on detritivorous prey (Wise *et al.*, 1999) or non-pest herbivorous prey (*e.g.* Andow, 1988;

Altieri, 1994) and subsequently depress pest populations. To bring clarity to this subject further investigations are needed.

4.5. Recommendations

Comparative studies on ground dwelling arthropod functional groups would benefit from a further restriction of geographical variation between farms. Definition of 'intensity' should be based on more farm characteristics than only crop rotation intensity. Our explorative studies might be repeated with emphasis on three extreme farm types: recently (1-2 years) converted farms, long organic duration (>8 years) and 'intensive' cropping, and long organic duration extensive cropping (*e.g.* >35% gramineous crops, including leys). Because the latter category is increasingly rare in commercial organic farming, farm experiments may be needed, particularly when investigating the effects of increased detrital input as suggested by Wise *et al.* (1999).

More specific research themes may address;

- the ecology of the aggregate functional group of saprophorous arthropods including staphylinids, Diptera, and Collumbola (*e.g.* Weber *et al.*, 1997; Idinger *et al.*, 1997);
- the importance of intraguild predation in crops (*e.g.* Tscharntke, 1997);
- the effect of different mowing regimes on arthropod communities (*e.g.* Haughton *et al.*, 1999), including vegetation dwelling functional groups as well as effects of predation pressure in the E.I. due to epigeic predators supported by rich resources in the crop area.

Additional attention should be paid to the often abundant but patchily distributed ants (*Formica*), because this species may compete with other predators and may protect aphids and related species in field margins. These studies should extend to a larger part of the farm food web, which might be necessary for soundly based practical recommendations with regard to enhancing farm biodiversity and its potential ecosystem services. Although no firm conclusions can be drawn yet from this field study, we think that results indicate future perspectives of a food web approach on farms.

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Chapter 4: Insectivorous breeding birds on organic farms in relation to crop area, ecological infrastructure and arthropods

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Abstract

Hypotheses on the relation of arthropod functional group abundance, crop area and ecological infrastructure (E.I.) variables to the territory density of functional groups of insectivorous birds were tested on organic arable farms. Bird territories were mapped on organic arable farms (eight in 1998, when epigeic arthropod were also studied, and nine in 1999, when vegetation dwelling arthropod studies were included). The farms were all situated in an open landscape dominated by agricultural land use; skylark, linnet and meadow pippit were the most numerous species. Most birds were more strongly related to vegetation dwelling arthropods in 1999, particularly those in the E.I., than to ground dwelling arthropods in 1998. The density of bird territories could usually be predicted by a combination of crop area and E.I. variables, including positive relations to improved E.I. characteristics. In 1999, according to the hypotheses, positive relations to organic farming duration were found; however in both years a general negative relation to extensive crop rotation was found. It will be discussed as to whether intensively managed crop areas may support birds due to the periodic and localised herbivore increases in a crop mosaic, but also whether extensively managed crops might offer less prey items due to the herbivore control exercised by epigeic predators as well as a less susceptible crop physiology. Late mown E.I. might possibly offer an important food resource that may supplement the, often interrupted, food resources of the crop area.

1. Introduction

1.1. Biodiversity loss in agriculture

A serious decline of the population in various plant and animal species on more intensively farmed land in industrialised countries, has been shown by, for example Fuller *et al.* (1995) and Andreasen *et al.* (1996). This decline concerns not only ecologists and agriculturists, but also the wider public (Paoletti, 1999; Wood & Lenné, 1999). The development of multi-species or sustainable farming systems is probably needed to reverse this trend (Vandermeer *et al.*, 1998; Altieri, 1994, 1999; Almekinders *et al.*, 1995). Such farming systems utilise ecosystem services provided by biodiversity (*e.g.* pest control, soil fertility), and allow a greater chance for nature conservation centered biodiversity. Several examples of multi-species farming system practices are given by Altieri (1994), Wood & Lenné (1999) and other authors.

Development of multi-species farming systems may require specific research approaches. Firstly the research should take site-specificity of biodiversity into account (Vandermeer *et al.*, 1998) and should preferably start from 'nearly natural systems' (Brown, 1999a). Secondly the variables, should specifically address the farm-, or higher levels of aggregation (Almekinders *et al.*, 1995). Thirdly the predictor variables should clearly relate to decisions in the farm management (Vereijken, 1997; Kabourakis, 1998; Smeding & Joenje, 1999; Park & Cousins, 1995).

1.2. Organic farms and ecological infrastructure

Organic farms that adhere to the production guidelines 2092/91 of the EC (Anonymous, 1991) are suitable research objects as the maintenance and utilisation of biodiversity is inherent to the philosophy of organic farming. Research shows that organic farming when compared to conventional farming, involves a greater number and diversity of species and habitats for birds, vegetation dwelling arthropods, epigeic arthropods, earthworms and arable weeds (*e.g.* Kromp & Meindl, 1997; Paoletti, 1999; Van Elsen, 2000; Smeding, 1993; Hendriks *et al.*, 2000).

Because of their increased similarity to 'nearly natural systems' farms that combine organic cropping with a deliberately enlarged, spatially diversified ecological infrastructure are of particular interest (Brown, 1999a). In this article ecological infrastructure (E.I.) is defined as the total of semi-natural (aquatic, woody, tall herb and grassy) habitats on the farm including their spatial arrangement (Smeding & Booij, 1999). Enlarged and diversified E.I. enhances the numbers and diversity of indigenous plants and animals at the farm level (*e.g.* Joenje *et al.*, 1997; Boatman *et al.*, 1999). This could contribute to soil fertility and pest control on organic farms (Brown, 1999b; Kromp & Meindl, 1997; Theunissen & Köhl, 1999).

1.3. Food web approach

Recent advances in research of food webs (Polis & Winemiller, 1996; Pimm, 1991) offer an appropriate methodology for biodiversity research, addressing variables at higher levels of aggregation. These advances, including some studies in agricultural habitats (*e.g.* De Ruiter *et al.*, 1995; Tscharntke, 1997), are providing inspiring examples of how (agro) ecosystems can be approached at higher integration levels than the species level. Some of this research indicates that farm food webs can mediate the effects of environmental factors on species (Wise *et al.*, 1999; Tscharntke, 1997).

Our general hypothesis about the farm food web on organic arable farms with improved E.I. is based on three sub-hypotheses:
Firstly, increased organic matter inputs from organic manure, crop residues, cereals, ley pastures, and compost, relate to increased numbers of invertebrate detritivorous meso- and macrofauna (*e.g.* Pfiffner & Mäder, 1997; Weber *et al.*, 1997; Idinger *et al.*, 1996; Heimbach & Garbe, 1996). Secondly, the numbers of various non-pest herbivorous functional groups are increased by improved E.I. (Holland & Fahrig, 2000; Boatman *et al.*, 1999) but also by organic crop characteristics (Hald & Redderson, 1990; Moreby & Sotherton, 1997). Thirdly, combined increases of detrital and herbivore invertebrates relate to a cumulative positive effect on the higher trophic level, including both invertebrate and vertebrate predators, which feed on prey from both detrital and herbivore subsystems (*e.g.* Wise *et al.*, 1999; Idinger *et al.*, 1996).

It is likely that succession to a hypothetical farm food web requires time (Idinger *et al.*, 1997; Edwards *et al.*, 1999), possibly at least the length of one or two crop rotations. The succession speed may be negatively influenced by previous applications of pesticides and the depletion of organic matter caused by reliance on artificial fertilisers (*e.g.* Paoletti, 1999).

1.4. Insectivorous birds and arthropod prey availability

The current field study was focussed on the abundance of insect-feeding birds in relation to crop area, E.I. characteristics and abundance of arthropod functional groups. Associated studies, to be published elsewhere, were devoted to lower trophic levels of the farm food web, including both vegetation and ground dwelling arthropods (Smeding *et al.*, 2001a,b). The guild of insect-feeding birds represents a higher trophic level that may be enhanced by productivity at the base of the food web (according to the concept of Oksanen *et al.*, 1996), and therefore reflects the 'ecological carrying capacity' of a farming system (Braae *et al.*, 1988). Birds, and their prey organisms, are influenced by farm characteristics. Birds are therefore affected both directly and indirectly by farm traits. These indirect effects on birds are probably mediated through the food web on the farm (*e.g.* Tscharntke, 1997).

Bird abundance on farms is not only determined by food but also by other environmental factors (as comprehensively outlined by Andrewartha & Birch, 1984). Important physical factors acting on farmland birds may be disturbance and nest destruction by machines or trampling (*e.g.* Green, 1980), availability of song posts or nest sites (Stoat, 1999), weather conditions or inaccessible vegetation (*e.g.* Schekkerman, 1997). Spatial features like field size, crop diversity and rotation may not necessarily relate to food distribution. However most studies on farmland birds indicate that food availability is a major factor determining bird density (reviewed by Poulsen *et al.*, 1998). Bird chicks are particularly vulnerable to shortage of proteins supplied by their invertebrate prey (*e.g.* Hald & Reddersen, 1990; Aebischer, 1991; Poulsen *et al.*, 1998).

Comparative studies between organic and conventional farms (Braae *et al.*, 1988; Hald & Reddersen, 1991; Wilson *et al.*, 1997; Chamberlain *et al.*, 1999; Moreby & Sotherton, 1997) emphasized the effects of pesticide usage on food availability, because pesticides depressed both prey and host plants of prey on conventional farms. Contributions of other farm characteristics affecting invertebrates were difficult to assess because most studied factors were correlated with pesticide application. However, Braae *et al.* (1988) traced a positive effect of manure/fertilizer on 8 of 35 numerously occurring bird species; Hald & Reddersen (1990) revealed the possible importance of host plants of *Fabaceae, Cruciferae, Polygonaceae*, which are common on organic farms as crop or weed. Chamberlain *et al.* (1999) detected effects of different landscape structures, which might be more relevant to organic farming practices (Hendriks *et al.*, 2000) on the bird community.

Traditional farming systems may reveal the key position of food resources for rich wildlife (*e.g.* of dehesas; Edwards *et al.*, 1999); in The Netherlands a traditional (*i.e.* orthodox biodynamic) mixed farm of 8 ha, possessed territories of endangered bird species, red-backed shrike (*Lanius collurio*) and ortolan bunting (*Emberiza hortulana*), probably due to increase of specific prey items (Esselink *et al.*, 1996).

Autecological research on farmland birds greatly contributed to deepening the understanding of the relation between crop management and chick food availability. In particular, work on grey partridge (*Perdrix perdrix*) (*e.g.* Rands, 1985) and skylark (*Alauda arvensis*) (*e.g.* Wilson *et al.*, 1997; Poulsen *et al.*, 1998; Wakeham-Dawson *et al.*, 1998) involved detailed investigations of habitat selection, nesting success, diet and chick condition in relation to farm characteristics and arthropod abundance. These studies were able to relate starvation of chicks and low territory densities to apparant food shortage in the breeding habitat (*e.g.* Poulsen *et al.*, 1998).

Arthropod functional groups, central to our research, include prey items for birds, but many taxa may be insignificant because of size, digestibility, repellant taste or other characteristics as summarized by the concept 'availability'. Consequently farmland birds have distinctive preferences. In our explorative study we chose to relate insectivorous bird-density to the abundance of entire arthropod functional groups. Contrary to *e.g.* Moreby *et al.* (1994) and Poulsen *et al.* (1998) who selected 'chick-food' within arthropod samples, according to diets of considered birds. Our research, therefore, does not discern between direct feeding relations and shared indirect association with certain habitat factors. Distinguishing different bird functional groups with known specific food and habitat requirements improves the basis for interpretation with regard to possible causal factors. However, this research was primarily concerned with relating bird functional group abundance (determined by its specific food with emphasis on chick diets) to arthropod functional groups (indicating the farm food web structure) in an attempt to link autecological research (*e.g.* Poulsen *et al.*, 1998) to farming systems research (*e.g.* Swift & Anderson, 1993; Vereijken, 1997; Wolfert, 1997; Van Keulen *et al.*, 1998).

1.5. Hypotheses and objectives

Five functional groups of birds feeding on invertebrates are examined. The distinction is based on difference in adult diet (insect, mixed insect-plant/seed or soil life) and habitat preference (field or field margin). For each group, specific hypotheses were derived from the above-explained general hypothesis with regard to the farm food web.

1.5.1. Insecti-granivorous birds with field affinity

These birds feed on the ground on plants. They were expected to be supported by ground- and vegetation dwelling diurnal predators and herbivores in the crop area. Farm management features which were expected to enhance the population of these birds were a reduced number of machine operations (which disturb their nests) and the occurrence of cereal crops and weeds which supply arthropods and seeds. Therefore extensive crop rotations were expected to favour this group. This group is represented by the skylark (*Alauda arvensis*) which is known to feed its chicks with large spiders, carabid beetles and large sized herbivores (sawfly and lepidopteran larvae, beetles). Young chicks receive both small and large soft-bodied insects, for example herbivorous larvae, and older chicks receive more large hard-bodied insects, for example beetles (*e.g.* Wilson *et al.*, 1997; Poulsen *et al.*, 1988). Skylarks are particularly attracted by grass leys (set-aside) and spring cereals. They prefer open crops to forage, and avoid dense crops.

1.5.2. Insecti-granivorous birds with E.I. affinity

These birds were expected to look for their animal food in the vicinity of their seed resources at the soil surface, on plants in the E.I. and in crop edges. Here these birds find ground living and vegetation dwelling diurnal predators and herbivores. Farm management features which were expected to enhance this group were the amount of E.I. on the farm, the timing of E.I. cutting and the variation of E.I. vegetation, including fruiting dicots. These factors would mainly influence their food availability since nests are usually not located in herbaceous vegetation. This group is mainly represented by the linnet (*Carduelis cannabina*), which feeds its chicks with invertebrates to a varying extent, captured on the ground as well as on plants; chick diets include beetles, spiders, fly adult and larvae, and caterpillars, but also small herbivores like aphids (Cramp, 1988).

1.5.3. Specialist insectivorous birds with field/E.I. affinity

These birds are able to capture flying insects. Therefore their density was expected to relate to the number of vegetation dwelling diptera, which dominate the airborne arthropod community; these diptera are mainly adults of detritivorous larvae and (root)herbivorous larvae (*e.g. Tipula* sp.). Probably to a lesser extent, the group would be supported by numbers of vegetation dwelling predators (*e.g.* syrphids) and folivorous herbivores. Farm management factors that were expected to favour field-inhabiting insectivorous birds would be organic duration and extensive crop rotation because these factors were presumed to support the detrital food web. Also the amount and quality of E.I. was expected to influence field-inhabiting insectivorous bird numbers, because adults of many flying insects from various trophic groups are attracted by flowers in the E.I. This group is represented by the *Motacillidae* species including wagtails (*Motacilla* sp.) and meadow pipit (*Anthus pratensis*). Wagtails are known to feed on flies and midges, including small individuals from 1-2 mm, but also on beetles (carabids as well as herbivorous species) (Cramp, 1988). Meadow pipit adults seem to feed on small predominantly dipteran insects (<5 mm) (Cramp, 1988) and are often seen to forage on the ground beneath crop canopies. However chicks are often to be fed with large (>1 cm) soft larvae (Cramp, 1988), that are generally herbivorous. Pipits on arable farms mostly occur in field margins (Scharenburg *et al.*, 1990).

1.5.4. Specialist insectivorous birds with E.I. affinity

These birds feed on vegetation dwelling arthropods of various trophic groups in the E.I. and are expected to prefer quantity (height and cover) above quality (*e.g.* species richness) of E.I. vegetation. The amount of E.I. (boundary width, area and spatial density) might contribute to the density of these birds (Stoat, 1999). This group is mainly represented by reed warbler (*Acrocephalus scirpaceus*) and reed bunting (*Emebriza schoeniclus*). In northern clay districts in The Netherlands, dominated by arable farming, abundance of both birds is clearly related to the length of ditches with old (>1 year) reed stands (Scharenburg *et al.*, 1990). Ditches in Flevoland with a mowing regime promoting reed growth were rapidly colonized by reed warbler and also marsh warbler (Remmelzwaal & Voslamber, 1996). Diets include a wide range of arthropod taxa that can be found within this vegetation (Cramp, 1988).

1.5.5. Soil life-feeding birds

Prey items of soil-life feeding birds include mainly soil macrofauna, including detritivores (earthworms) and root herbivorous insect larvae (particularly *Tipula* sp.) and additionally epigeic arthropods (carabid beetles and spiders). Open fields without vegetation or with sparse or very low vegetation provide best access to soil life. However, fields that remain open during spring and early summer, receive intensive farming procedures that disturb nesting. The group is mainly represented by Lapwing (*Vanellus vanellus*). Food availability for lapwing chicks is often critical because of agricultural practices. Dry soil is harder to penetrate and limits the access to soil macrofauna. (Schekkerman, 1997; Beintema *et al.*, 1991, 1995).

1.5.6. Insecti-granivores versus specialist insectivores

With regard to food requirements of combined groups of insecti-granivorous and specialist insectivorous birds, our hypothesis was that the insecti-granivorous group will show a clearer relationship with ground dwellling arthropods (sampled by pitfall traps) than specialist birds. Furthermore, we expected that vegetation dwelling predators would be the most important common food resource of the four functional bird groups because of their generally larger size. Total bird density is expected to be related both to this group of vegetation dwelling predators as well as to farm characteristics that favour detrital web numbers (*i.e.* duration, extensive crop rotation) and flowers/seeds in the ecological infrastructure.

1.5.7. Landscape effects

Birds may be affected by differences in the terrain. For example, in the northern clay district in The Netherlands, skylark, blue-headed wagtail, meadow pipit and quail (*Coturnix coturnix*) prefer open terrain. Marsh bird abundance is favoured by continuous reed habitat of 1.5-3 km length (Scharenburg *et al.*, 1990). Therefore also landscape differences between farms were taken into account.

1.5.8. Objectives

Thus, the objectives of this study were:

1. to determine the territory density of insectivorous birds of organic farms, and relate this density to the abundance of arthropod functional groups;
2. to relate the territory density of insectivorous birds of organic farms to the extent of on-farm ecological infrastructure, and vegetation and crop characteristics.

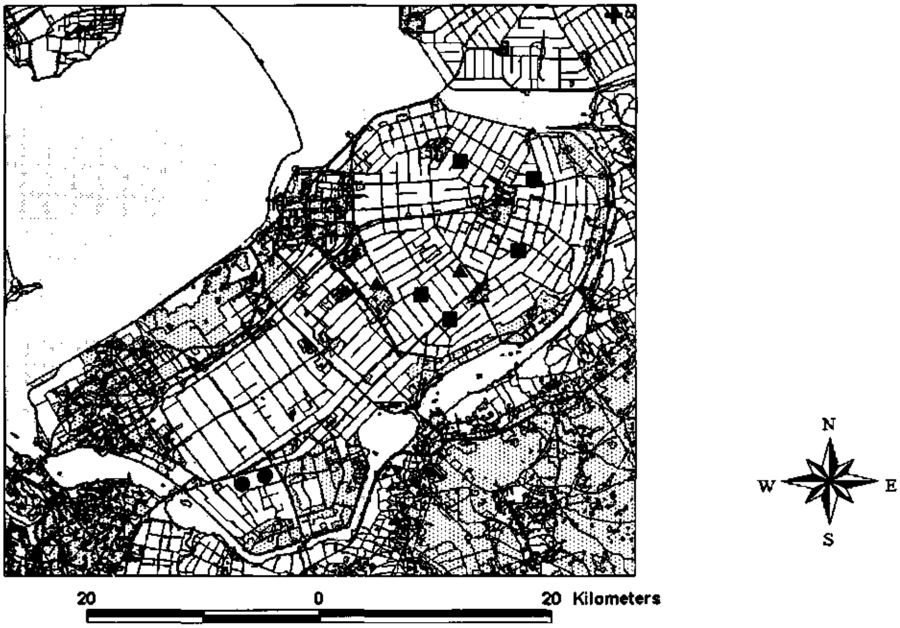

Fig. 1. Study area in 1998-1999: five farms with bird and arthropod studies in 1998 as well as 1999 are represented by squares; one farm with bird and arthropod studies only in 1998 is represented by a cross; two farms with bird and arthropod studies in 1998 and only bird studies in 1999 are represented by circles; two farms with bird and arthropod studies in 1999 are represented by triangles.

2. Materials and methods

2.1. Study area

The study was carried out on organic farms in the province of Flevoland, The Netherlands. The farms are located in the three polders Noordoostpolder, Oostelijk Flevoland and Zuidelijk Flevoland (Fig. 1). These three polders were reclaimed around 1940, 1957 and 1968, respectively, and are dominated by agricultural land use. The landscape is very flat and open with wood lots confined to farmyards, villages and main roads. The soil is a calcareous clay-sandy clay of marine origin. Flevoland was chosen as our study area because it has a concentration of organic farms that are similar with respect to their history and topography. There are currently 75 economically viable organic arable farms in Flevoland, which are generally large (c. 30-70 ha) and intensive relative to other organic arable farms in Europe.

Table 1
Characteristics of the farms, ecological infrastructure and landscape (200 ha, including the studied farm).

1998 **Level**	**Variable**	**Abbrev.**	**A**	**N**	**T**	**F**	**K**	**Z**	**R**	**L**	**E**	**D**
Farm	n year organic farm (n)	DUR	12	12	8	7			1	10	4	8
Farm	Cereals and ley pasture (%)	INT	38	59	38	24			18	11	70	35
Farm	% of crop area within 100 m range E.I. (%)	EI100	47	40	74	74			51	80	90	72
Farm	Semi-natural habitat (E.I.) (%)	AREA	2	1	2	1			2	3	5	4
E.I.	Mowing date (farm level) (month)	MOW	7	5	9	5			5	6	6	7
E.I.	Mowing frequency (n/year)	MOWFRQ	2	3	1	2			3	2	2	2
E.I.	Height vegetation (m)	EIGHT	1.8	1.1	1.8	1.0			0.7	0.7	1.2	1.1
E.I.	Cover vegetation (%)	EICOV	98	82	97	88			85	92	97	94
E.I.	Species diversity vegetation (n/4 m^2)	EISPN	12	8	11	9			6	10	10	15
E.I.	Dominant species diversity (n/4 m^2)	EIDOM	3.4	2.8	3.4	3.1			2.3	3.0	3.4	3.8
Landscape	Age polder (year)	LSAGE	30	30	41	41			41	41	41	57
Landscape	Semi-natural habitat landscape (%)	LSNAT	4	8	5	5			5	4	7	4
Landscape	Cereals/ley pasture landscape (%)	LSINT	34	44	32	26			27	23	51	27
Landscape	Vegetables landscape (%)	LSVEG	38	23	17	16			29	22	21	28
1999												
Farm	n year organic farm (n)	DUR	13	13	9	8	16	1	2	11	5	
Farm	Cereals and ley pasture (%)	INT	2	24	32	42	33	18	12	20	72	
Farm	Weed abundance (class)	WABUN	0.4	2.3	1.2	3.9	1.8	1.3	2.3	2.3	2.4	
Farm	% of crop area within 100 m range E.I. (%)	EI100	47	40	74	74	72	66	80	80	90	
Farm	Semi-natural habitat (E.I.) (%)	AREA	2	1	2	1	2	1	1	3	5	
E.I.	Mowing date (farm level) (month)	MOW	7	5	9	5	5	5	5	7	6	
E.I.	Mowing frequency (n/year)	MOWFRQ	2	3	1	3	3	2	3	2	2	
E.I.	Height vegetation (m)	EIGHT	1.8	1.1	1.8	1.0	0.7	0.4	0.7	0.7	1.2	
E.I.	Cover vegetation (%)	EICOV	98	82	97	88	84	82	85	92	97	
E.I.	Species diversity vegetation (n/4 m^2)	EISPN	12	8	11	9	9	8	6	10	10	
E.I.	Dominant species diversity (n/4 m^2)	EIDOM	3.4	2.8	3.4	3.1	2.8	2.5	2.3	3.0	3.4	
Landscape	Age polder (year)	LSAGE	31	31	42	42	42	42	42	42	42	

Ten farms were selected based on differences in farm structure and ecological infrastructure (E.I.) traits (Table 1). The selection included nine commercial organic farms and one experimental farm. The selected commercial farms are all arable although three (farms N, T, and K) possess a stable with livestock fed on fodder crops from the same farm but grazing

elsewhere during the summer. The organic experimental farm of Wageningen University is a mixed dairy and arable farm. Four commercial farms (A, T, L and D) were Ecological Arable Farming Systems (EAFS) prototype farms during 1992-1997 (Vereijken, 1997, 1998). Among these farms, farm A is different because it is situated in the youngest polder Zuidelijk Flevoland, and joined the EAFS-project a few years later than the others. Farms A and N started in 1985 on an experimental reclamation area where pesticides had never been used (Remmelzwaal, 1992).
Bird and arthropod studies in 1998 involved 8 farms (total 542 ha) in three polders (Fig. 1). Bird and arthropod studies in 1999 involved 7 farms (total 392 ha) that were confined to the polder Oostelijk Flevoland. On two farms in polder Zuidelijk Flevoland (farms A and N; 216 ha study area) only bird studies were done in 1999.

2.1.1. Crop area characteristics

The organic duration of the selected farms ranged from one to sixteen years (Table 1). Ploughing is generally at 25-30 cm depth. On all farms a 6-7 year crop rotation is maintained, with 6-14 different crops per farm. The proportions of different types of crop per farm ranged in both years from 10-70% for gramineous crop (cereals and ley pastures), 10-28% for traditional lifted crops (potato, beet) and 20-77% for vegetables (mainly onions, peas, sweet corn, various cabbages, red beet and runner beans).

The farms with the most intensive crop rotations had up to 60% vegetables and therefore a low percentage of gramineous crops (cereals, ley pasture). As compared to other crops, gramineous crops provide a large amount of carbon in crop residues and require fewer procedures that cause soil disturbance. Because input of nutrients (N,P,K) has to be adjusted to crop requirements, and vegetables need more nutrients than cereals, intensity of crop rotation is assumed to relate to both the amount of crop residues and the amount of N-application at the farm level.

2.1.2. Ecological infrastructure characteristics

Canals and banks (together c. 3-4 m width) that are laid out as linear herbaceous boundaries adjacent to the crops mainly determine the ecological infrastructure (E.I.) of arable farms in Flevoland. On five farms, boundaries are wider because of adjacent (2-3 m wide) grass strips, often including clovers (*Trifolium* spp.), on one or both sides of the canals. Farm E also had grass strips between crop plots. Percentages of E.I. higher than c. 2% (Table 1) were mainly due to the presence of these grass strips. Only farms K, L and E possessed a boundary planted with a hedgerow. Spatial density of E.I. is purposively increased on farm E (Smeding & Joenje, 1999) and farm L; the spatial arrangement of E.I. on the other 6 farms mainly reflects landscape-scale features.

Extreme types of vegetation management are:

- 'traditional management' involving three or four more cuts per year with a flail mower leaving the shredded cuttings *in situ*;
- 'late mowing management' involving one or two cuts per year after June 21st with a finger-bar mower with hiab grab for removal of cuttings.

The grass strips along the canals are required for transport on farms with a 'late mowing management'. E.I. area is therefore related to mowing date. In this article the E.I. with enlarged area and late mowing is defined as 'improved E.I.'. The improved E.I. on four farms (A, T, L, and D) was created during the EAFS-prototyping research program in 1992-1997 (Vereijken, 1997). The improved E.I. on the experimental farm E started in 1995 simultaneously with conversion of the conventional dairy farm to an organic mixed farm (Smeding & Joenje, 1999).

Dominant plant species in canal bank swards are: couch (*Elymus repens*), perennial meadow grasses (*Festuca rubra, Poa trivialis, Lolium perenne, Agrostis stolonifera*), common reed (*Phragmitis australis*) and few perennial herbs: dandelion (*Taraxacum officinale*) and stinging nettle (*Urtica dioica*). Canals that are traditionally managed have a low, relatively open, species poor vegetation (<10 species/4 m^2), dominated by a few grass species. Late mowing particularly relates to increased vegetation biomass in June and July as expressed by vegetation height (up to 1-3 m) and cover (up to 90-100%). However, late mowing does not always relate to increased higher plant species diversity for two reasons: a) tall grass species may dominate the sward; b) swards that have been traditionally managed may be cut locally to ground level and therefore be invaded by ruderals and annuals (increased species number up to 15 species/4 m^2), *e.g.* thistles (*Cirsium arvense, Sonchus arvensis*), annual weeds (*e.g. Sonchus asper, Polygonum aviculare*) and annuals that are rarely pernicious weeds in Flevoland (*e.g. Myosotis arvensis, Veronica persica, Cardamine hirsuta*).

High perennial plant diversities found in some locations may be caused by various interrelated factors (Kleijn, 1997); such as reduced vegetation productivity, removal of the hay, nutrient buffering by the grass strip, and long organic duration. Artificial species introduction is however, also involved. In the EAFS-project, around 90 different native perennial dicots were artificially seeded into the canal banks to obtain higher plant diversity and flower abundance of plants with limited dispersal capacity (Vereijken, 1998). Although few species could settle well (*e.g. Senecio jacobea, Crepis biennis, Heracleum sphondylium*), the introduction clearly affected species diversity: vegetation including sites with >15 species/4 m^2 was confined to prototype farms.

2.2. Sampling and measurements

2.2.1. Birds

Territory mapping of skylark was done four times in 1998 and three times in 1999, in the beginning of May (week 19), around the end of May (week 22), around the middle of June (week 25) and, only in 1998, around the beginning of July (week 28), using the method described in Van Dijk (1993). A representative part (80-100%) of the farm, excluding the farm yard, was selected. Farms were visited in the morning between 8:30-12:00 h. Observations were done while slowly walking along transport tracks and canal banks, within a free observation range of 200 m to both sides of the transect. Bird observations were plotted on a 1:5000 field map, including territorial behaviour (singing, fighting, mating) or other nesting indications (nest visits, feeding and presence of chicks).

Field maps were interpreted according to Van Dijk (1993): observations were collected on individual bird species maps. Separate sightings within specific merger distances were attributed to the same territory, unless two individuals were seen simultaneously.

Breeding birds were grouped according to food types and habitat preferences:

1. Insecti-granivorous birds with crop area preference: skylark (*Alauda arvensis*);
2. Insecti-granivorous birds with E.I. preference: linnet (*Carduelis cannabina*) and goldfinch (*Carduelis carduelis*), both finch species (Fringillidae);
3. Specialist insectivorous birds with combined crop area and E.I. preference: blue-headed wagtail (*Motacilla flava*), white wagtail (*Motacilla alba*) and meadow pipit (*Anthus pratensis*) members of the bird family Motacillidae;
4. Specialist insectivorous birds with E.I. affinity, defined as 'marsh birds' (according to Remmelzwaal & Voslamber, 1996): reed warbler (*Acrocephalus scirpaceus*), reed bunting (*Emberiza schoeniclus*) and bluethroat (*Luscinia svecica*).

5. Insecti-granivorous birds on the farm, including groups 1. and 2. mentioned above and also a few observations of quail (*Coturnix coturnix*) which is not a songbird but has requirements similar to the first group;
6. Specialist insectivorous birds on the farm, including groups 3. and 4. mentioned above;
7. Total songbirds including insecti-granivorous birds and (specialist) insectivorous birds;
8. Soil life-feeding birds: lapwing (*Vanellus vanellus*), oystercatcher (*Haematopus ostralegus*) and blacktailed godwit (*Limosa limosa*).

Observations of swallow (*Hirundo rustica*), house martin (*Delichon urbica*), starling (*Sturnus vulgaris*) and house sparrow (*Passer domesticus*) were not included because these species nest in farmyards and stables and mostly stay around the farmyard or are accidentally present in the fields of adjacent farmland. Linnet, goldfinch and white wagtail also do not nest in the open field but are much more resident in particular parts of the arable fields. Observations of soil life-feeding birds were interpreted with caution because the most common species, lapwing, requires observations in April (Van Dijk, 1993).

2.2.2. Arthropods

Sampling was done in wheat crops and on adjacent canal banks (E.I.). Wheat (*Triticum aestivum*) was chosen as a representative crop because this crop is common on organic arable farms in Flevoland and arthropod numbers in cereals are larger compared to numbers in other common crops like potatoes and onions (Booij & Noorlander, 1992).

In 1998 ground dwelling arthropods were sampled by six pitfall traps placed in a row with intervals of 10 m at distances of 0 m (E.I.) and 30 m (wheat). Weekly samples were taken during 8 weeks, starting from 6th of June until 28th of July 1998. Individuals were sorted to taxa at order- or family-level and placed into six different arthropod functional groups (for further details see Smeding *et al.*, 2001a):

- Predacious beetles including carnivorous Carabidae and large (>6 mm) Staphylinidae;
- Lycosid spiders which are large and represent diurnal wandering spiders;
- Linyphiid spiders which are small and represent sheet-web spiders;
- Small staphylinid beetles which represent an important detritivorous functional group;
- Granivorous herbivores represented by granivorous carabid beetles;
- Folivorous herbivores represented by weevils (Curculionidae) and hoppers (Cicadellidae).

The observations of the six traps and eight sampling dates were accumulated giving one total number per functional group per habitat (crop or E.I.) per farm.

In 1999 vegetation dwelling arthropods were collected by means of a vacuum sampler (ES 2100, Echo, Lake Zurich U.S.A.) for 120 s at each 1 m^2 sample. Nine samples of 1 m^2 at distances of 0 m (E.I.) and 30 m (wheat) were selected. Sampling was done once between June 7th and July 6th. Taxa were placed into trophic categories (for further details see Smeding *et al.*, 2001b):

- Detritivores;
- K- or senescense-feeding herbivores (White, 1978);
- r- or flush-feeding herbivores (White, 1978), represented by aphids (Aphididae)
- Predators;
- Parasitoids, represented by Parasitica (Hymenoptera).

The observations of the nine suction samples were accumulated, giving one total number per functional group per habitat (crop or E.I.) per farm.

2.2.3. Vegetation measurements in the E.I.

Vegetation studies included the banks of small canals (width <4 m) that were adjacent to the crops; investigation was done from May to August: late mown vegetation was investigated in June and July before the first cut. Early and or frequently mown vegetation was investigated before the first cut (May) or later (until August) when species composition could sufficiently be identified. Investigation was done once in 1997-1999. Species number were assumed to be more or less constant over the two years. Observations on vegetation height and cover were influenced by sampling date and differences between years; however by investigating many plots including all canal banks (width <4 m) on the farm, there was sufficient representation of general performance, standing crop and occurrence of gaps in the sward.

The herb layer was sampled in plots of 4 m^2 area with intervals of 50 m between plots. Plots included the ditch bank vegetation from the top to the helophytic zone; and vegetation affected by submersion was excluded. Parameters were: cover, maximum height, plant species and dominant plant species (totalling 80% of the cover). Averages were calculated for each farm. The database comprised 397 plots with 30-50 plots per farm.

2.2.4. Farm management and lay out

A 1:5000 map was made of each farm, depicting the different crops and the ecological infrastructure (E.I.) and on these maps the area of the crops and of semi-natural habitats were measured.

Measurements of farm characteristics were restricted to a representative farm area in which the bird territories were mapped, which was 80-100% of the total farm area. However, crop rotation intensity (% gramineous crops, including ley pasture and cereals) was calculated for the whole arable crop area because this figure indicated both the input of carbon as well as a specific habitat within the bird mapping area.

The 'E.I. area' is calculated as the percentage of semi-natural habitat of the representative farm area. The spatial density of the E.I. was expressed by the percentage of the farm which lay within a 100 m distance of the E.I. In case the canal bank vegetation was cut both after September 15th as well as before May 15th, a distance of 70 m was considered.

Weed abundance in the crop area was measured in the field using a simplified Tansley scale (with 0.5 = few individuals, 1 = rare, 2 = occasional, 4 = frequent, 8 = abundant; 10 = co-dominant); weed abundance was estimated during half of June in each crop. A weighted average value was calculated for each farm, based on the proportions of the crops within the area where the bird territories were mapped.

Data on conversion to organic, operations in the wheat crop in 1998, and the mowing of canals banks and grass strips was obtained by using a questionnaire. Duration is defined as the number of years since the whole crop area of the farm was certified according to the European regulations for organic farming (Anonymous, 1991). The timing of mowing is represented by the month of the first cut and the frequency per year.

2.2.5. Landscape

Landscape parameters were sampled around 8 farms in 1998, in an area of 200 ha which included the investigated farm. The area had a rectangular shape with a length and width ratio congruent to the farm and positioned in the same orientation as the farm. The farm was situated in the centre. Inside the rectangle the area of different crops, semi-natural habitats, roads, pavements and urban occupation were measured. The semi-natural aquatic, woody, tall herb and grassy habitats were defined as 'natural'.

2.3. Statistical analyses

All measurements were tested for normality. Arthropod numbers were ln-transformed. All subsequent analyses were conducted using Statistical Analysis System (SAS Institute, Cary, North Carolina). The relative importance of arthropods, crop area and E.I. characteristics on bird territory density were determined using multivariate REG MAXR regression.
Eight explored response variables were: skylarks, wagtails/pipit, finches, marsh birds, insectivores, insecti-granivores, total songbirds and soil life-feeding birds.
There were four separate analyses concerning arthropods and farm environmental factors in two different years and one additional analysis concerning the landscape factors. These analyses include the following predictor variables:

1. with regard to ground dwelling arthropods (1998), twelve variables in crop and E.I.: predacious beetles, lycosid spiders, linyphiid spiders, small staphylinids, granivorous carabids and folivorous insects;
2. with regard to vegetation dwelling arthropods (1999), ten variables in crop area and E.I.: r-herbivores, K-herbivores, detritivores, predators and parasitoids;
3. with regard to farm and E.I. characteristics in 1998, ten variables: organic duration, intensity, spatial density of E.I., area of E.I., mowing date, mowing frequency, maximum height, cover, plant species number and dominant plant species number;
4. with regard to farm and E.I. characteristics of seven farms in Oostelijk Flevoland in 1999, the same ten variables as in 1998 were used and also weed abundance: the same analysis was performed including two more farms in Zuidelijk Flevoland because these farms were also involved in studies of 1998 but not in arthropod studies of 1999 that were confined to Oostelijk Flevoland;
5. with regard to landscape structure of eight farms in 1998, five variables: age of the polder, proportion of semi-natural habitats, proportions of vegetable crops, lifted crops and gramineous crops.

In the multiple regressions all predictor variables were included in both linear and quadratic form to find both linear and quadratic relations between response and predictor variables. Multiple regression models included maximally 4 variables (Maxr; STOP=4). For each response variable the best model was selected according to the following criteria:

- the R-square of the model was larger than 50%;
- the significance level of the effects of all individual variables and the model should be smaller than 0.05;
- the model with the highest probability was considered as the best model. But if the model with the highest probability, as compared to the best model with one variable less, had the same probability class and added less than 5% to the R-square, than the model with fewer variables was considered as better.

3. Results

3.1. Observed bird species and territory densities

In 1998 within 422 ha study area, 169 territories of insectivorous and insecti-granivorous birds were counted and in 1999 within 467 ha study area, 133 territories were counted. Observations in both years included 10 species (Table 2). Additional observations of soil life-feeding birds yielded 39 territories in both years, including 3 species (Table 2).
Most territories (c. 39%) concerned skylark (*Alauda arvensis* L.), that had territory densities ranging from 0.06-0.24 per ha with average densities of 0.15 and 0.12 territory per ha in 1998 and 1999 respectively. Other numerous species were linnet (*Carduelis cannabina* L.) (c. 18% of observations) and meadow pipet (*Anthus pratensis* L.) (c. 13% of observations). Soil life-feeding birds were mainly (c. 90%) lapwing (*Vanellus vanellus* L.).

3.2. Bird functional groups in relation to arthropod functional groups

Skylark territory density was found to be positively related to arthropod functional groups (Table 3) in the E.I., particularly to the diurnal predacious groups: lycosid spiders in 1998 (Table 4) and vegetation dwelling predators in 1999, but also to herbivores in 1999 (Table 5). With regard to arthropods in the crop area, r-herbivores were an important predictor in 1999 (Table 5). Multiple regression selected as best 1-variable model:
ALAU = 0.0003 + 0.0029 $(\text{rHERB})^2$ (R^2=0.66; P<0.034).

Table 2
Observations of bird territories: the territory numbers of different species per farm, the size of the study area, and the densities of the functional groups. The assemblages are explained in the method section.

	1998								**1999**								
Farm	**A**	**N**	**T**	**F**	**R**	**L**	**E**	**D**	**A**	**N**	**T**	**F**	**K**	**Z**	**R**	**L**	**E**
Birds																	
Skylark	4	15	9	9	9	4	4	8	2	12	8	5	7	5	7	5	4
Linnet	3	4	3	4	2	3	5	5	2	5	2	2	6	1	2	5	4
Goldfinch	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0
Quail	1	4	2	0	2	1	2	0	0	0	0	1	1	0	1	1	1
Blue-headed wagtail	1	2	2	1	1	2	1	2	1	1	1	2	0	0	1	1	1
White wagtail	2	2	1	2	1	1	3	1	2	3	2	1	1	1	2	1	2
Meadow pipit	0	1	2	5	4	7	1	9	0	0	1	2	0	0	0	6	0
Reed warbler	1	0	0	0	0	0	0	0	4	1	2	0	0	0	0	0	0
Bluethroat	1	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	0
Reed bunting	3	3	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Lapwing	0	7	5	4	5	4	2	7	1	8	3	3	5	3	8	4	2
Oystercatcher	0	0	0	0	0	0	3	1	0	0	0	0	0	0	0	0	2
Black-tailed godwit	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Bird mapping area (ha)	39	93	37	47	57	34	68	47	39	93	37	47	45	47	57	34	68
Skylarks n/10 ha	1.0	1.6	2.4	1.9	1.6	1.2	0.6	1.7	0.5	1.3	2.1	1.1	1.6	1.1	1.2	1.5	0.6
Finches n/10 ha	0.8	0.4	1.1	0.9	0.3	0.9	0.9	1.3	0.5	0.5	0.8	0.4	1.3	0.2	0.3	1.5	0.6
Motacillidae n/10 ha	0.8	0.5	1.3	1.7	1.0	2.9	0.7	2.6	0.8	0.4	1.1	1.1	0.2	0.2	0.5	2.3	0.4
Marsh birds n/10 ha	1.3	0.3	0.3	0.0	0.0	0.0	0.0	0.0	1.5	0.1	0.5	0.0	0.4	0.0	0.0	0.0	0.0
Insecti-granivores n/10 ha	2.0	2.5	4.0	2.8	2.3	2.3	1.8	3.0	1.0	1.8	2.9	1.7	3.1	1.3	1.7	3.2	1.3
Insectivores n/10 ha	2.0	0.9	1.6	1.7	1.0	2.9	0.7	2.6	2.3	0.5	1.6	1.1	0.7	0.2	0.5	2.3	0.4
Total songbirds n/10 ha	4.1	3.3	5.6	4.5	3.3	5.3	2.5	5.6	3.3	2.4	4.5	2.8	3.8	1.5	2.3	5.6	1.8
Soil life-feeders total n/10 ha	0.0	0.8	1.3	0.9	0.9	1.2	0.9	1.7	0.3	0.9	0.8	0.6	1.1	0.6	1.4	1.2	0.6

Table 3

Observations of arthropods per farm: data from 1998 representing total numbers of ground dwelling arthropod functional groups captured in 6 pitfall traps in weekly trappings over a eight week period in the wheat crop (30 m from the field margin) as well as in the ecological infrastructure; data from 1999 representing the total number/9 m^2 per farm of vegetation dwelling arthropods in the wheat crop (30 m from the field margin) and in the ecological infrastructure, captured by vacuum sampling.

Crop area 1998

Arthropod functional groups (n/trap)		Farms:									
Ground dwelling 1998	abbrev.	A	N	T	F	K	Z	R	L	E	D
Predacious beetles in wheat 30 m	COL	952	1064	1333	3765	*	*	1011	1035	2889	1731
Lycosidae in wheat 30 m	LYC	53	146	57	38	*	*	18	83	35	8
Linyphiidae in wheat 30 m	LIN	3061	3311	2979	2622	*	*	2515	2055	1687	1944
Staphylinidae <6 mm in wheat 30 m	STSM	1308	329	893	425	*	*	640	772	205	541
Carabidae granivorous in wheat 30 m	CARH	5	83	7	4	*	*	3	19	504	15
Folivorous insects in wheat 30 m	FOLI	4	3	7	21	*	*	13	6	8	5

Crop area 1999

Arthropod functional groups (n/9 m^2)		Farms:									
Vegetation dwelling 1999		A	N	T	F	K	Z	R	L	E	D
r-Herbivores total	rHERB	*	*	2379	219	836	743	413	377	189	*
K-Herbivores total	KHERB	*	*	20	12	28	15	36	42	58	*
Detritivores total	DETR	*	*	19	24	45	23	66	48	63	*
Predator total	PRED	*	*	33	31	85	33	93	39	221	*
Parasitoids total	PAR	*	*	94	60	68	66	156	152	79	*

EI 1998

Arthropod functional groups (n/trap)		Farms:									
Ground dwelling 1998		A	N	T	F	K	Z	R	L	E	D
Predacious beetles in wheat 30 m	COL	1365	1319	1205	2808	*	*	832	1706	2603	926
Lycosidae in wheat 30 m	LYC	87	535	208	302	*	*	46	168	226	64
Linyphiidae in wheat 30 m	LIN	2508	2577	880	4235	*	*	1191	1607	1930	2554
Staphylinidae <6 mm in wheat 30 m	STSM	739	703	444	334	*	*	365	217	411	709
Carabidae granivorous in wheat 30 m	CARH	52	149	83	79	*	*	253	291	279	66
Folivorous insects in wheat 30 m	FOLI	104	275	150	33	*	*	38	61	35	100

EI 1999

Arthropod functional groups (n/9 m^2)		Farms:									
Vegetation dwelling 1999		A	N	T	F	K	Z	R	L	E	D
r-Herbivores total	rHERB	*	*	488	11	45	106	127	59	35	*
K-Herbivores total	KHERB	*	*	471	71	24	341	831	509	145	*
Detritivores total	DETR	*	*	395	67	43	79	45	440	98	*
Predator total	PRED	*	*	254	104	158	158	121	336	96	*
Parasitoids total	PAR	*	*	88	14	27	95	49	47	35	*

Finches (mainly linnet) territory density was found to be positively related to vegetation dwelling predators in both crop area and E.I. and was found to be negatively related to herbivorous groups in the E.I. (granivorous beetles and K-herbivores in 1998 and 1999 respectively) and also negatively related to linyphiid spiders in the crop area in 1998 and parasitoids in E.I. in 1999 (Tables 4 and 5).

Motacillidae (wagtails/pipit) territory density was found to be positively related to lycosid spiders in the E.I. in 1998 (Table 4) and to detritivores in the E.I. in 1999 (Table 5). In 1998

Motacillidae were negatively related to linyphiid spiders and curvilinearly to granivorous carabids in the crop area (Table 4).

Marsh bird territory density was best predicted by small staphylinid beetles in the crop area in 1998 (Table 4) and by r-herbivores and parasitoids in the E.I. in 1999 (Table 5).

Insecti-granivorous birds territory density (including skylark, linnet, goldfinch and quail) was best predicted by vegetation dwelling predators in the E.I. (Table 5). No model with regard to ground dwelling arthropod observations, was obtained in 1998 (Table 4).

Insectivorous birds territory density (including blue-headed and white wagtail, meadow pipit, reed warbler, reed bunting and bluethroat) was found to be curvilinearly related to detritivores in the E.I. and to r-herbivores in the E.I. (Table 5). The most important predictor was vegetation dwelling detritivores in the E.I.: Multiple regression selected as best 1-variable model: $\mathrm{INSECT} = 0.0066(\mathrm{DETREI})^2 - 0.0054$ ($R^2=0.71$; $P<0.017$). No model for insectivorous birds in relation to ground dwelling arthropod observations was found (Table 4).

Table 4

Multiple regression models (P<0.05) with ground dwelling arthropods as predictor variables based on bird and arthropod observations on eight farms in 1998; Birds (territory/ha): Alau = skylark, Mota = Motacillidae, Fin = Finches, Marsh = Marsh birds, Insect = Specialist insectivorous birds; Insgran= Insecti-granivorous birds; Avis = total songbirds; Soilf = soil life-feeding birds; Ground dwelling arthropods: COL = predacious beetles; LYC = lycosid spiders; LIN = Linyphiid spiders; STSM = small staphylinid beetles; CARH = granivorous carabids; additional symbols: 'ca' = crop area; 'ei' = ecological infrastructure.

Birds	**Model**	**R^2**	**Pr>F**
Alau	-0.063*ln(LYCca) – 0.005*ln(CARHca)^2 + 0.010*ln(LYCei)^2 - 0.004*ln(LINei)^2 + 0.437	96	0.0162
Fin	-0.11*ln(LINca) - 0.04*ln(CARHei)^2 + 1.0612	72	0.0401
Mota	-0.42*ln(LINca) + 0.13*ln(CARHca) - 0.025*ln(CARHca)^2 + 0.039*ln(LYCei) + 3.071	99	0.0011
Marsh	-0.96*ln(STSMca) + 0.08*ln(STSMca)^2 + 2.839	74	0.0327
Insgran	No model		
Insect	No model		
Avis	No model		
Soilf	-0.36*ln(LINca) - 0.03*ln(CARHca) - 0.15*ln(COLei) + 0.1*ln(LYCei) + 3.53	94	0.0390

Table 5

Multiple regression models (P<0.05) with vegetation dwelling arthropods as predictor variables based on bird and arthropod observations on eight farms in 1999; Birds (territory/ha): Alau = skylark, Mota = Motacillidae, Fin = Finches, Marsh = Marsh birds, Insect = Specialist insectivorous birds; Insgran= Insecti-granivorous birds; Avis = total songbirds; Soilf = soil life-feeding birds; Vegetation dwelling arthropods: rHERB = r-herbivores; KHERB= K-herbivores; PRED = predators; DETR = detritivores; PAR = parasitoids; additional symbols: 'ca' = crop area; 'ei' = ecological infrastructure.

Birds	**Model**	**R^2**	**Pr>F**
Alau	0.063*ln(rHERBca) + 0.0014*ln(KHERBei)^2 + 0.038*ln(PREDei) - 0.077*ln(PARei) - 0.244	100	0.0068
Fin	0.034*ln(PREDca) - 0.014*ln(KHERBei) + 0.139*ln(PREDei) - 0.004*ln(PARei)^2 - 0.632	100	0.0018
Mota	0.006*ln(DETRei)^2 - 0.059	62	0.0346
Marsh	-0.044*ln(PARei) + 0.003*ln(rHERBei)^2 + 0.076	99	0.0002
Insgran	0.147*ln(PREDei) - 0.527	62	0.0354
Insect	-0.671*ln(DETRei) + 0.075*ln(DETRei)^2 -0.029*ln(rHERBei)^2 + 1.703	97	0.0074
Avis	0.366*ln(PREDei) - 0.017*ln(PARei)^2 - 1.284	94	0.0035
Soilf	0.0068*ln(PARca)^2 - 0.154*ln(KHERBei) + 0.015*ln(KHERBei)^2 + 0.332	99	0.0011

Total songbird territory density was best predicted by vegetation dwelling arthropods in the E.I. (Table 5) and was positively related to predators and curvilinearly to parasitoids. Total songbird territory density was also predicted fairly well by a one-variable model: $AVIS= 0.027(PREDEI)^2 - 0.38$ ($R^2 = 0.71$; $P<0.035$). No model for total bird density in relation to ground dwelling arthropod observations was found (Table 4).

Territory density of soil life-feeding birds had ground dwelling arthropods in both crop area and E.I. as predictor variables and was found to be positively related to lycosid spiders in the E.I. and negatively related to linyphiid spiders granivorous carabids in the crop area and predacious beetles in the E.I. (Table 4). With regard to vegetation dwelling arthropods, soil life-feeding bird territory density could best be predicted by parasitoid abundance in the crop area (which clearly is an association because these birds definitly do not feed on this group) and K-herbivores in the E.I. (Table 5).

3.3. Bird functional groups and relations to farm and E.I. characteristics

Skylark territory density was found to be positively related to late mowing and negatively related to high vegetation cover of the E.I. in both 1998 and 1999 (Tables 6 and 7), and positively to organic duration of the farm in 1999. If the two Zuid Flevoland farms were included in the study area, then Skylark territory density was also predicted by the spatial density of E.I. (Table 8).

Finches (mainly linnet) territory density was found to be positively related to spatial density of E.I. and plant species richness of E.I. vegetation in 1998 (Table 6) and organic duration and area of E.I. in 1999 (Table 7); in 1999 a negative relation was found to percentage of gramineous crops in the crop rotation (Table 7).

Motacillidae (wagtails/pipet) territory density in 1998 and 1999, was found to be positively related to spatial E.I. features (E.I. area in 1998 and E.I. density in 1999) and negatively related to percentage of gramineous crops (Tables 6 and 7). In 1998 it was negatively related to mowing frequency and in 1999 also negatively to height of E.I. vegetation but positively to number of dominant plant species. If the two farms in Zuid Flevoland were included in the study area than wagtails/pippit were also found to be related positively to weed abundance whereas spatial density of E.I. was no longer included in the model (Tables 7 and 8).

Marsh bird territory density was found to be exponentially related to height of the E.I. vegetation in 1998 and 1999 (Tables 6 and 7) and curvilinearly to organic duration in 1999 (Table 7) and was found to be negatively related to area and curvilinearly to late mowing of the E.I. in 1998 (Table 6).

Insecti-granivorous bird territory density (including skylark, finches, goldfinch and quail) was found to be positively related to late mowing of E.I. in 1998 and 1999 (Tables 6 and 7) and organic duration in 1999 (Table 7) and was found to be negatively related to frequent mowing and open vegetation in 1998 (Table 6) and also to E.I. dominant plant species number in 1999 (Table 7). If the two farms in Zuid Flevoland were included in the study area than insecti-granivorous bird territory density was also predicted by E.I. density and was found to be negatively related to mowing frequency and E.I. plant species number (Table 8).

Insectivorous bird territory density (including blue-headed and white wagtail, meadow pipit, reed warbler, reed bunting and bluethroat) was found to be positively related to E.I. dominant plant species number and negatively to percentage gramineous crops in 1998 and 1999

(Tables 6 and 7) and negatively to E.I. spatial density in 1999. If the two Zuid Flevoland farms were included then the selected model included weed abundance as a predictor for insectivorous bird territory density, whereas E.I. spatial density was not included (Table 8).

Total songbird territory density was found to be positively related to plant species number of E.I. vegetation in 1998 and 1999 (Tables 6 and 7) and late mowing and mowing frequency in 1999 (Table 7), and negatively to percentage gramineous crops, mowing frequency and cover of E.I. vegetation in 1998 (Table 6). If the two Zuid Flevoland farms were included then the selected model included organic duration as a predictor for total bird territory density, whereas E.I. plant species number was not selected (Tables 7 and 8).

Soil life-feeding bird territory density was found to be positively related to late mowing and curvilinearly to height of E.I. vegetation in 1998 (Table 6) and positively related to organic duration and negatively related to percentage gramineous crops and spatial density of E.I. in 1999 (Table 7). If the two Zuid Flevoland farms were included then no significant model could be found (Table 8).

Table 6
Multiple regression models (P<0.05) with farm and E.I. characteristics as predictor variables based on bird observations (response variables) on eight farms in 1998. The keys are in Table 5 (birds) and Table 1 (farm and E.I. characteristics).

Birds	**Model**	**R^2**	**Pr>F**
Alau	$0.0033*(MOW)^2 - 0.00006*(EICOV)^2 + 0.479$	78	0.0231
Fin	$0.0015*(EI100) - 0.0126*(AREA) + 0.0106*(EISPN) - 0.094$	99	0.0003
Mota	$-0.0002*(INT)^2 - 0.6678*(AREA) + 0.1478*(AREA)^2 - 0.1219*(MOWFRQ) + 1.214$	99	0.0029
Marsh	$-0.0033*(AREA)^2 + 0.185*(MOW) - 0.0146*(MOW)^2 + 0.0446*(EIHGT)^2 - 0.584$	97	0.0163
Insgran	$0.0036*(MOW)^2 - 0.0174*(MOWFRQ) - 0.00008*(EICOV)^2 + 0.841$	95	0.0048
Insect	$-0.0037*(INT) + 0.126*(EIDOM) - 0.1008$	83	0.0117
Avis	$-0.0029*(INT) - 0.159*(MOWFRQ)^2 - 0.00007*(EICOV)^2 + 0.026*(EISPN) + 1.23$	98	0.0045
Soilf	$0.0038*(MOW)^2 + 0.309*(EIHGT) - 0.187*(EIHGT)^2 - 0.135$	97	0.0011

Table 7
Multiple regression models (P<0.05) with farm and E.I. characteristics as predictor variables based on bird observations (response variables) on seven farms in Oostelijk Flevoland in 1999. The keys are in Table 5 (birds) and Table 1 (farm and E.I. characteristics).

Birds	**Model**	**R^2**	**Pr>F**
Alau	$0.0001*(DUR)^2 + 0.0035*(MOW)^2 + 0.0059*(MOWFRQ)^2 - 0.0059*(EICOV) + 0.483$	100	0.0007
Fin	$0.0088*(DUR) - 0.0020*(INT) + 0.0063*(AREA)^2 + 0.0308$	99	0.0005
Mota	$-0.0068*(INT) + 0.00003*(EI100)^2 - 0.044*(EIHGT)^2 + 0.057\ (EIDOM)^2 - 0.37$	99	0.0119
Marsh	$-0.0077*(DUR) + 0.0006*(DUR)^2 + 0.021*(EIHGT)^2 + 0.0014$	98	0.0056
Insgran	$0.014*(DUR) + 0.036*(MOW) - 0.018*(EIDOM)^2 + 0.053$	98	0.0049
Insect	$-0.00007*(INT)^2 - 0.00005*(EI100)^2 + 0.198*(EIDOM) + 0.666$	95	0.0186
Avis	$0.0148*(MOW)^2 + 0.253*(MOWFRQ) - 0.334*(EIHGT) + 0.057*(EISPN)^2 - 1.015$	100	0.0009
Soilf	$0.0002*(DUR)^2 - 0.002*(INT) - 0.00003*(EI100)^2 + 0.023$	94	0.0251

Table 8
Multiple regression models (P<0.05) with farm and E.I. characteristics as predictor variables based on bird observations (response variables) on nine farms in Oostelijk and Zuidelijk Flevoland in 1999. The keys are in Table 5 (birds) and Table 1 (farm and E.I. characteristics).

Birds	**Model**	**R^2**	**Pr>F**
Alau	$0.0033*(DUR)^2 + 0.000012*(EI100)^2 + 0.0034*(MOW)^2 - 0.00006*(EICOV)^2 + 0.347$	98	0.0015
Fin	$0.0084*(DUR) - 0.000009*(EI100)^2 + 0.0227*(MOW) - 0.0751*(EIHGT) - 0.109$	99	0.0006
Mota	$-0.00002*(INT)^2 + 0.0559*(WABUN) + 0.3127*(MOW) - 0.0201*(MOW)^2 +1.122$	93	0.0121
Marsh	$-0.216*(MOW) + 0.0138*(MOW)^2 - 0.144*(EISPN) + 0.0101*(EISPN)^2 + 1.243$	98	0.0008
Insgran	$0.0268*(DUR) + 0.0036*(EI100) - 0.129*(MOWFRQ)^2 - 0.0625*(EISPN) + 0.597$	88	0.0418
Insect	$-0.0024*(INT)^2 + 0.0404*(WABUN) + 0.0026*(EISPN)^2 + 0.128$	95	0.0012
Avis	$0.0158*(DUR) + 0.112*(MOW) - 0.0994*(EIHGT)^2 - 0.371$	89	0.0081
Soilf	No model		

3.4. Bird functional groups and relations to landscape characteristics in 1998

Table 9 is presenting the significant best multiple regression models for bird functional groups, using landscape characteristics as predictor variables; semi-natural habitats included canals, canal banks, road verges, tall herbs, shrubs and woodlots.

Table 9

Multiple regression models ($P<0.05$) with farm and E.I. characteristics as predictor variables based on bird observations (response variables) on eight farms in 1998. Keys in Table 5 (birds) and Table 1 (landscape characteristics).

Birds	**Model**	**R^2**	**Pr>F**
Alau	$0.048*(\mathrm{LSINT}) - 0.00069(\mathrm{LSINT})^2 - 0.00011*(\mathrm{LSVEG})^2 - 0.557$	94	0.006
Fin	$0.000018*(\mathrm{LSAGE})^2 - 0.031*(\mathrm{LSNAT}) + 0.0037*(\mathrm{LSINT}) - 0.003*(\mathrm{LSVEG}) + 0.154$	97	0.012
Mota	$-0.0067*(\mathrm{LSINT})$	51	0.045
Marsh	$-0.024*(\mathrm{LSVEG}) + 0.0005*(\mathrm{LSVEG})^2 + 0.268$	83	0.011
Insgran	$0.004*(\mathrm{LSAGE}) + 0.068*(\mathrm{LSINT}) - 0.001*(\mathrm{LSINT})^2 - 0.007*(\mathrm{LSVEG}) - 0.866$	96	0.021
Insect	$-0.28*(\mathrm{LSNAT}) + 0.021*(\mathrm{LSNAT})^2 - 0.0001*(\mathrm{LSVEG})^2 + 1.065$	97	0.001
Avis	$-0.057*(\mathrm{LSNAT}) + 0.717$	58	0.028
Soilf	$0.00005*(\mathrm{LSAGE}) + 0.00005*(\mathrm{LSVEG})^2 + 0.049$	88	0.005

Skylark territories were curvilinearly related to a landscape with many gramineous crops, and negatively to a landscape with a high proportion of vegetable crops. Finches (mainly linnet) territory density was found to be positively related to the age of the polder and to the proportion of gramineous crops, and negatively related to the proportions of semi-natural habitat and vegetable crops.
Wagtails/pipet territory density was predicted by a marginally significant model which included a negative relation to the proportion of gramineous crops in the landscape. Marsh birds had a curvilinear relation to a high proportion of vegetable production.

Insecti-granivorous bird territory density (including skylark, linnet, goldfinch and quail) was found to be positively related to the age of the polder, negatively to the proportion of vegetable crops and curvilinearly to gramineous crops. Insectivorous bird territory density (including blue-headed and white wagtail, meadow pipit, reed warbler, reed bunting and bluethroat) was curvilinearly related to a high proportion of semi-natural habitat in the landscape and negatively to the proportion of vegetable crops. Total songbird territory density was best predicted by the proportion of landscape with semi-natural habitat and was found to be negatively related to this variable. Soil life-feeding bird territory density was found to be positively related to the age of the polder and the proportion of vegetable crops.

4. Discussion

4.1. Observations in comparison with hypotheses

Observations of wagtails/pipet showed most accordance with hypotheses because the territory density of this group (insectivores with combined crop and E.I. affinity) was indeed related to both the crop area and E.I. characteristics and more positively and more clearly related to vegetation dwelling arthropods (including abundant flying species) than to ground dwelling arthropods. However in general terms, similar observations were done with regard to the other three groups of skylarks, finches and marsh birds. This means that field observations did not provide indications for the expected E.I. preference of finches and marsh birds and crop area preference of skylark. Also the expected association between insecti-granivorous birds and ground dwelling arthropod abundance was not observed.

With regard to crop area characteristics there was, according to the hypotheses, a general positive relation to organic farming duration in the 1999 observations. Our hypothesis was that both organic duration as well as extensive crop rotation would enhance detrital subweb prey for birds. However a negative relation to extensive crop rotation was found with regard to several bird functional groups, and particularly to the insectivorous groups.

With regard to ecological infrastructure variables, observations were largely in accordance with our hypotheses, because selected models often included positive relations to characteristics of improved E.I., particularly late mowing and plant or dominant plant species number. However some models had seemingly inconsistent combinations of characteristics as for example, early mowing with high vegetation.

These general tendencies, which have been discussed, can be viewed in Table 10, which shows the occurrence of the different (types of) variables in all selected models. The general tendencies are also well summarized in the best models for total songbird territory density. These models included positive relations to vegetation dwelling predators in the E.I., plant species number in the E.I., and organic duration (in 1999) and a negative relation to proportion of gramineous crops (in 1998).

4.2. Crop area effects

4.2.1. Food resources in the crop area

Preference of birds for arthropods from the E.I. may suggest that birds were attracted away from fields with poor food resources (O'Connor & Schrub, 1986). Preference of skylarks and blue-headed wagtails for field margins on conventional farms was found by De Snoo (1995) in the Haarlemmermeerpolder and by Remmelzwaal & Voslamber (1996) in 50 ha crop plots in Zuidelijk Flevoland. However, mean skylark territory densities on studied organic farms in 1998 (0.15/ha) and 1999 (0.12/ha) were quite high when compared to means in Zuidelijk Flevoland and the Groningen clay district: 0.09/ha and 0.11/ha, respectively (Remmelzwaal & Voslamber, 1996). Densities of around 0.2 territories/ha found on farms with high skylark abundance, correspond to densities of good skylark habitats involved in studies of Poulsen *et al.* (1998) and Wakeham-Dawson *et al.* (1998) in Great-Britain. This might be an indication that the studied organic arable crop areas contributed to bird abundance.

4.2.2. Food resources related to detritivore and herbivore subsystems

Negative relations to extensive crop rotation of insectivorous and insecti-granivorous birds were opposit to the hypothesis. Apparently distributions of birds and carabid beetles and linyphid spiders (involving >80% of ground dwelling invertebrate numbers) did not match. Explanations may involve food as well as other environmental factors, however in this article we primarily explore explanations concerning food resources. A possible explanation might be that the increased detrital subweb, related to increased carbon supply, depresses the herbivore subweb (Wise *et al.*, 1999) while herbivores are preferred prey items in 'chick-food' (Hald & Reddersen, 1990; Moreby & Sotherton, 1997). This explanation will be explored below.

Table 10

An overview of the variables that were selected by significant multiple regression models based on bird territory density (response variable) with farm and E.I. characteristics as predictor variables as well as arthropod functional groups as predictor variables. Key: On the horizontal axis birds: alau = skylark, mota = Motacillidae, fin = finches, marsh = marsh birds, insect = specialist insectivorous birds; insgran= insecti-granivorous birds; avis = total songbirds; soilf =soil life-feeding birds ; On the vertical axis, characteristics at the farm and at the E.I. habitat level (key see Table 1); down at the left side: ground dwelling arthropods: col = predacious beetles; lyc = lycosid spiders; lin = linyphiid spiders; stsm = small staphylinid beetles; carh = granivorous carabids; foli=folivorous insects; down at the right side: vegetation dwelling arthropods: Kherb= K-herbivores; detr = detritivores; pred= predators; par = parasitoids; rherb = r-herbivores; additional symbols: 'ca' = crop area; 'ei' = ecological infrastructure.

1998 1999

Factor	alau	mota	fin	marsh	insect	insgran	avis	soilf	**Factor**	alau	mota	fin	marsh	insect	insgran	avis	soilf
dur									dur	X		X	X		X		X
int		X			X		X		int		X	X		X			X
									wabun								
ei100			X						ei100		X			X			X
area		X	X	X					area			X					
mow	X			X		X		X	mow	X					X	X	
mowfrq		X				X	X		mowfrq	X						X	
eihgt				X				X	eihgt		X		X			X	
eicov	X					X	X		eicov	X							
eidom					X				eidom		X			X	X		
eispn			X				X		eispn							X	
colca									Kherbca								
lycca	X								detrca								
stsmca				X					predca			X					
linca		X	X					X	parca								X
carhca	X	X						X	rherbca	X							
folica																	
colei								X	Kherbei	X		X					X
lycei	X	X						X	detrei		X			X			
stsmei									predei	X		X			X	X	
linei	X								parei	X		X	X			X	
carhei			X						rherbei				X	X			
foliei																	

The observation that Skylark territory density related to r-herbivore (*i.e.* Aphididae) abundance suggested that this bird is associated with an increased herbivore subweb in intensive crop rotation. However aphids are probably not important food item for skylarks (*e.g.* Cramp, 1988; Poulsen *et al.*, 1998) and may therefore indicate other (food resource) factors.

Probably crops in intensive organic farms are generally more vulnerable to pest outbreaks than crops in extensive organic farms due to crop physiology (*e.g.* Phelan, 1997) as well as a lower predation pressure from detrital subweb-based polyphagous predators. This type of crop vulnerability is demonstrated in the conventional plots of various comparative studies including various crop species (Kromp & Meindl, 1997). Time series of arthropod numbers in crop edges of conventional crops (Remmelzwaal & Voslamber, 1999) with regard to various crop species, show similar exponential increases of arthropod numbers which are temporarily higher than arthropod densities in grass margins. Hald & Reddersen (1990) also found higher arthropod densities in conventional cereal fields than in organic fields if the exponentially developing aphids were taken into account. They note that aphids are supplementary prey but that the unpredictability of their densities limit the carrying capacity of conventional crops. On organic farms in Flevoland spatial variation of individual crop species may compensate for the short time intervals of crop-specific herbivore increases. Accordingly, spatial analysis of skylark territories (Nan *et al.*, in prep.) showed an affinity of skylarks for within-field crop borders, which may facilitate foraging in different crops and crop edges (Wilson *et al.*, 1997).

The effect of predation by polyphaguous predators might be stronger on numbers of large-sized invertebrate herbivores (K-strategists) than on numbers of small-sized r-strategists, because K-strategist populations may be vulnerable due the scarcity of host plants, both weedy and undersown. Poor nutritive quality of a diet comprised of mainly r-herbivores (*i.e.* aphids) may also be involved (Toft, 1996). Herbivorous prey resources on organic arable farms in Flevoland may therefore include only a small proportion of favourite items (sawfly and lepidopteran larvae). However, in this case r-herbivores may be relevant as food resource for insectivorous birds.

In crops or crop rotations where epigeic predators exploit detritivores and subsequently inhibit herbivores, birds have to feed on these predators. However, food web structures in these habitats represent a poor resource for chick food. Observations of Poulsen *et al.* (1998) may be coherent with our theory: skylark chick diet and survival was compared in three distinct crop habitats (four year old set-aside, grass silage and spring barley): nestlings in set-aside received many small loadings of small soft-bodied (*i.e.* herbivorous but no aphids) organisms which were abundant in that crop habitat; nestlings in both other crops received larger loads including hard-bodied organisms, particularly carabid beetles. In spring barley arthropod abundance was lowest and nestling diet included a high proportion of spiders that perhaps, compensated for the lack of larger items; the observed chick mortality in spring barley was probably caused by starvation.

Examination of arthropod communities provided preliminary evidence for these ideas: detailed analysis of ground dwelling arthropod communities in 1998 (Smeding *et al.*, 2001a) indicated that wheat crops in intensively managed farms, as compared to extensive farms, had low numbers of epigeic predators (and high numbers of fungivorous small staphylinids) whereas wheat crops of farms with less intensive (*i.e.* vegetable) production could be associated with an abundance of carabid beetles, granivorous carabid beetles and lycosid spiders. Detailed analysis of the vegetation dwelling arthropod community on arable farms in Flevoland in 1999 (Smeding *et al.*, 2001b) indicated that wheat crops in extensive crop rotations of long duration farms had a low abundance of herbivores and a moderately high abundance of detritivores (*i.e.* small diptera species) and parasitoids, whereas wheat crops of intensive crop rotation farms were characterised by (potential) outbreaks of r-herbivores and absence of high numbers of other arthropod functional groups.

The ideas presented correspond to the hypothesis of Power *et al.* (1996), that partly contradicts the hypothesis of the positive relation between increased primary productivity and top predation (*e.g.* Oksanen *et al.*, 1996). Power *et al.* (1996) found in temporal succession on river flood plains, that food chains shorten from three to two steps, because in a later successional stage armoured secondary consumers inhibit food supply of the top predators; in the dynamic situation of early successional stage the primary organisms are better accessible and give rise to longer food chain lengths more than two steps. In more or less stabilized farm food webs due to detrital subsidy and herbivory-resistant crop physiology, dominant predacious invertebrates may be epigeic predators. This guild is 'armoured' from a birds perspective; their 'armour' may relate to both hard bodies (carabids) as well as hiding in dense vegetation or in the soil, size (*e.g.* for wagtails) and nocturnal behaviour (Vickerman & Sunderland, 1975).

4.3. Ecological Infrastructure effects

Territory densities of most investigated bird functional groups showed the positive effect of increased numbers of detritivores and predators in late mown E.I. (Table 10). Accordingly increased arthropod abundance in late mown (uncut) vegetation, as compared to early mown, is reported in several studies (Boatman *et al.*, 1999; Wakeham-Dawson *et al.*, 1998; Schekkerman, 1997; Curry, 1994). Wagtails/pipet may have foraged on abundant small flies. Negative relations of birds to parasitoids and K-herbivores indicated an avoidance of early mown E.I. because these groups were relatively abundant in traditionally managed canal banks (Smeding *et al.*, 2001b). However, skylarks also showed some affinity for open E.I., possibly attracted by hoppers, lycosid spiders, granivorous carabids and ants.

Apart from marsh birds, there is a tendency to avoid high E.I. vegetation. This may have a behavioural background that the typical arable farmland birds prefer habitats that afford a good view. Marsh birds did not relate strongly to the average value of E.I. vegetation height because local stands of reed or shrubs may already be sufficient to establish a number of territories.

Emergent vegetations may attract or catch flying arthropods (Hradetzky & Kromp, 1997). Many detritivorous diptera and aphids in late-mown vegetation are perhaps not autochthonous for the habitat. r-Herbivores density in the E.I. and crop area were highly correlated (Smeding *et al.*, 2001b). This may explain why marsh birds, which mostly stay in and around E.I. vegetation, could be predicted by r-herbivores in the E.I. and, intensive production indicating (Smeding *et al.*, 2001b), small staphylinids in the crop area. Densities of marsh birds in emergent vegetation surrounded by arable crops might be promoted by a prey 'precipitation' of both detrivores and herbivores from the crop area.

Hald & Redderson (1990) noted that additional sweep-net sampling, including more bird prey items, exaggerated the difference between conventional and organic crops. Accordingly catches of four yellow water traps on farm E (Venhorst & Smeding, unpublished data) included taxa under represented by suction trapping, containing 75% diptera of which c. 10% involved larger taxa (>2 mg dry weight). This under represented group, involving anthomyid flies, scatophagid flies, craneflies and predacious flies might be important for various insectivorous birds (Poulsen *et al.*, 1998; Cramp, 1988).

Soil life-feeding birds were expected to relate to crop area characteristics. However, also association with certain E.I. characteristics were found. This is in accordance with impressions in the field that chicks of lapwing often occurred in ditches, particularly those with 'traditional mangement', where mud and shallow water in non-vegetated open ditch bottoms provide soft ground and abundant aquatic prey, including molluscs.

4.4. Landscape effects

Differences in bird territory densities between farms were also affected by landscape factors. The Zuid Flevoland polder had a shorter life and larger fields which means a lower spatial density of E.I. Territory densities of skylarks, wagtails/pipet, linnet and lapwing relate positively to one or both of these variables and therefore older polders were preferred.

Negative relations to linyphiid spiders can be explained by the fact that linyphiids preferred the larger scale found in the younger polder (Smeding *et al.*, 2001a).
At the landscape level skylarks seemed to be associated with a high proportion of gramineous crops and a low proportion of vegetable crops. This was more or less opposite to the farm-level observations of skylarks but in accordance with the expectation from literature. Landscape level crop areas included both conventional and organic crops. On conventional farms cereals may offer the largest food resource for birds. However, on organic farms other crops than cereals could be relevant for prey provision.

According to expectations, marsh birds were enhanced by a high percentage of semi-natural habitats in the farm surroundings. Impressions in the field were that vicinity of canals with reed stands, ponds or dense shrubs (*e.g.* in a 2 ha nature reserve near farm A) encouraged nesting of this functional group in the farm E.I. However, total songbird territory density is related negatively to the proportion of semi-natural habitat at the landscape level. Accordingly spatial analysis of skylark observations with GIS (Nan *et al.*, in prep.) revealed that skylark territories are clustered on farms, particularly at some distance from the farmyards, tree lines and roads. This may reflect the preference shown by typical arable farmland birds for open landscape with no disturbance.

4.5. Conclusions

Results of bird studies in 1998 and 1999 on ten organic arable farms in Flevoland suggest that bird territory density is particularly supported by organic arable farms with intensive crop production and improved (late mown, species rich) ecological infrastructure. Bird food resources on intensive farms may be based on periodic and local herbivore increases in a crop mosaic. Extensive systems might be more balanced due to the pest-control by beneficials (*i.e.* polyphagous predators) and to a less susceptible crop physiology. However, in these systems with greater detrital subsidized food webs (*cf.* Wise *et al.*, 1999), the higher trophic levels (*i.e.* insectivorous birds) might be inhibited by secondary consumers which exploit the primary level and have limited availability for vertebrate predators (*cf.* Power *et al.*, 1996).

Crop areas on organic arable farms in Flevoland may not resemble the food rich habitats observed by Hald & Redderson (1990) or in set-aside (*e.g.* Poulsen *et al.*, 1998) due to perhaps intensity and/or abundance of epigeic predators that inhibit populations of soft-bodied herbivorous larvae.

Late mown E.I. most probably offers an important food resource, supplementing both quantitatively and qualitatively, the crop area food resources and possibly filling temporary gaps in food availability.

Our observations provided preliminary evidence for these ideas; further research is required.

4.6. Recommendations

Further research on the topic requires restricted geographical variation between farms. Experimental manipulation of bird populations at the farm level is extremely expensive. The study area may therefore include extreme types of commercial farms, with regard to intensity and E.I. management and one or two experimental (pilot)farms which have, for example, increased detrital subsidy based on crop residues and organic manure.

The suggested importance of r-herbivores for birds in the crop area is hard to translate in practical recommendations because r-herbivores are usually pests. It may therefore be a challenge for farmers and agroecologists to design crop rotations with controlled herbivory in for example mixed crops, living mulches (Theunissen, 1994; Theunissen *et al.*, 1997), ley crops and grazing-resistant cultivars.

Closer examination of local bird diets and foraging habitats is required, assessing the contribution of aphids, craneflies and carabid beetles in bird diets, and tracing important taxa. Other catching methods, preferably including a density assessment, should be tried (*e.g.* Duelli *et al.*, 1999). Also non-food habitat factors (machine disturbance and predation) should be considered.

Special attention should be given to the effect of local 'hot spots' of food, represented by wagtails feeding on dung deposits (*e.g.* Hald & reddersen, 1990) or lapwings feeding at ditch bottoms.

Modification by farmers of E.I. management is very rewarding in terms of bird abundance and therefore of nature conservation value. In particular because late mowing contributes to bird food resources in early summer. However, managements with cautious, frequent mowing at >10 cm above ground surface may also stimulate herbivores and predators important for birds. Optimally managed E.I. may include a permanent, simple division into some frequently mown and late mown boundaries (see *e.g.* Feber *et al.*, 1999) and also local, broad stands of tall vegetation or shrubs which facilitate nesting of marsh birds (see *e.g.* Stoate, 1999). Reed or shrubs should preferably be situated close to the present semi-natural habitat so that open space, attractive for typical farmland birds will not become fragmented (Smeding & Joenje, 1999).

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Chapter 5: Effect of field margin management on insectivorous birds, aphids and their predators in different landscapes

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Abstract

An increased field margin area at farm level, is thought to promote vertebrate and arthropod predators and to reduce pests. In a field trial in 1997 a comparison was made between animal communities on four organic farms that possessed different amounts of ecological infrastructure (E.I.). One pair was situated in young landscape and the other in old landscape. Only specialist insectivorous birds showed a clear positive relationship. With regard to important arthropod species in wheat (e.g. carabid, staphylinid and coccinellid beetles, spiders) abundance differences in relation to amount of E.I. were not related to old and young landscapes. High aphidophagous syrphid fly abundance and aphid (pest) densities occurred in young landscape farms.

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1. Introduction

1.1. Agriculture and biodiversity

Biodiversity in European agricultural landscapes is decreasing. One important solution for reversing this biodiversity loss is to develop farming systems that integrate agriculture and nature conservation interests. Organic farming tries to implement this idea because biodiversity is thought to enhance pest control (Altieri, 1994). Farm-nature plans support these farms to develop site-specific habitat diversification which means the establishment of an ecological infrastructure (E.I.) (Smeding & Joenje, 1999). The E.I. is defined as the total of semi-natural (aquatic, woody, tall herb and grassy) habitats on the farm including its spatial arrangement. Habitat diversification is likely to increase natural enemy abundance and to reduce pest populations (Booij & Den Nijs, 1996); this means that the herbivorous pest organisms represent a small part of the mainly non-pest herbivore and detritivore communities in the farm food web. The increase of beneficial and harmless (prey) species enhances the food availability for the vertebrate species on the farm (*e.g.* Moreby & Sotherton, 1997; Hald & Reddersen, 1990), which are of conservation interest.

1.2. Farm ecological infrastructure

Practical recommendations to optimize the Ecological Infrastructure often rely on experience and common sense. Detailed studies about key species are available, *e.g.* skylark (Wilson *et al.*, 1997) and partridge (Potts, 1983), however, it is difficult to combine and extrapolate this knowledge to farm practice and translate it to actions of the farmer.

Our study was intended to contribute to a systems approach that links information on the ecology of species (groups) with farm topography and management. Therefore we undertook a simultaneous examination of several integration levels (landscape, farm and habitat/field) and animal species groups. Farm and fauna measurements which are both effective in the field (Den Nijs *et al.*, 1998) as well as explanatory factors in future theory were selected.

In a field trial in 1997 a comparison was made between four contrasting organic farms that possessed different amounts of established E.I. and might serve as good examples for the above theory. It is probable that the effect of equal efforts by the farmer would differ between landscapes; a biodiverse neighbourhood may overrule or amplify the effect. Therefore one pair of organic farms was situated in a young (culture) landscape and another pair of organic farms in an old (culture) landscape; old landscape is assumed to be more biodiverse. Our hypothesis was that an increased E.I. would be associated with more insectivorous birds, more arthropod predators and a reduced pest infestation.

2. Materials and Methods

2.1. Study sites

The research was carried out on four different organic farms (indicated in the text as Y-, Y+, O- and O+) on clay soils in April-August 1997. Two farms were situated in the young landscape (=Y) of the polder Zuid-Flevoland which was reclaimed in 1968. The other two farms were part of an old landscape (=O) near the rivers in the centre of The Netherlands. In each landscape farms with a small E.I.(=-) and a farm with a greater E.I.(=+) were selected. Within each farm winter wheat fields were chosen as a representative crop for arthropod and arable weed measurements. Cereal aphids were chosen as an example of a pest.

For Dutch standards all studied farms can be considered as old organic farms. Farms Y- and Y+ started in 1985 on an experimental reclamation area which never received pesticides. Farm Y+ joined a group of 10 'innovation' pilot farms in 1993 which implies that all ditches have adjacent three meter wide grass strips and that ditch vegetation includes several artificially introduced indigenous plant species (Vereijken, 1998). Farm O- converted to organic farming practice in 1980; its intensive production is focussed on cabbage and leek; old hedgerows were maintained, mainly at the borders of the farm. Farm O+ was run between 1971-1995 as part of a secondary school for biodynamic farming; extensive boundaries including hedgerows were created during this period.

2.2. Sampling and measurements

2.2.1. Landscape

Landscape parameters were sampled in a circle around the mathematical centre of the farm. The radius of this circle differed between the four farms because it included a section of the farm and an extra 200 m from the farm border; the 200 m distance approximates to the home range of several small mammals and songbirds. Inside the circle, the area of different agricultural, semi-natural and other habitats was measured. The semi-natural aquatic, woody, tall herb and grassy habitats were defined as E.I. The scale of the landscape was determined by measuring the total areas ('blocks') of interconnected agricultural fields.

2.2.2. Farm

The limits of the study area were equal to the administrative borders of the farm because this is the unitary system under control by the farmer (Swift & Anderson, 1993). The areas of semi-natural habitats were measured, as for landscape.

The spatial arrangement of the ecological infrastructure was expressed by the percentage of the farm which lay within a 100 m distance of the ecological infrastructure. The influence of boundaries on the abundance of large carabid beetles and spiders probably does not exceed 100 m.

2.2.3. Vegetation

Vegetation studies included boundaries surrounding the crops. The herb layer was sampled in one meter lengths at intervals of 25-100 m between samples, depending on the length of the boundary. Parameters were: cover, maximum height, plant species and dominant plant species (which determine 80% cover).

Weed species composition in winter wheat was recorded by listing the species in 40 samples of 0.25 m^2 in each field.

2.2.4. Birds

Territory mapping of birds was done three times at the beginning and the end of May and the beginning of June, using the method described in Van Dijk (1993). Breeding birds were grouped according to three food types: insectivorous, insectivorous/granivorous and soil life-feeding.

2.2.5. Arthropods

Weekly samples were taken on each farm in winter wheat between 29 April and 24 July. In each winter wheat field four random plots of 10 by 20 m were laid out, in which three pitfall traps and a yellow water trap were placed. Aphids were counted on 80 to 200 tillers per plot, depending on the expected number of aphids present. The carabid and staphylinid beetles and spiders caught in pitfall traps were sorted into size categories; syrphid flies and coccinellids in the water traps were determined to species level.

In September three suction samples (3 minutes in 1 m^2) were collected in adjacent boundaries including a tall herb and grassy and a shrub sample; herbivorous beetles (curculionids and chrysomelids) were determined to species level.

3. Results

3.1. Landscape characteristics

3.1.1. Farm surroundings

The young landscape was dominated by agricultural land use and had large blocks of continuous agricultural land (Table 1). The percentage semi-natural habitat appeared to be unaffected by landscape type.

3.1.2. Farm and its habitats

Crop rotation in young landscape tended to include fewer extensive crops (cereals and ley pasture) (Table 1), however farm Y- included a relatively large percentage due to its large size. Wheat yields were higher in the young landscape whereas arable weeds in this crop were much more abundant and divers in the old landscape (Table 1). Farms in young landscape had a larger crop area that was remote from the boundaries (Table 1). Boundaries in the polder included more aquatic habitat (ditches and banks) and in the river region included more woody (hedgerow) habitat. The structure diversity and species richness of the boundary vegetation appeared to be unaffected by the landscape type (Table 1).

Table 1
Characteristics of four farms in young (Y) and old (O) landscape with small (-) or increased (+) E.I. with regard to landscape and habitats.

		Y-	Y+	O-	O+
Landscape	% agricultural land use	71	94	54	52
	block size (average)(ha)	23	26	3	2
	% semi-natural habitat	27	4	40	18
Farm	farm area (ha)	210	55	22	28
	% cereals/ley pasture in crop rotation	50	29	50	75
	% farm area within 100 m range of E.I.	61	72	81	100
	% semi-natural habitat = E.I.	1.2	2.6	1.7	5.8
Crop	no. of weed species/0.25 m^2	3.2	1.6	5.4	5.1
Boundary	no. of plant species/m (average)	7.6	11.4	9.0	9.9

3.2. Effects of Ecological Infrastructure

3.2.1. Young landscape

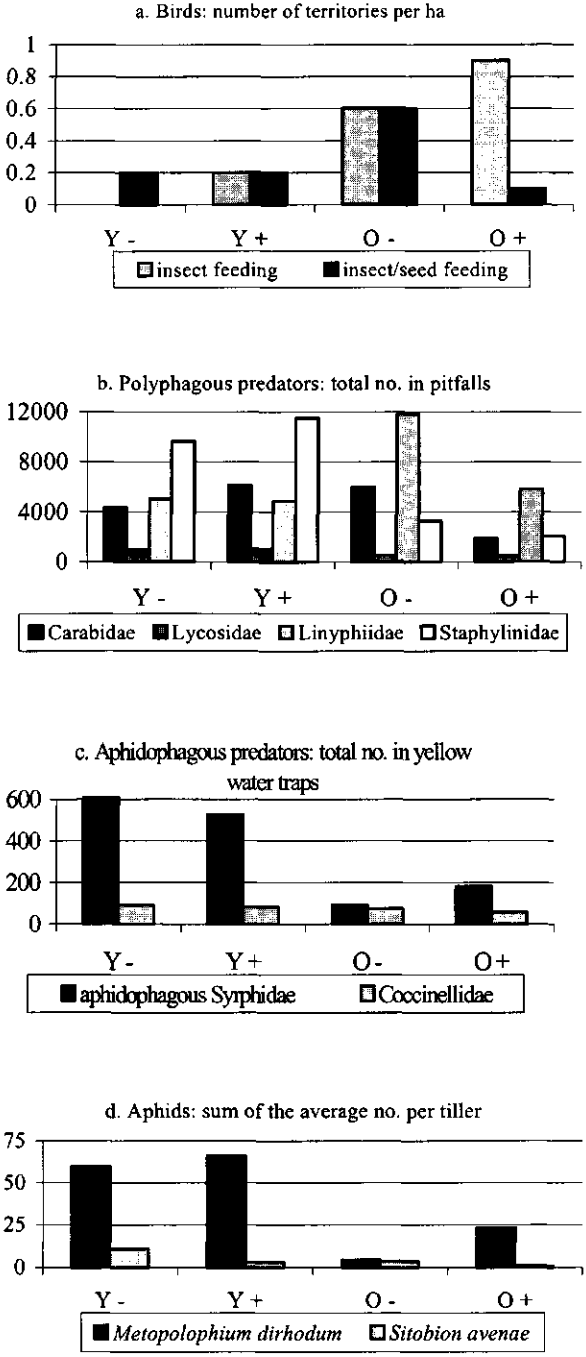
Characteristics of farm Y+ (2.6% E.I.) in comparison with farm Y- (1.2% E.I.) were: a more diverse boundary vegetation and less weeds in wheat (Table 1); a higher density and species number of breeding birds due to the occurrence of specialist insectivores in the boundaries (Fig. 1a); a slightly greater abundance of most polyphagous predator groups in wheat (carabids, staphilinids and lycosid spiders) (Figs 1b and 1c), whereas aphidophagous syrphids and ladybirds were slightly more abundant in wheat on farm Y- (Fig. 1c); similar high aphid abundance in wheat (Fig. 1d); a higher species number and similar (low) abundance of herbivorous beetles in boundaries.

3.2.2. Old landscape

Characteristics of farm O+ (5.8% E.I.) in comparison with farm O- (1.7% E.I.) were: a more diverse boundary vegetation (Table 1); a higher density of specialist insectivorous birds and a lower density of mixed insecti-granivorous birds resulting in a lower total breeding bird density (Fig. 1a); lower abundance of polyphagous aphid predators in wheat (carabid and staphilinid beetles and linyphiid spiders) (Fig. 1b); monophagous aphid predator abundance were variable: more syrphids, less ladybirds (Fig. 1c) and less lacewings; similar low aphid abundance in wheat (Fig. 1d) apart from an early moderate peak of *Metopolophium dirhodum*; a higher species number and abundance of herbivorous beetles in boundaries. The abundance of syrphids could have been underestimated because the yellow water traps competed with numerous flowers (Den Nijs *et al.*, 1998).

3.2.3. Relationships with landscape types

Increased ecological infrastructures on two of the four farms in two contrasting landscape types involved a doubled percentage of semi-natural habitats and a more diverse vegetation (Table 1). This promoted in both landscapes species that strongly depend on the E.I. itself (insectivorous birds density and herbivore beetles diversity). In the crop only abundance of the aphid *R. dirhodum* seemed to increase (Fig.1d). A decrease was found with regard to the abundance of coccinellids (Fig.1c) and the density of the aphid *Sitobion avenae* (Fig.1d). However most fauna parameters that were studied did not show a relationship. Abundance of polyphagous aphid predators on farms with increased E.I. decreased in old landscape whereas they increased in young landscape (Fig.1b); aphidophagous syrphids showed the reverse (Fig.1c).



a. Birds: number of territories per ha

b. Polyphagous predators: total no. in pitfalls

c. Aphidophagous predators: total no. in yellow water traps

d. Aphids: sum of the average no. per tiller

Fig. 1. Occurrences of birds (a), polyphagous predators (b), aphidophagous predators (c), and aphids (d) on four farms: Y = young landscape; O = old landscape; - = small ecological infrastructure; + = large ecological infrastructure.

4. Discussion

Only observations of specialist insectivorous birds and in the young landscape also polyphagous predators supported our hypothesis. Few parallels between effects in the old and young landscapes were found. How can these contradictory results be understood? In our attempt to give an explanation we focus on soil invertebrates and weed abundance which are only groups among several others. However, these groups are likely to influence numbers of birds and predatory arthropods.

4.1. Young landscape

Soils in the polder landscape are known to contain few earthworms and probably have a lower soil meso- and macrofauna biomass than old landscapes. This is in accordance with the observed low density of soil life-feeding birds. The low abundance of arable weeds limits dependent foliar herbivores and granivores. These factors lead to a crop habitat where aphids become an important component in the summer diet of polyphagous predators (Booij & Den Nijs, 1996). Several authors report this predominance of aphids in conventionally managed wheat (Moreby & Sotherton, 1997; Reddersen 1997).

Predator counts on farm Y+ suggested an influence of increased E.I. but its area may have been too small and its distance from field centres too far to have a strong effect; moreover weed abundance and a high percentage of cereals/ley pasture on farm Y- offered better circumstances for ground dwelling invertebrates as compared to farm Y+.

4.2. Old landscape

Crops in the old landscape contained more weeds and probably a higher soil invertebrate biomass. Farm O- had a high weed abundance; its intensive vegetable production caused a higher general fertility level of the fields which may have a quantitative effect on soil invertebrates. These factors could explain the high abundance of the polyphagous carabid beetles (comparable with the young landscape numbers) and linyphiid spiders in spite of the absence of aphids. Also the apparently high abundance of insectivorous/granivorous birds at farm O- supports this idea of abundant food availability in the fields. These requirements possibly overrule the E.I. influence on crop communities in the growing season.

4.3. Improving the hypothesis

In the light of these results we conclude that the hypothesis should also consider crop factors including crop diversity (e.g. crop rotation, weeds) and soil life characteristics. Ideally comparative research on E.I. influence should be restricted to farms where these characteristics are similar. The hypothesis could only work on farms with intermediate levels of alternative prey on the fields (associated with soil life and weeds or intercrops) and with boundaries that are not too far from field centres. In our study in 1997 it seemed that animal communities in the crops were independent from E.I. In the polder the intensively cropped fields were probably too large to be influenced by the E.I. whereas in the river region the fields already had a high level of alternative prey related to crop factors. With abundant alternative prey caused by crop factors (which might be undesirable for the farm, *e.g.* weeds) a smaller E.I. may already be sufficient to maintain biodiversity.

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Chapter 6: A concept of food web structure in organic arable farming systems

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Abstract

A proposal for a descriptive or topological farm food web is derived from field observations and from references in literature. Important themes in the food web theory are tentatively applied to this preliminary model, explaining differences between local farm food web structures and how they are related to farm and/or ecological infrastructure (E.I.) management. Predictions are made for four different farm food web structures for extremes of farm and environmental gradients corresponding to the length of organic duration and amount/quality of E.I. The implications with regard to farming practices and nature conservation are that both organic duration and the amount/quality of ecological infrastructure may contribute to ecosystem services and nature conservation. However, an optimisation of the farm food web with regard to ecosystem services, may possibly run counter to nature conservation goals.

1. Introduction

1.1. The problem of biodiversity loss in agroecosystems

Species diversity of indigenous plants and animals on farmland is declining dramatically due to agricultural intensification (Paoletti, 1999; Wood & Lenné, 1999; Vandermeer *et al.*, 1998; Swift & Anderson, 1993). Amongst those that are greatly concerned about this biodiversity loss are agriculturists, ecologists and members of the public. Nature conservation organisations usually address the intrinsic value of biodiversity and their viewpoint is translated into national programs for species and habitat conservation (*e.g.* in The Netherlands: Bal *et al.*, 1995). Agroecologists stress the economic value of biodiversity, related to its ecological services, *e.g.* pest control and biotic regulation of soil fertility (Altieri, 1994, 1999; Paoletti, 1999; Pimentel *et al.*, 1995). Biodiversity loss has been thought to result in artificial ecosystems, requiring constant human intervention and costly external inputs.

Ecosystem services might be sustained or improved by a general, indiscriminate, high species diversity (Altieri, 1994; Paoletti, 1999) or by a few essential components of the local biodiversity, as determined by site characteristics (Vandermeer *et al.*, 1998; Almekinders *et al.*, 1995). Functional redundancy of species means that not all species have evident significance for ecosystem services (Duelli *et al.*, 1999). However, it can be argued that agriculture has, to a certain extent, responsibility for all species and communities which co-evolved with farming during around 10,000 years (Wood & Lenné, 1999), irrespective their utility.

1.2. Multi-species agroecosystem research

One important solution for the reversal of the loss of biodiversity in agriculture of the industrialised countries is the development of farming systems that are economically based on utilisation of biodiversity and that harbour, partly due to increased biodiversity, conservation-worthy species. This idea is compatible to the concept of multi-species agroecosystems (Vandermeer *et al.*, 1998; Altieri, 1994, 1999; Almekinders *et al.*, 1995; Swift & Anderson, 1993).

Research aimed at this concept requires an appropriate approach; three criteria, which take into account the studied objects and environmental variables, might be essential. Firstly, the research should apply methods that are appropriate for higher levels of aggregation and avoid reduction of the system through emphasis on variables of lower levels (Almekinders *et al.*, 1995). Secondly, investigations should address real farming systems because biodiversity, relevant for apparent ecosystem services, might be site-specific (Vandermeer *et al.*, 1998) and may not be observable in small 'isolated' subsystems, or foreseeable by a bottom-up approach. Preferably study areas should include objects that express functioning of ecosystem services (Brown, 1999a). Thirdly, assessed variables should be clearly related to both the structural and the daily decisions of the farmer so that the outcomes can be translated into farming practice and policy (*e.g.* Vereijken, 1997; Kabourakis, 1996; Park & Cousins, 1995; Smeding & Joenje, 1999).

Recent advances in research on food webs (Polis & Winemiller, 1996) offer a suitable approach for biodiversity studies at higher levels of aggregation (Pimm, 1991; Gezondheidsraad, 1997). This article therefore examines the perspectives of a food web approach for research that aims at multi-species agroecosystem development.

1.3. Food web approach

1.3.1. Definitions

Definitions and general information on food webs has been examined extensively in the volume edited by Polis & Winemiller (1996); some of their main points are summarised here. A food web is defined as a network of consumer-resource interactions among a group of organisms, populations, or aggregate trophic units. Species are usually aggregated in 'trophospecies' or functional groups which essentially share resources and predators but usually more criteria are used *e.g.* life history traits. Guilds are trophospecies of a higher order, and usually include several related functional groups.

In a food web diagram functional groups are arranged in trophic levels which have the same number of steps ('chain lengths') away from the basal resources plants or detritus. A descriptive or 'topological food web' depicts species and feeding relations; in a 'flow web' components and relations are quantified as to number or energy flow. The most elaborate food web representation is a 'functional web' that also reveals the relative strength of relations.

1.3.2. Research on farm food webs

Traditional studies on farmland communities often included considerations of the trophic structure which indirectly addressed local food webs. Examples of this kind of studies are the comprehensive empirical study by Potts & Vickermann (1974), including a wide range of invertebrate and vertebrate taxa present in wheat crops in West Sussex, UK, or the extensive survey of the trophic structure of above-ground insect biomass in various agricultural landscapes by Ryszkowski & Karg (1991) and Ryszkowski *et al.* (1993).
Most studies directly addressing food webs were restricted to a part of the farmland community, involving a section of the herbivore food (sub) web or a section of the detrital (sub) web, for example studies of pest-predator complexes (examples in *e.g.* Wood & Lenné, 1999; Kromp & Meindl, 1997) or the studies of food requirements of farmland birds

(reviewed by Poulsen *et al.*, 1998). Some of these studies provided clear conceptual advances. For example Andow (1988) hypothesised 7 'primitive relations' (*i.e.* food web structures) among weeds, crops, herbivores and predators. Comprehensive topological food webs of arable cropping systems, including detrital and herbivore subwebs, were first developed in 1977 for rice, in the context of Integrated Pest Management programmes (*e.g.* Cohen *et al.*, 1994; Schoenly *et al.*, 1996).

A major breakthrough in agroecological application of food web theory, were studies on the detrital subwebs in arable crops (*e.g.* De Ruiter *et al.*, 1993, 1995) and grasslands (*e.g.* Hunt *et al.*, 1987), including also analyses of nutrient and energy flows. Progress in scientific understanding of food webs is expanding into agroecosystems as is demonstrated by several recent review articles, for example: detrital subweb control of the herbivore subweb by influencing vegetation performance (Brussaard, 1998) or by increased predator pressure on herbivores due to externally subsidised detrital chains (Wise *et al.*, 1999); and interference between predacious functional groups, causing 'trophic cascades' in the herbivore subweb (Tscharntke, 1997).

1.4. Objectives

However, despite the above-mentioned advances, there is, to our knowledge, no comprehensive farm food web available for arable farming systems. Such a 'topological' food web, or a more elaborate 'flow' web, may enable a synthesis of fragmented data on taxa and habitats, and could subsequently form the foundation of agroecological farming system research (*e.g.* Swift & Anderson, 1993; Van Keulen *et al.*, 1998) as well as applied agroecosystem planning (Smeding & Joenje, 1999; Visser, 2000).

The objectives of this article are:
- to propose a simplified topological farm food web, encompassing both herbivore and detrital subwebs and their interrelations, as occurring at the farm level of aggregation;
- to demonstrate, using both empirical data and theory, how this preliminary food web model could be used to relate the abundance of functional groups to farm management;

A case study will be used to meet these objectives.

2. Methods and materials

2.1. Research area and delimitation of the system

2.1.1. Organic arable farms in Flevoland

The agroecosystem of arable farms in Flevoland is well studied because of several large experiments (*e.g.* Booij & Noorlander, 1992; Booij, *1994*; Brussaard *et al.*, *1988, 1990*; De Ruiter *et al.*, 1993, 1995; Lantinga & Oomen, 1998; Smeding & Joenje, 1999; Remmelzwaal, 1992; Remmelzwaal & Voslamber, 1996; Vereijken, 1989, 1997, 1998). Flevoland consists of three polders that were reclaimed between 1940 and 1968 and are dominated by agricultural land use. The landscape is flat and open with woodlots confined to farmyards, villages and main roads. The predominant soil type is calcareous clay of marine origin.
Organic farms may function as a stepping stone on the road to developing multi-species agroecosystems (*e.g.* Stobbelaar & Van Mansvelt, 2000; Vandermeer, 1995) and were therefore chosen as objects for the case study. Around 75 organic farms are situated in Flevoland including farms with improved ecological infrastructure, resulting from a

prototyping research project (Vereijken, 1997, 1998). The case study is based on empirical data of 17 organic farms and one integrated farm, and literature concerning around 10 organic, integrated and conventional (experimental) farms.

Crop rotations of organic arable farms in Flevoland include six or more years. Common crops are spring and winter wheat (10-35%), ley pasture (0-20%), traditional lifted crops (potatoes and sugar beet) (10-35%) and intensive vegetable crops (25-70%). Major vegetable crops are onions, peas, sweet corn, runner beans, carrot and various cabbages. Ploughing is generally at 25-30 cm depth. The ecological infrastructure (E.I.) (Smeding & Booij, 1999) on arable farms in Flevoland mainly consists of linear herbaceous boundaries of canal banks and verges along tracks and roads (Smeding & Booij, 2001). The case study is based on empirical data of around 20 organic farms.

2.1.2. Delimitation of the system

The farming system is positioned between commonly recognised aggregation levels of habitat and landscape and may therefore be too small to be considered as an (agro) ecosystem. However Swift & Anderson (1993) consider the farm as the basic unit in studies of system functioning in agricultural systems. The farm level might therefore be considered as aggregation level in the ecological sense. Accordingly, Bockemühl (1986) argues that taking local ecological and historical factors into account in farm management can consolidate the system borders of a farm unit.

The second criterion for spatial delimitation of the considered system is that it matches the space required by a well-defined food web. According to these criteria Cousins (1988) defined the Ecosystem Trophic Module: the ETM is based on the territory size of the top predator. Resident top predators on arable farms in Flevoland are Kestrel (*Falco tinnunculus*) and Stoat (*Mustela erminea*) (Remmelzwaal & Voslamber, 1996). Their territory sizes correspond to the scale and size of the studied farming system.

2.2. General description of the topological farm food web

The topological food web, including preliminary flow web characteristics, of a Flevoland organic arable farm was developed using the following sources of information:

- empirical data from farmland species in Flevoland including data from our own research in Flevoland (references mentioned above and Smeding *et al.*, 2001a, 2001b; Smeding & Booij, 1999, 2001; Smeding, unpublished data);
- literature on diets and predators of the taxa observed in Flevoland;
- publications of research concerned with farmland species in arable crops and field margins in Western Europe.

The species (-groups) were listed in a food web matrix. Functional groups and guilds were assembled according to commonly accepted criteria (Polis & Winemiller, 1996; Brussaard, 1998). The examples of assemblages from the literature were followed if possible (*e.g.* Brussaard *et al.*, 1997; Brussaard, 1998; White, 1974). Some taxa may belong to more than one functional group because of shifts in their life history traits.

The biomass of the trophospecies reflects their ecological functions (Ryszkowski *et al.*, 1993); biomass estimations are therefore applied to illustrate the relative importance of groups and interactions in a two-dimensional diagram of a farm food web. Rough estimations, in a tenfold order of magnitude, were based on the available literature, preferably with data from organic farms in Flevoland, organic farms in general (*e.g.* Kromp & Meindl, 1997) or unsprayed crop edges (*e.g.* Boatman *et al.*, 1999). The mean biomass of arthropod taxa observed by Schekkerman (1997) was used to relate density data to biomass. Relative importance was assessed to derive a food web diagram from the more complex food web matrix. The farm food web diagram was drawn in a fashion similar to the food web diagrams of Oksanen *et al.* (1996).

2.3. Relating the farm food web to farm management

The relationship between food web structure and farm management was explored by comparing four management types of organic arable farms in Flevoland: short organic duration without improved ecological infrastructure (E.I.), short organic duration with improved E.I., long organic duration without improved E.I., and long organic duration with improved E.I. These four basic farm types were considered to represent the extremes of two different gradients (*cf.* Holt in Polis & Winemiller, 1996) with regard to duration of organic farming practice and quality of the ecological infrastructure. In addition, a distinction was made between long duration farms with improved E.I. with extensive and little herbivory in the crop area. Thus in total five food webs were constructed.

Organic farming duration was presumed to relate to the amount of input of organic matter in the crop area soil. This input includes organic manure, compost and crop residues of in particular, the gramineous crops (ley pasture and cereals). Additionally, organic duration also relates to an increase of the crop diversity as well as the weed diversity. The effects of both an increased input of organic matter and crop/weed diversity may accumulate over years (Hald & Reddersen, 1990; Idinger & Kromp, 1997).

The quality ('improvement') of the ecological infrastructure relates particularly to vegetation structure and diversity within the boundary, and is largely determined by the mowing regime. Mowing with a finger-bar mower after June 21st, seems to be optimal for arthropod abundance and diversity in Flevoland, when compared to the traditional management of more frequent mowing with a flail mower (Smeding *et al.*, 2001b). In addition to the vegetation features, E.I. quality relates to the dimensions of field margins and consequently to the proportion of semi-natural habitat on the total farm area.

Performances of farm food web structures of the four theoretical farms were derived by roughly relating the available detritus and plant resources to the abundance of detritivore and herbivore functional groups, respectively. An abundance of functional groups at the higher trophic level was assumed to be primarily determined by prey abundance ('bottom-up'). However 'top down' control and horizontal effects (*i.e.* competition) were also considered, with reference to the evidence in literature (Wise *et al.*, 1999; Tscharntke, 1997; Power *et al.*, 1996; Booij & Den Nijs, 1996). Analogous to the approach of Fretwell (1977), who coined the theory on predator and resource limitation, the four presented hypothetical food web structures were based on expert judgement with reference to theory from literature and empirical data.

3. Results

The results section includes three parts:

- an outline of the topological food web;
- consideration of the effect of farm management on the food web structure (*i.e.* relative abundance of functional groups and strength of their interactions);

- an illustration of the predictions with empirical data from arable farms in Flevoland.

3.1. Topological farm food web on organic arable farms in Flevoland

Because of frequently occurring omnivory and intraguild predation, trophic levels are difficult to assess in the farm food web. It is therefore convenient to make a broad distinction among four aggregate subsystems (Table 1):

- a primary guild of herbivores;
- a primary guild of detritivores;
- an intermediate level of macrofauna predators of invertebrates;
- a top level of predators of vertebrates.

The composition of these four aggregate subsystems is discussed below, and also some remarks will be made with regard to the relative size and the extent of the energy flow through the herbivore and detritivore based food chains.

Table 1

The food web matrix of the farm food web on an organic arable farm in Flevoland (The Netherlands); in rows are the resources and prey functional groups respectively, in columns are the detritivores, grazers and predators, as represented by the same functional groups; 1 = interaction and 2 = strong interaction (according to both observations and the literature references). The lines represent the separate resources and the four aggregate subsystems (detritivores, herbivores, predators of invertebrates and the top predators).

Subsystem	Resource or functional groups	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
1 primary prod.	roots			1	2					1								
2 primary prod.	leafs and stems				1	2	2		1	2								
3 primary prod.	flowers of dicots				1	1	1	2					1	1				
4 primary prod.	seeds	1		1	1		1		2	2						2		
5 detritus	crop-residues, litter (C/N high)	2	1	2	1													
6 detritus	slurry, stable dung (C/N low)	2	2	1														
7 detritivores	earthworms	x									1				2	1		1
8 detritivores	microbivore predators		x								2	1	1		1			
9 detritivores	detritivorous arthopods			x							2	2	2	1	1	1	2	
10 herbivores	root herbivorous arthropods				x						1	1	1		2	2	1	1
11 herbivores	invertebr. flushfeeders (r)					x					1	1	2	1		2	2	
12 herbivores	invertebr. senescence feeders (K)						x				1	1	2	1		2	1	
13 herbivores	specialist anthophiles							x				1	1			1	1	
14 herbivores	granivorous arthropods								x						1	1	1	
15 herbivores	herbivorous vertebrates									x								2
16 predators	epigeic predacious beetles										x				1	1	1	1
17 predators	wandering and web spiders										1	x				1	1	
18 predators	vegetation dwelling arthropods										1	1	x			2	2	
19 predators	parasitoids										1	1	1	x		1	1	
20 predators	soil-life feeding vertebrates														x			1
21 predators	insecti-granivorous birds															x		1
22 predators	specialist insectivorous birds																x	1
23 toppredators	raptors, mustelids, opportunists																	x

3.1.1. Herbivore subweb primary guilds

Guilds can be assembled according to the exploited part of the plant: roots, green material (leafs and stems), flowers and seeds (De Snoo & Canters, 1988; Crawley, 1983) (Table 1).

The root herbivorous guild belongs to the soil biota (Brussaard, 1998) and it mainly includes herbivorous nematodes, mites and insect larvae. Nematodes may determine the amount of root herbivory on farms (Wardle *et al.*, 1999). However nematodes and mites are so much interlinked with the micro predator food web (presented below) that we considered them as a component of that assemblage. Root herbivorous arthropods in arable agroecosytems are mostly polyphagous larvae of Diptera, Coleoptera and Lepidoptera. Their food also includes seeds and seedlings (Gange *et al.*, 1991) (Table 1). Feeding on detritus may also be significant in some taxa (Strong *et al.*, 1996). The root-herbivore guild biomass (Table 2) in the farm food web is generally larger than the biomass of all the above ground herbivores (Tscharntke & Greiler, 1995; Wardle *et al.*, 1999), particularly when leather jackets (*Tipula* spp.) are enhanced by gramineous crops.

Table 2
Estimates of the biomass magnitudes (kg dry weight per ha) of functional groups at organic arable farms in Flevoland; the estimates are average values with regard to a farm of around 40 ha with 5% ecological infrastructure and 30% gramineous crops. Sources: (a) Van der Burgt, 1998; (b) De Ruiter et al., 1993, 1995; (c) Kromp & Meindl, 1997; (d) Schekkerman, 1997; (e) Smeding et al., 2001b; (f) Buys et al., 1996; (g) Hospers, 1991; (h) Booij, oral communication; (i) Remmelzwaal & Voslamber, 1996; (k) Lange et al., 1994; (m) Smeding & Booij, 2001.

Functional group	**Range of biomass**	**Reference**
earthworms	10 – 1000	a
microbivore predators	0.1 – 1	b
detritivorous arthopods	0.1 – 10	c
root herbivorous arthropods	1 – 100	d
flushfeeding folivores	1 – 100	c
senescense-feeding folivores	0.1 – 10	c, e
specialist anthophiles	0.001 – 0.01	f, g
granivorous arthropods	0.01 – 1	h
herbivorous vertebrates	0.01 – 0.1	i, k
epigeic predators	0.1 – 10	c, h
oligophagous predators	0.01 – 1	c, e
parasitoids	0.001 – 0.01	e
soil life-feeding vertebrates	0.01 – 0.1	i ,m
insectivorous birds	0.001 – 0.1	i, m
top predators	0.001 – 0.01	i

Folivores can be subdivided into two invertebrate assemblages (Table 1): flush and senescence feeding folivores. The flush feeding folivores (White, 1978) feed on young tissues with low C/N ratio and low fibre content. The characteristic modes of feeding are usually sucking, boring and mining (Crawly, 1983). They have a small body size, a fast development and good dispersal abilities. Senescence feeders feed on mature plant tissues. Originally White (1978) had defined this group as feeding on tissues that have increased nitrogen levels caused by stress or ageing. In this article we also include folivores which feed on presumably healthy mature tissues which could have a high C/N ratio. Characteristic modes of feeding are clipping, holing or removal (Crawly, 1983). Senescence feeders tend to have a slower development or a larger body size (Crawley, 1983) and possess, related to a more sedentary behaviour, defensive traits to predation (Power *et al.*, 1996). The flush feeders largely determine the biomass of the folivorous guilds on the farm; and their exponential increase, dependant on how susceptible the crop is, and on weather conditions, may temporarily determine the aboveground herbivore biomass on the farm.

The anthophiles guild (Kevan, 1999) involves insects which are dependant on flowers in their entire life cycle (specialists) or only in the adult stage (non-specialists). The former are particularly bees, either solitary (Tscharntke *et al.*, 1998) or social (Svensson *et al.*, 2000). The latter are insects whose larvae can be herbivorous (*e.g.* butterflies and moths), predacious (*e.g.* syrphid flies, cantharid beetles), parasitoids, or detritivorous (*e.g.* anthomyid flies). Specialist anthophile biomass, which, in Flevoland, mainly consists of bumblebees, is small in comparison with the biomass of other herbivorous guilds (Table 2).

The aboveground granivores guild involves insects, birds and mammals. Because of the difference in their life history, vertebrates are placed in other functional groups. The granivorous invertebrate functional group include the carabid beetle genera *Amara* and *Harpalus* which are notorious granivorous (as well as being omnivorous); and other granivorous insects like weevils and lygeid bugs which are mainly oligophagous (Westerman, in prep.).

Herbivorous vertebrates on the farm mainly involve rodents and a few bird species (*e.g.* pigeon and house sparrow). Their large body size and digestive capabilities allow them to feed on a wide range of plant tissues. The diet of for example the wood mouse, an abundant species in Flevoland field margins, also includes animal food (invertebrates, bird eggs) (Lange *et al.*, 1994). Seeds are an important component in mixed diets because of their high nutritional value.

3.1.2. Detrital subweb primary guilds

The detrital food web can be divided into three major divisions (Brussaard *et al.*, 1997; Brussaard, 1998; Wardle *et al.* 1999): the micro predator food web, saprovorous arthropods and the soil engineers (*i.e.* earthworms).

The micropredator food web is in fact a complex system in itself (De Ruiter *et al.*, 1993, 1996; Brussaard, 1998) comprising bacteria-based and fungi-based compartments. Primary consumers are microfauna like protozoa and nematodes; top species are micropredators comprised of mesofauna mites (Acari) and springtails (Collembola). Because of respiration losses by several preceding transfers, the biomass of micropredators is relatively small (Table 2).

The saprovorous arthropod guild involves meso- and macrofauna which feed directly on plant debris and on microflora which develops on decaying tissues. Large springtails, Diptera larvae (*e.g.* Chironomidae, Sciaridae) and staphylinid beetle adults and larvae are important groups (Sinnige *et al.*, 1992; Weber *et al.*, 1997; Frouz, 1999; Bohac, 1999). Taxonomic composition of this guild is affected by substrate quality, for example the nitrogen (Bohac, 1999) and sugar content (Weber *et al.*, 1997).

The engineers guild (Brussaard, 1998), although principally saprophagous, eats bulk-soil which may also include other kinds of food (microflora, seeds). The major characteristic of this guild is their capability of soil disturbance. Although earthworms play a minor direct role in soil metabolism, their biomass may predominate the total biomass of detritivorous meso- and macrofauna in arable fields (Table 2).

In semi-natural habitats with a permanent litter layer, it might be convenient to distinguish within the saprovorous guild, an epigeic detritivore functional group that involves in particular woodlice (Paoletti & Hassal, 1999), diplopods (Sinnige *et al.*, 1992), slugs and snails. This group also exhibits transitions from herbivorous to detritivorous traits, for example abundant slugs feeding on sow thistles that had been weeded out of the crop area, and placed in the crop edge (Smeding, unpublished data). For reasons of simplicity, this article does not distinguish this group.

3.1.3. Predator guilds

Six distinctive predator functional groups or guilds represent a shift in emphasis from detritivore to herbivore subweb:

- Epigeic predacious beetles including polyphagous carabid and staphylinid beetles;
- Spiders, both wandering and web-building spiders, that are ground and facultatively vegetation dwelling polyphagous predators;
- Vegetation dwelling arthropod predators including polyphagous species (*e.g.* cantharid beetles, myrid bugs) and oligophagous species. Oligophagous species in crops are often aphidophagous (*e.g.* ladybirds, syrphid flies) but not always so, for example predacious Diptera (*e.g.* Empididae, Dolichopodidae) which feed on small Diptera and Hymenoptera;
- Parasitoids (mainly Hymenoptera) which do not only exploit, as is often thought, aphids and lepidopterans but also, for example, detritivorous Diptera (Potts & Vickerman, 1974) or spiders (Topping & Sunderland, 1996);
- Insectivorous birds including two functional groups: specialist insectivores that are capable of catching flying insects; insecti-granivorous species which concentrate on feeding among the vegetation on invertebrates and seeds;
- Soil life-feeding vertebrates, including birds (*e.g.* lapwing and starling) and mammals (*e.g.* mole and shrew).

For reasons of simplicity it is convenient to combine the predacious beetles and spiders in a guild of 'epigeic polyphagous predators' (*e.g.* Poehling in Booij & Den Nijs, 1996). The epigeic predators have a key position in the farm food web, in that they exploit both the herbivore and the detrital subweb (Sunderland *et al.*, 1996; Kromp, 1999; Wise *et al.*, 1999). So although they basically depend on the abundance of the soil mesofauna, *e.g.* springtails (Potts & Vickermann, 1974; Holland & Thomas, 1997) they also temporarily exploit the increased herbivore population in the summer (Wise *et al.*, 1999; Schoenly *et al.*, 1996), and so might prevent outbreaks of r-herbivores if these populations build up slowly (Burn, 1988). Insectivorous birds also exploit both subwebs but are less numerous, compared to the other predator groups. Compared to other predacious groups, epigeic predators may achieve the highest biomass in arable farm food webs (Table 2).

Intraguild predation, including hyperparasitism and cannibalism probably strongly affects the abundance of individual predator guilds (*e.g.* Tscharntke, 1997; Sunderland *et al.*, 1996). Examples are the predation of already parasitised aphids by vegetation dwelling predators, carabid beetles feeding on spiders, or insectivorous birds feeding on adult syrphid flies. Birds probably consume relatively more arthropod predators than primary invertebrates when compared to the relative abundance of these prey species, because they may prefer larger individuals. Since epigeic predators can hide under the soil surface or have nocturnal behaviour (carabid beetles), vegetation dwelling arthropods are an important prey for birds on arable farms.

Haematophagous (blood feeding, parasitic) and scatophagous (dung feeding) insects and scavengers are small functional groups (*e.g.* Potts & Vickermann, 1974; Weber *et al.*, 1997) that exhibit transitions from predacious to detritivorous traits. This guild which feeds on the produce of vertebrates may contribute significantly to the prey of insectivorous birds (*e.g.* the swallow). This could occur where cattle are temporarily grazing on ley pasture or in the stable, or when dung is stored on farm headlands (Hald & Reddersen, 1990; Smeding, unpublished data). For reasons of simplicity we are not considering these functional groups.

3.1.4. The top predator guild

Top predators are the vertebrates which are true carnivores (*e.g.* kestrel, barn owl, weasel, stoat) or opportunistic omnivores (*e.g.* carrion crow). Their common characteristic is the ability to prey on other vertebrates and their preference for prey of a larger size. Some top predators, which visit the farm by chance, belong to the food web at the region or landscape level (*e.g.* hen harrier, blue heron, and gulls). The abundance of herbivorous vertebrates strongly determines the resource availability for the true carnivores (Plesnik & Dusik, 1994). The breeding density of kestrels in Oostelijk Flevoland, in the years following reclamation, related positively to their food supply which was mainly common voles. However, nestling mortality was not affected by a decreased vole abundance as the nestlings could also be fed with chicks, in particular those of starlings (Cavé, 1968).

3.1.5. The relative sizes of herbivore and detritivore subsystems

As in most terrestrial ecosystems, the farm foodweb consists of a herbivore subweb and a detrital subweb (Odum, 1973; Polis & Winemiller, 1996). Food chains in the total farm food web may, by chance, achieve a length of 9 steps. However the number of functional trophic levels (Power *et al.*, 1996) is much less, presumably approximating the common chain length of 4 (Winemiller & Polis, 1996).

In agroecosystems the detrital subweb is expected to be much larger than the herbivore subweb in terms of biomass and species diversity (Wardle *et al.*, 1999; Swift & Anderson, 1993). This could be explained from the viewpoint of resource availability. In most natural systems, on average, about 10% of net primary production (NPP) is generally taken by herbivores and about 90% by decomposers; insect herbivores consume usually less than 1% of NPP, whereas ruminants can easily assimilate more than 10% (Crawly, 1983; Edwards & Wratten, 1980). On arable farms the average herbivore consumption might also be less than 1% because harvesting removes a large proportion of NPP and herbivory is inhibited by both the direct and indirect measures of the farmer. However even a small amount of consumption may cause great damage to the plant (Tscharntke & Greiler, 1995; Crawly, 1983) and therefore involve large economic loss.

In contrast to the herbivore subweb, the detrital web receives extra food in terms of organic manure, organic wastes and crop residues of both allochthonous and autochthonous origin. However 90-95% of energy in detritus is used by the respiration of soil micro organisms (Swift & Anderson, 1993). Consequently the biomass of the mesofauna (*i.e.* the top organisms of the micropredator food web) is amazingly small (De Ruiter *et al.*, 1993, 1995) (Table 2) compared with, for example, earthworms. The relative difference between the biomass of macrofauna (*i.e.* large invertebrates) of the detritital subweb compared to the macrofauna of the herbivore subweb may therefore not be very marked. In other words: although the size at the food web base may differ extremely between both subwebs, the quantitative difference seems to be much smaller at a higher trophic level. This supposition is supported by studies of Ryszkowski *et al.* (1993) on the aboveground insect biomass in several agricultural landscapes: herbivore subweb biomass (including also the adults of root herbivorous larvae) was generally larger than the biomass of insects originating from the detritivore subweb. However, comprehensive data on this subject are scarce and could be biased by seasonal and annual effects.

3.2. Farm food web structure related to farm management

In the text below, the five food web structures are presented and illustrated with food web diagrams. Firstly, attention is drawn to the crop area contributions to the farm food web; contrasting the food web of a short organic duration farm and low E.I. quality (type A; Fig. 1a), with the food web of a farm with long organic duration and low E.I. quality (type B; Fig. 1b). Next the effect of improved E.I. (*i.e.* with an increased area and vegetation diversity) on the farm food web is considered by contrasting the above two models without improved E.I. with short and a long duration farms with improved E.I. (types C and D; Figs. 1c and 1d).

3.2.1. Short duration farm without improved E.I.

The farm food web of type A (Fig. 1a) represents a relatively small and low food web structure. The food web is largely determined by the detrital food web, however soil meso- and macrofauna densities are low when compared to the long duration farms (types B and D). After the conversion to organic farming herbivore densities in crops may initially remain low.

However, crops may become susceptible to herbivory because the farm has to adapt to a changed fertility management and the epigeic polyphagous predator pressure is relatively weak. In cases of unbalanced luxurious development of the crop, herbivores, (including senescence feeding folivores, flush feeding folivores and root herbivores) may rapidly establish in the crop and induce temporarily high vegetation dwelling predator densities.

Characteristics of traditionally managed E.I. are:
- a high abundance of foliar herbivores related to the prolonged vegetative development of the gramineous sward;
- epigeic predators that are attracted by the warm microclimate of sparse vegetation;
- herbivores (*e.g.* granivores) related to annual or ruderal plants in disturbed swards;
- specific detritivorous arthropod taxa related to relatively easily decomposable cuttings.

Arthropod communities of traditionally managed E.I. probably have less influence on the crop area than arthropod communities of improved E.I., because of a more restricted food supply (both quantitative and qualitative), and consequently lower densities as well as a reduced variety of functional groups.

Vertebrate predators may be mainly birds feeding on soil organisms (*e.g.* lapwing) and foraging insectivorous birds, exploiting accidental herbivore outbreaks (*e.g.* swallows feeding above infested crops). For insectivorous birds traditionally managed E.I. may offer a useful but limited quantity of food.

3.2.2. Long organic duration farms without improved E.I.

The farm food web of type B (Fig. 1b) compared to type A is characterised by an increased detrital web in the crop area. Particularly densities of saprovorous arthropods and earthworms might be increased when this is compared to short duration farms (e.g. Heimbach & Garbe, 1996; Idinger *et al.*, 1997). The increase of these groups may support, in particular, epigeic predator functional groups but also some vegetation dwelling predators like Empididae that feed on small Diptera. Long duration organic farms might possess a relatively diverse population of potential crop pests and weed herbivores, due to the accumulated effect of increased crop and weed diversity (Hald & Reddersen, 1990; Moreby & Sotherton, 1997).

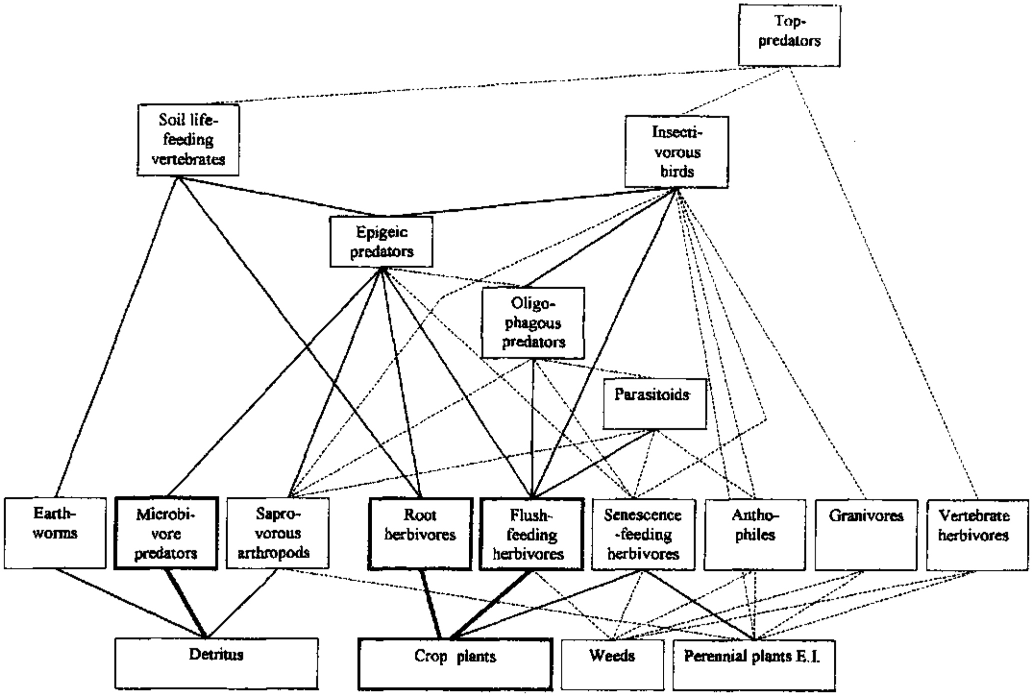

Fig. 1a. Predicted food web structure for an organic arable farm with short organic duration, without an improved ecological infrastructure. Thick lines indicate probable cases of strong interactions. Continuous thin lines refer to interactions of intermediate strength. Dotted lines refer to interactions of minor importance. Boxes with thick lines indicate a relatively high quantitative importance of the functional group within the farm food web.

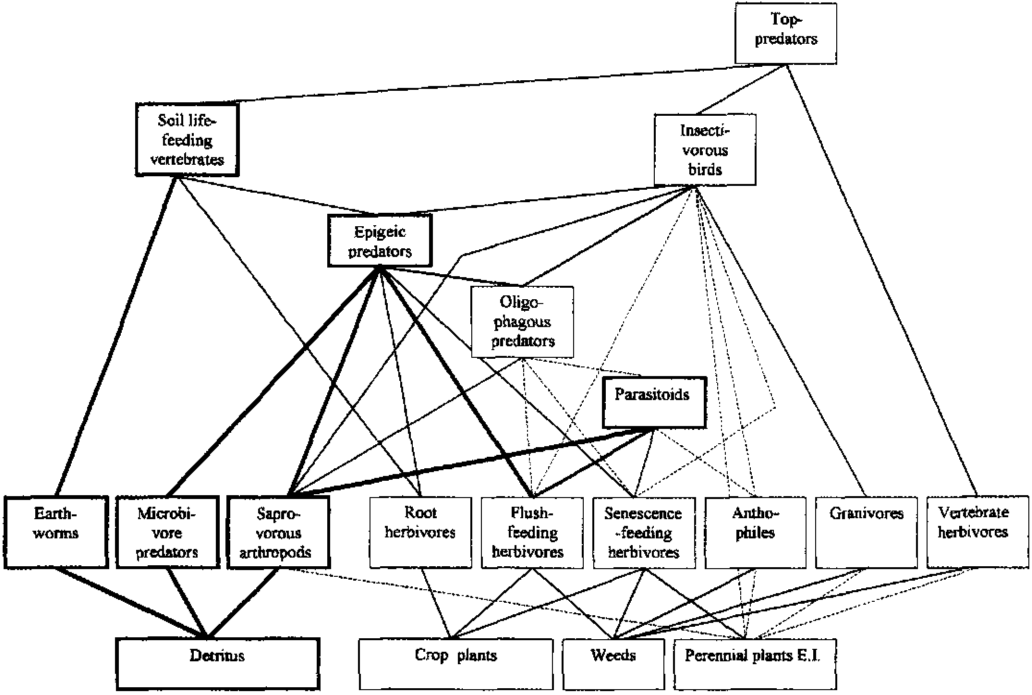

Fig. 1b. Predicted food web structure for an organic arable farm with long organic duration, but without an improved ecological infrastructure. Symbols as in Fig. 1a.

However, the relationships between and within predator and herbivore guilds may alternate between two extreme trophic structures. Figs. 1d and 1e illustrate this alternation with regard to the crop area of farm type D. The extremes depend on the relative strength of predation pressure by the polyphagous epigeic predators and the degree of pest susceptibility of the crop (Van Emden, 1988), which is related to weather, soil nutrients, soil organic matter levels (Phelan, 1997) and interaction between crop and intercrop/weeds (*e.g.* Theunissen, 1994):

- If epigeic predator abundance is relatively low or if crops are susceptible to herbivory, the flush feeding herbivores may become a pest (Fig. 1b). Herbivores support a diverse predator system because neither epigeic predators nor oligophagous predators are dominant. This system may control increase of senescence-feeding herbivores but not outbreaks of the more vigorous flush feeding herbivores (*e.g.* aphids). These situations may occur more frequently in intensive organic crop rotations;
- If epigeic predator abundance is high or the crop not susceptible, then all herbivores and connected epigeic predators might depress oligophagous predator numbers. Epigeic predator numbers are probably limited by food shortages (Den Nijs *et al.*, 1997; Booij *et al.*, 1997) and may therefore exert a potentially high predation pressure on the herbivore subweb, a principle referred to as 'allochthonous energy subsidy via multi channel omnivory' by Wise *et al.* (1999). Herbivores higher in the crop canopy may experience less predation pressure (Kromp, 1999) and might be preyed upon mainly by parasitoids. Parasitoids may be released from interference by oligophagous predators (*cf.* Tscharntke, 1997), or have better abilities to cope with low densities of prey (*cf.* Powell & Nickless, 1996). This food web structure may occur more frequently in extensive organic crop rotations due to large detritus resources and sparser crops.

With regard to vertebrate predators, increased densities may occur in soil life-feeding and insectivorous birds when compared to farm type A. However, in particular, the situation with increased herbivory in the crop area may support insectivorous birds, because herbivores are an essential component of nestling diets (Poulsen *et al.*, 1998; Hald & Reddersen, 1990), whereas the numerous epigeic prey items are hidden by nocturnal behaviour (Vickerman & Sunderland, 1974), or sheltered by physical structures or protected by low palatability (*e.g.* too hard for the chicks to eat). Therefore the functional food chain length of the farm food web may get shorter when epigeic predators predominate and depress the herbivore subweb, and reduce food availability for insectivorous birds. Accordingly, Power *et al.* (1996) hypothesised that food chains may shorten in a succession from the pioneer stage to an established community due to the increasingly armoured features of sedentary taxa at the 2nd or 3rd trophic level.

Herbivorous bird and mammal numbers may also be supported by an increased seed availability of weeds and cereals on long duration farms. A small top-predation layer may subsequently be based on an increase of herbivorous and insectivorous vertebrate abundance.

3.2.3. Short duration farms with improved E.I.

The farm food web of a short duration farm with an improved E.I. (Type C; Fig. 1c) will combine the relatively small food web in the crop area (occurring on farm type A) with an increased and more functionally diverse food web in the field margins. The resulting food web structure may become extended and more satiated.

The effect of improved E.I. on the farm food web structure is most significant with regard to resources and connected functional groups that are lacking or scarce in the crop area: flowers, seeds, anthophiles, granivores and senescence feeding herbivores. Specific taxa of detritivorous arthropods are supported by the variety of litter types. Both increased arthropod numbers, as well as varied vegetation structure, support vegetation dwelling predators.

Primary functional groups and invertebrate predators may disperse from the E.I. into the crop (Sotherton, 1994, 1995; Lys & Nentwig, 1992).

Vertebrate functional groups include species that by preference reside in the E.I., feeding on the locally present seeds and arthropods but probably also on imported flying insects that adhere to tall vegetation.

3.2.4. Long duration farm with improved E.I.

Improved E.I. probably adds similar resources to the food web of a long duration farm (Type D; Fig. 1d) as to the food web of a short duration farm (Type C; Fig. 1c). However, on a long duration farm the addition of herbivore subweb functional groups may further satiate the food web structure and cause cumulative effects. The greater the amount and variety of resources could, for example, give a better absorption by the food web of fluctuations or interruptions in the food supply, due to operations in the crop area. In particular, populations of large mobile arthropod predators, insectivorous birds and top predators might be supported and stabilised by improved E.I. Food webs of farms including some degree of herbivory on crops and weeds (Fig. 1e), are likely to support more insectivorous birds and top predators than farms with depressed herbivore subwebs due to abundant polyphagous predators or herbivore resistant crops (Fig. 1d) (as explained in paragraph 3.2.2.). In crop areas with little herbivory, insectivorous birds may have to depend more on improved E.I. for high quality sources of prey.

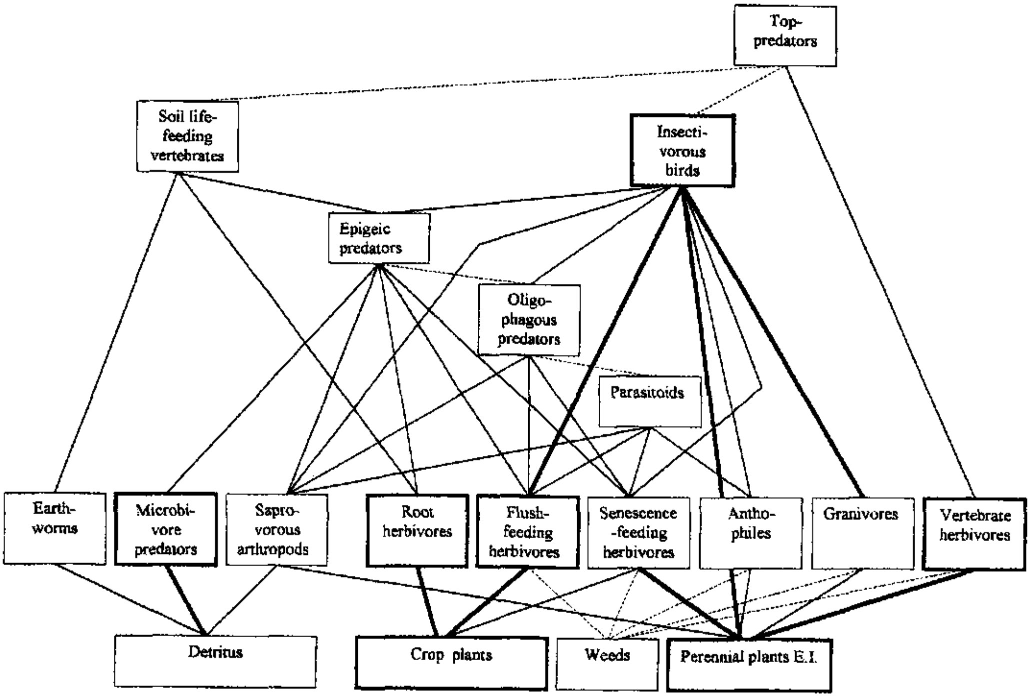

Fig. 1c. Predicted food web structure for an organic arable farm with short organic duration including an improved ecological infrastructure. Symbols as in Fig. 1a.

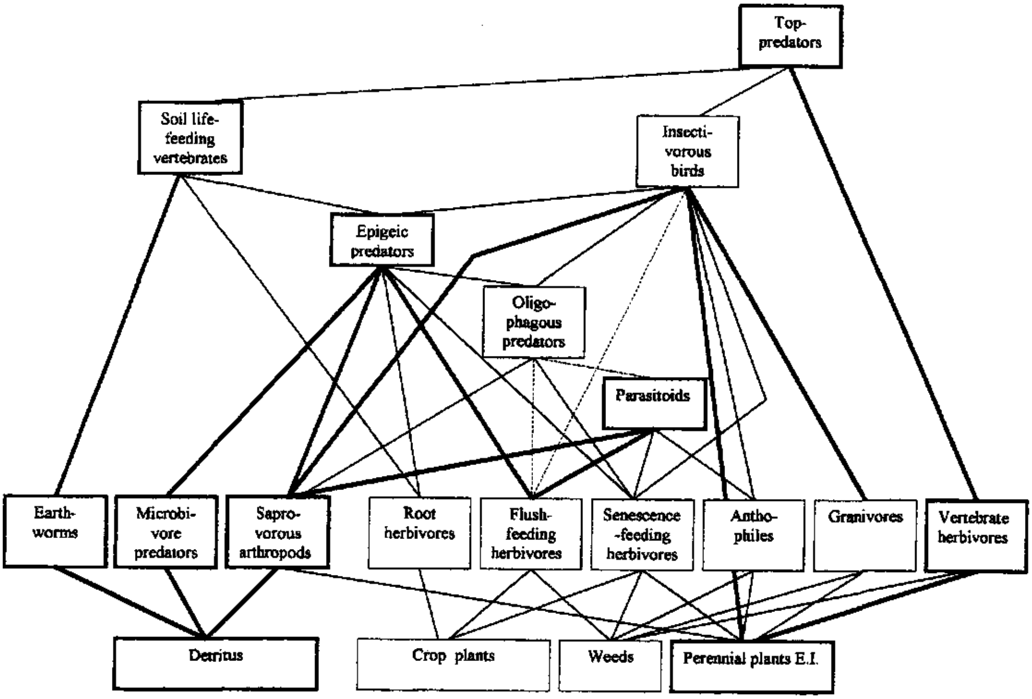

Fig. 1d. Predicted food web structure affected by increased detrital subsidy, for an organic arable farm with long organic duration including an improved ecological infrastructure. The food web structure expresses the indirectly inhibiting effect of detrital subsidy on the herbivore subsystem. Symbols as in Fig. 1a.

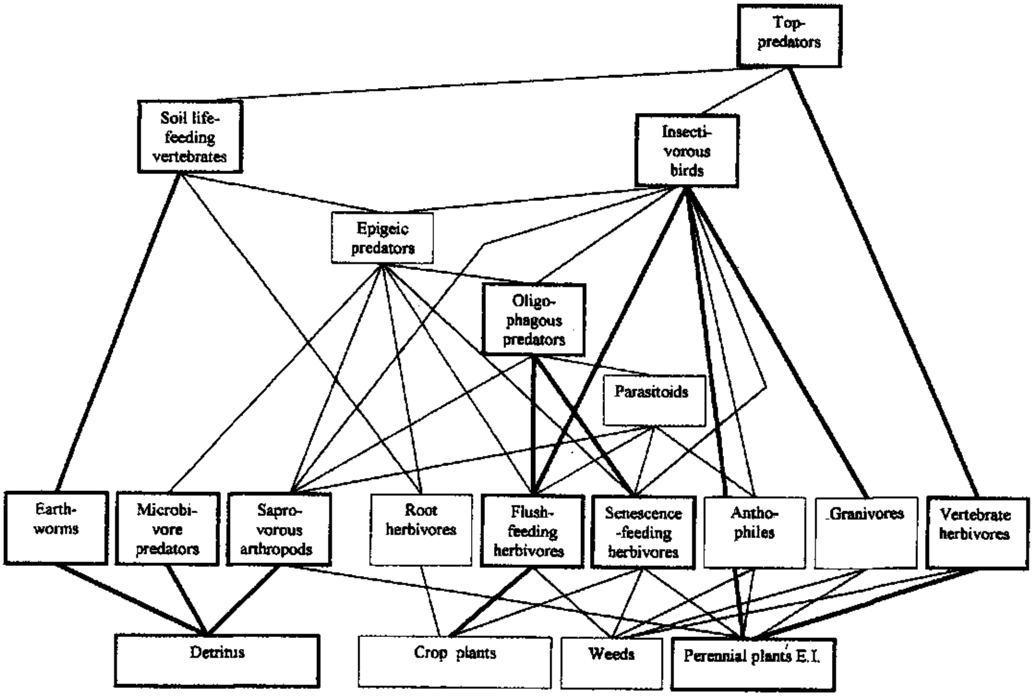

Fig. 1e. Predicted food web structure affected by an r-herbivore outbreak, for an organic arable farm with long organic duration including an improved ecological infrastructure. The food web structure expresses the 'bottom up' effect of increased herbivorous prey availability. Symbols as in Fig. 1a.

3.3. Support from empirical research on organic arable farms in Flevoland

Results from empirical research on arable farms in Flevoland give some supporting evidence for the models presented above. Observations of the four farm types showed:

- short organic duration farms (type A and C) had in the crop area low densities of all the functional groups of vegetation dwelling arthropods or, in more dense luxurious crops, high densities of senescence feeding folivores associated with increased predator abundance (Smeding *et al.*, 2001b). Bird densities on these farms were low compared to other farm types (Smeding & Booij, 2001);
- long organic duration farms (type B and D) had in the crop area two distinctive compositions of vegetation dwelling arthropods: one with abundant flush feeding folivores related to intensive crop rotation, and another with moderately abundant detritivores and parasitoids related to extensive crop rotation (Smeding *et al.*, 2001b). Accordingly epigeic arthropods had a low abundance in long duration farms with intensive crop rotation (Smeding *et al.*, 2001a) as compared to farms with a less intensive vegetable production. However, evidence for increased epigeic predator abundance on long duration organic farms with a high proportion of gramineous crops, was not found, because these were not well represented in the study area;
- long duration and improved E.I. farms (type D), including mainly intensive vegetable producing farms, had the highest territory densities of insectivorous birds, probably related to both E.I. and crop characteristics (Smeding & Booij, 2001). Insectivorous bird abundance seemed to be negatively correlated to more extensive crop rotations;
- improved E.I. bordered by large conventionally managed crop plots (resembling type C) had high densities of insectivorous bird territories and supported also herbivorous mammals (Remmelzwaal & Voslamber, 1996).

4. Discussion

4.1. On the validation of the model

In this article we proposed a topological farm food web (based on the farm food web of organic arable farms in Flevoland, The Netherlands) and related this food web to two important farm traits: the duration of organic farming and the amount of ecological infrastructure. This exercise led to the distinction of four basic food web structures. An additional subdivision could be made based on the level of crop herbivory in long-duration organic farms. It might be clear that the outlined responses of the farm food web to farm management were based on a mix of field evidence, theory and interpretation. The above presented empirical data illustrate the food web but are principally not applicable as validation, because the theory was partly inspired by the same data. Further research is required to validate our model food webs. However, we think that the ideas that have been presented, despite the weaknesses in their validation, provide valuable hypotheses and incentives for further research.

4.2. Integration of ecosystem services and nature conservation

The duration of organic farming as well as the amount of ecological infrastructure affect the farm food web. Both variables are useful for implementing the integration of ecosystem services (Altieri, 1999) and nature conservation-centred aims. However, the effect of duration does not always coincide with the effect of a more extensive crop rotation (*i.e.* the proportion of gramineous crop in the crop rotation), since current organic practice could include various degrees of intensity. Food web structures may differ significantly between extensive and intensive long duration organic farms; difference in 'intensity' among organic farms involves input of C (particularly crop residues and straw in manure) as well as weed control and crop performance due to nutrient availability.

The results of this article suggest that food webs that support beneficials (*i.e.* the polyphagous epigeic predators) may not necessarily support conservation-worthy species like insectivorous birds. Long duration organic farms with an intensive cropping system as well as an improved E.I. seem to combine together, to a reasonable degree, both the aims of ecosystem services and of nature conservation. However, if these systems were to be optimised, the increased employment of beneficials might run counter to nature conservation aims. An increased efficacy of weed control in the future, might also further diminish the food resources in the organic crop area available for these birds.

The presented models of the farm food web showed the positive effect of E.I. on nature conservation aims. This effect may occur relatively independently from organic duration. It must, however, be noted that short duration farms are not the same as conventional farms, where pesticide and fertiliser drift might happen (De Snoo, 1995). Indirect effects of E.I. on 'ecosystem services' in the crop area could be presumed but may be less evident than the effects of E.I. on conservation-worthy species at the farm level.

4.3 Recommendations for research

Hypotheses of further research might concentrate on the effects of increased detritus supply in the farm food web (*e.g.* Wise *et al.*, 1999), the importance of detritivorous mesofauna for epigeic predators (*e.g.* Holland & Thomas, 1997; Idinger & Kromp, 1996) and the relation between herbivory and higher trophic levels of the farm food web (*e.g.* Poulsen *et al.*, 1998; Tscharntke & Greiler, 1995). Applied research based on food web management, may address the management of crop residues and other non-harvestable components (NHC) (Vandermeer *et al.*, 1998) as well as the possibilities for controlled herbivory in living mulches, leys etc. (*e.g.* Theunissen, 1994, 1997). It would be worthwhile to link the farm food web model, as proposed in this article, to a farming system model (*e.g.* Oomen & Habets, 1998; Wolfert *et al.*, 1997) which can broadly estimate the resource availability of various detritus and plant tissue qualities, based on farm management traits.

Finally, also the spatial distribution of resources for functional groups should be addressed (*e.g.* Topping, 1997; Kreuss & Tscharntke, 1994) as well as the effect of physical disturbance and shelter on mortality (*e.g.* Den Nijs *et al.*, 1996) or bird nesting success (e.g. Wilson *et al.*, 1997). However, according to authorities in food web research (Polis *et al.*, 1996), when referring to the current state of knowledge, care is needed so that the complex field study scenario is not entangled with the methodology used by the researcher.

Acknowledgements

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Chapter 7: Farm-Nature Plan: landscape ecology based farm planning

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Abstract

A procedure is presented for restyling the lay-out and management of farms in order to increase the biodiversity in the agricultural landscape as well as the sustainability farming. The protocol for the development of an on-farm nature management plan uses landscape ecology characteristics, local biotic and abiotic data and potential, as well as the farming system data and farmer's personal interests. It may also enhance the farmer's interest and understanding of agroecological pattern and processes and a more conscious approach to elements of nature on the farm, which may be the starting point in ecologising agricultural practice.

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1. Introduction

The integration of nature and farming is an important issue in scientific as well as political circles of industrialized European countries, in the first place, populations of many plant and animal species associated with agricultural land are declining in many Western European countries. Changes in agricultural land-use are often suggested as the main cause of this decline (*e.g.* Wilson *et al.*, 1997; Fuller *et al.*, 1995; Andreasen *et al.*, 1996). These changes have concomitantly had an effect at the landscape-level, resulting in a loss of landscape differentiation in Europe (Baldock *et al.*, 1993).

At the IUCN conference 1992 on biodiversity in Rio de Janeiro, most European governments committed themselves to implementing biodiversity conservation measures. In The Netherlands, these commitments are now being translated into deeds. Agriculture, the land-use accounting for about 50% of the country's area, is not excluded from these efforts to conserve biodiversity, since the occurrence of many species and communities is related to farmland and farming practices.

Apart from its intrinsic value, biodiversity has a function in a number of ecological processes highly relevant for food production. These 'life support functions' of biodiversity include for example the soil nutrient cycles (Brussaard, 1997) and regulation of pests by means of biological control (Altieri, 1994). Agro-technology has broadly increased the independence of these functions at the cost of high inputs of fossil fuel, artificial fertilizers and pesticides. The concept of 'sustainable' agriculture aims to re-establish an equilibrium: life support functions and technology should be farm attributes of equal importance. Here, the integration of farming and nature comes into play.

From both perspectives - the intrinsic and functional value of biodiversity in agriculture - there is a strong need to develop farming systems that include biodiversity (Almekinders *et al.*, 1995; Vandermeer *et al.*, 1998). These ideas are particularly manifest in the current practice of organic farming (EEC, 1994). The standards for organic farming guarantee safer conditions for biodiversity development by banning the application of pesticides and artificial fertilizer application and by encouraging long crop rotation and moderate stocking rates. Nevertheless, organic farms also lack a clear perspective when it comes to integrating nature on the farm.

In this article, we argue that the integration of farming and nature in the context of a sustainable agriculture (including the management and conservation of biodiversity), should comprise two levels: the landscape level (100-1000 ha) and the farm level (10-100 ha) (Table 1). As regards the landscape level, there should be coherence between the structure and distribution of the non-productive (green) habitats on the farm and in the surrounding landscape. The reason is that conditions supporting biodiversity on the farm are strongly related to processes and structures at the landscape level. The first question therefore, is: what are the implications of this landscape-level focus for farm-nature? At the farm level, these green habitats should be clearly and purposefully integrated with farm management. Only if habitat structures and distribution are compatible with (or beneficial to) the agricultural production, will they be able to survive and, as a result, biotic complexity be able to increase.

The second question to be addressed is: what does this farm-level focus imply for nature on the farm? The third question is an extension of the preceding ones: how can these implications be worked out for real farms, *e.g.* in a 'Farm-Nature Plan'? How can farms actually be 're-styled' in order to achieve a better coherence with landscape patterns and processes and a better adjustment of farming to nature? The outlines of a procedure for such an on-farm implementation will be presented. This protocol for a Farm-Nature Plan is currently being tested in Dutch agricultural practice, mainly on organic farms, without subsidies on a voluntary basis.

2. Farm in the landscape

The question of why this 'coherence' between the green habitat's structure and distribution on the farm and at the landscape level is so important for the biodiversity can only be approached at landscape ecology level and has to include agroecosystem functioning.

At the beginning of this century, traditional farming was broadly in accordance with landscape ecology characteristics and processes. The technical and economic constraints to farming were directly related to limiting natural resources and conditions. Crops, livestock, tillage and manuring had a spatial distribution reflecting the prevailing abiotic conditions. This land-use pattern resulted in a gradient in use intensity and productivity from the farm settlements onwards. In addition to this spatially differentiated land-use, the use of each area was consistently the same over the years, *i.e.* constancy of processes. This traditional land-use resulted in a high biodiversity (Westhoff *et al.*, 1970; Van Leeuwen, 1966). However, increasingly and especially since 1950 improved technology and welfare allowed agricultural land-use to gain independence from natural resources and the increasing inputs of artificial fertilizer and mechanisation have levelled out the habitat variation. Nevertheless, modern agricultural landscapes still harbour abiotic and biotic diversity. This variation often refers to vital ecological processes, particularly related to the eco-hydrology (Everts & De Vries, 1991).

The data from plant and animal species inventories are extremely valuable. Because vegetation succession and species immigration mostly take decades to be accomplished (Van Dorp, 1996; Hermy, 1994), it is difficult to conclude the potential suitability of a location for certain species. Therefore, structures and processes at the surrounding landscape level have to be used as references and resources for biodiversity at the farm level.

Table 1
Important structures and processes (italics) on the landscape and the farm levels as related to ecosystem components.

Component:	Landscape level (reference):	Farm level (field of operation):
Climate	exposure to sun and wind, mesoclimate	shade, shelter, *erosion*, *deposition*
Soil	soil type, inclination, soil/height transitions (*soil formation*)	*managing* nutrient and organic matter status, *tillage*, *disturbance*
Water	catchment area (river), *water transport: inundation, seepage, infiltration, leaching or accumulation minerals, land-use planning*	ditches, drains, ponds, wells, *water management*
Physical structures (man-made)	roads and banks, dikes, urban zones, *construction*	buildings, tracks, fences, dumps/piles, *transports of matter, construction*
Vegetation	present communities (including forest, nature reserve), *succession, population dynamics, dispersal*	pastures, arable crops, weeds, vegetation of linear habitats, *dispersal, management and control*
Fauna	vertebrates and migratory invertebrates, *migration, population dynamics*	present species, domestic animals, *dispersal, population dynamics*

How can pattern and process at the landscape level (Table 1) be assessed in order to achieve such coherence between the habitat infrastructure of farm and landscape? If we look at the landscape level there are three ecological keynotes to be addressed:

- *Similarity*: the promotion on the farm of plant and animal populations already occurring in the region, most effectively enhances the farm biodiversity. Semi-natural (green) habitat types found in the surrounding landscape could be present or constructed or reinstated on the farm; a farm in an open landscape could have a solitary tree or some shrubs, but is better not planted with woodlots or hedges;
- *Connectivity*: ecologically related habitats (wet, wooded, herbaceous) should be connected or be located within a certain distance in order to guarantee a minimum territory size within the reach of dependent animal species (Opdam *et al.*, 1993); the on-farm green habitats should link up with the habitat network present in the surrounding landscape;
- *Variation potential*: the variation in soil and hydrological conditions at the landscape level as well as the processes at work on a landscape scale acting as agents for variation (*e.g.* causing groundwater seepage zones, flooding) should be utilized in planning habitat arrangement and habitat management at the farm level.

If these three keynotes are addressed on a number of contiguous farms, their common landscape context will lead to compatible green infrastructures that will positively influence each other and may also restore characteristics of the landscape. This synergy or positive feedback may have the character of a restoration, but includes economically feasible farming.

When the three landscape level keynotes are applied to the ecosystem components at the farm level, a number of recommendations can be identified (Table 2):

- Climate: general exposure to sun and wind, rainfall are the same for farm and landscape;

- Soil: different soil types and transitions may extend into the farm area, which could be expressed by botanical composition; this can be enhanced by applying special management on selected (promising) habitats (*e.g.* establishing grassy strips, removing biomass after mowing);
- Water: influx of nutrient-rich or polluted water from the surrounding area may strongly influence on-farm habitat conditions; this should be restricted if possible; differences in groundwater quality extending into the farm area could be expressed in the local species composition (Everts & De Vries, 1991); deepening of a ditch or construction of a pond should be linked with the surface-water network; distances up to *c.* 300 m enable amphibians to disperse;
- Vegetation: woody elements (hedgerows, woodlots, individual shrubs and trees), can be planted to expand the woody network or reinforce existing patterns or isolated woody elements in the landscape; management of woody, dry or wet herbaceous vegetation should refer to examples in the surrounding area that demonstrate subsequent developmental stages and species-rich communities;
- Fauna: measures for the promotion of certain species could focus on resident (vulnerable) species; to avoid disturbance of large species, particularly meadow birds, these efforts could best be at least 200 m away from settlements and main roads.

3. On-farm nature

The previous section considered the coherence in pattern and process between the farm and landscape and recommendations were derived for the farm. Now, we will emphasize pattern and process at the farm level proper, including the related activities and management. The challenge here is to establish an explicit link between the farming measures and the desired developments in farm nature.

A number of structures and processes at the farm level can be important. Features at the farm level are summarized in Table 1. How can these structures and processes be assessed and addressed in a Farm-Nature Plan? Here we will use four farm-ecology keynotes comparable to the three keynotes at the landscape level:

- *Surface area*: a certain part of the farm area should comprise green (*i.e.* semi-natural or extensively managed) habitats and serve as a refuge and a source of variation. In a number of cases an area of 5% of the farm has been recommended (Vereijken *et al.*, 1994);
- *Connectivity*: similar habitats on the farm (wet, woody, herbaceous) should be connected or located within a certain distance in order to ensure that dependent animal species have at least the minimum territory size and can disperse across the farm (Opdam *et al.*, 1993);
- *Variation*: a variety of habitats should occur on the farm; variation can be added within the predominant habitat types by applying different management forms and thus accommodating different plant species and animals that *e.g.* require variation in prey and resources; this holds true for generalist predators of pests who need 'alternative prey' when pest populations are low (Altieri, 1994). Variation also relates directly to biodiversity;
- *Habitat quality*: extensively managed habitats should be protected from manuring and soil disturbance in order to allow communities of older successional stages to develop; to facilitate vegetation succession and small scale differentiation in ecological gradients there should be as much continuity in the year-to-year management as possible, including the use of the fields (Westhoff *et al.*, 1970); some vertebrate species require additional measures to compensate for or protect against threats in the production area, *e.g.* protection of meadow bird nests (Beintema, 1991).

Table 2
Developing a Farm-Nature Plan by translating ecological information (about structures and processes) to recommendations.

Component:	Landscape level recommendations:	Farm level recommendations:
Climate	-	utilize differences in microclimate
Soil	utilize relief, soil-type, transitions	nutrient application in consistent patterns in space and time; no input outside fields
Water	correspond to flow patterns, seepage water quality (*i.e.* the general ecohydrology)	manage water quality, quantity and links: retention, rising water table, creating new ponds and marshes
Physical structures	consider vicinity of roads and buildings (disquiet)	enable nesting and hiding of animals
Vegetation	reference communities under consistent (nature) management; improve spatial linkages or maintain separation	creating and/or linking of similar habitats; consistent management method in a consistent distribution pattern; mowing mainly with biomass removal
Animals	reference communities, including species with a large home range	facilities and protection measures

When the four farm-ecological keynotes are applied to the ecosystem components at the farm level, a number of recommendations can be identified (Table 2):

- Microclimate and climate: establishment of sheltered and sunny places; in open landscapes shelter can be provided by shrubs, reed or even high perennial herbs; ditch banks or ponds with a sunny aspect should have priority when extra efforts are made in vegetation management;
- Soil and soil fertility: any manuring or emission of nutrients outside the production area should be avoided. The margins of pastures and, if possible, the edges of arable crops could, therefore, receive less manure; difference in fertility levels of fields should be emphasized; on marginal fields on arable farms a less intensive crop rotation can be considered;
- Farm buildings: access and nesting facilities for birds (swallow, barn owl) and mammals (hedgehog, stoat) could be offered;
- Water: the potential for conserving relatively nutrient-poor groundwater and rainwater on the farm should be exploited; sometimes the direction of flow can be changed and the effects of good water quality extended; the water level in some ditches could be raised by damming. If the landscape type permits, wet elements or deeper water can be created;
- Vegetation: if the landscape permits new linear woody elements of at least 3 m width to be established; the rule of thumb regarding the movement of birds, bats and butterflies the 100 meter between trees and shrubs; the pattern of wet, woody and herbaceous elements around fields should be as interconnected as possible; a gap should never exceed 200 m (radius of action for stoat and songbirds). Plots should preferably be no larger than 8 ha. There should be a realistic and not too complex annual planning of the vegetation management of verges and ditch banks, that provides for differences in growing stage between or even within linear elements; there should be a consistent differentiation in land-use patterns, if stocking rate permits.

4. Protocol for a Farm-Nature Plan

How can organic or other farms be modified in order to achieve coherence at the landscape level and integration of nature at the farm level? The above recommendations were derived from both levels. The Farm-Nature Plan protocol (Smeding, 1995) was developed for this purpose. It is a stepwise procedure that leads to a map of the farm including site-specific recommendations.

The Farm-Nature Plan protocol has five steps:

- *The attunement*: a talk with the farmer about his perception of nature on the farm, his wishes, technical possibilities and constraints;
- *The survey*: a field visit of two days to identify and describe all relevant features resulting in (1) a 1:5,000 map of the farm, (2) a 1:25,000 map of the landscape, (3) a list of the different habitat types and their areas and (4) a short report on observations of habitat structure and composition; only conspicuous indicator species need to be identified; information is also collected about land-use planning policy and nature management subsidies relevant for the farm;
- *The appraisal*: an evaluation of the farm with regard to: (1) the area of non-farmed habitats, (2) the connectedness of similar (wet, woody or tall herbaceous) habitats on and around the farm area, (3) the variation and (4) quality of farmed and non-farmed habitats;
- *The choice of objectives*: a decision on site-specific and realistic objectives for the farm; the decision is based on ecological criteria (appraisal), the farmer's preferences and management possibilities (attunement) and local land-use policy and subsidies (survey);
- *The design*: starting from the objectives and the farm map several points of attention are checked; at this stage, the list of recommendations (Table 2) is consulted to establish landscape coherence and compatibility with farming practices; the result is a map of the farm area including the existing and planned distribution of green infrastructure, with practical recommendations; particularly in this last step the scientific/ecological judgement is to be combined with creativity when finding alternatives for acceptable solutions.

By way of an example, let us consider the Farm-Nature Plan made for the A.P. Minderhoudhoeve experimental farm (Lantinga & Oomen, 1998), a 89 ha mixed organic farm in a polder dominated by arable production. The plan (Fig. 1) involved increasing the total area of non-farmed biotopes from 2.8 to 5.8%. Four sown grassy banks are cross-linking the herbaceous network and dividing extended areas of arable land into plots of 9 ha or less.
The management in the ditches is varied, with the aim of achieving a tall herb structure (common reed) and a poorly productive vegetation with increased flowering performance. The vegetation quality of the ditch slopes is guaranteed by means of a grassy field margin and an overall mowing regime with biomass removal. The ditch with tall herbs together with shrubby corners and a newly planted hedgerow have to provide a shelter network for insectivorous songbirds and small mammals like stoat and weasel. Additional measures are taken to protect and facilitate nesting of swallow and black-tailed Godwit.

The protocol was developed in collaboration with the Dutch National Extension Service. The procedure was tested in 1995 at three organic farms (Smeding, 1995). In 1996-1997 extensionists made 27 Farm-Nature Plans for Dutch organic farms, ranging from dairy and arable to fruit production, and distributed over various regions in the Netherlands (Van Almenkerk & Van Koesveld, 1997). In 1998 70% of the involved farmers responded to a questionnaire: 40% of the farmers had implemented the recommendations and 35% intended to do so in the future. About 70% of the involved farmers are using the Farm-Nature Plan in discussions with the local government, water boards and nature conservation authorities.

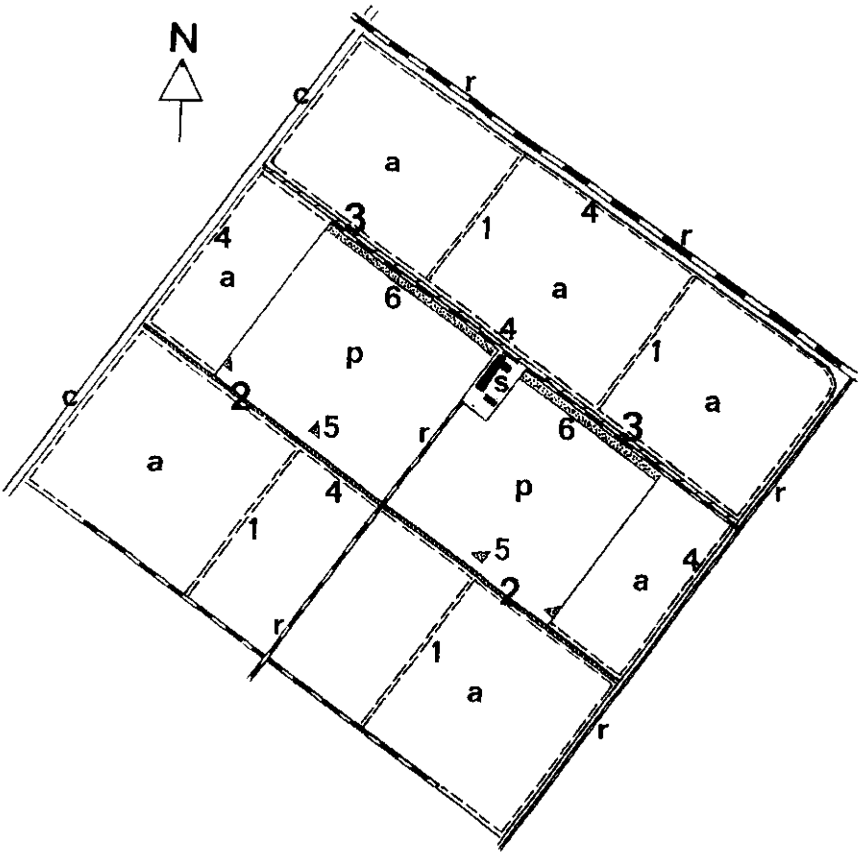

Fig. 1. Farm-Nature Plan for the A.P. Minderhoudhoeve-WU experimental organic farm (89 ha). a, arable field; p, permanent pasture; s, farm buildings; c, canal; r, road with verge(s). Measures (width): 1, grassbanks (3 m); 2, ditch/common reed (5 m); ditch rich in flowering herbs (5 m); 4, grassy field margins (3 m); 5, shrub corners (25 m^2); 6, hedgerow (3 m).

5. Discussion

The development of farming systems that include biodiversity management is a complex topic. The approach presented in this article emphasizes coherence between farm and landscape features and integration of non-production habitat and farm management. As explained above, this approach is subsequently elaborated into an advisory instrument (protocol for Farm-Nature Plan) which assumes that the farmer will collaborate and participate actively.

The approach does not pretend to be final and comprehensive; the Farm-Nature Plan protocol follows only one particular line of reasoning, applying field experience and scientific evidences mixed with professional judgement. However, the complex system of a farm can also be approached from another perspective, for example, historical development, spatial relations or from different integration levels (crop, community, region). Certainly, more scientific research could always be done before giving practical recommendations at the farm level. However, despite such criticism every alternative line of planning of farm-nature, including the implementation, tends to pose comparable problems.

A valuable point of the approach presented is the well-structured framework that enables open discussion and improvements. The results of practice-oriented scientific research can be fitted into this framework, improving the criteria and guidelines. Important research topics include: the selection of indicator-parameters at different levels, food webs on farms, dispersal requirements for plants and animals, necessity of plant species introduction, etc.

A further advantage is that the protocol is transparent and can be applied by non-academics, because the emphasis is on observation of structures and general characteristics of species and vegetation. Last, but not least: the farmer's involvement in designing a Farm-Nature Plan is essential. The results are strongly dependent on the farmer's good intentions, understanding and accuracy in timing and positioning of actions. The protocol and Farm-Nature Plan seem to be effective tools in restoring landscape and farming sustainability. As well as having a high-tech context, precision farming (Rabbinge, 1997) may also refer to a keen understanding and use of ecological patterns and processes and a tolerant attitude towards nature elements on the farm: managing biodiversity as the starting point in ecologising agriculture.

Chapter 8: General discussion

1. Observations and their implications from a food web perspective

1.1. Empirical data on food web structures

1.1.1. Initial hypotheses

It was expected that the duration of organic management, an extensive crop rotation and an improved ecological infrastructure (E.I.) (*i.e.* enlarged area, a regime of late mowing), would relate positively to the abundance of non-pest arthropod functional groups, including primary levels of the detrital as well as the herbivore subweb. The crop area was expected to support in particular the detritivores in the farm food web, and the E.I. was expected to support particularly the (K-)herbivore functional groups that might be scarce in the crop area. An increase of the primary functional groups would consequently enhance invertebrate predator and parasitoid numbers as well as the numbers of insectivorous vertebrates (*i.e.* birds) that feed on both primary and predacious groups. The increased abundance of the predator complex was expected to inhibit outbreaks of pest herbivores.

1.1.2. Observations in the crop area

Field studies on organic arable farms in Flevoland indicated that all the factors included in the above hypothesis, affected abundance and functional group composition of both arthropods and birds. However the effects differed from what was expected.

In the crop area (*i.e.* wheat crops), K-herbivore abundance was associated with farms that had been recently converted, while r-herbivore abundance was associated with farms of a longer organic duration with an intensive crop rotation. Both observed herbivore increases might be explained by a combination of crop susceptibility to the herbivore group and limited predation pressure (Smeding *et al.*, 2001b). There was, according to the hypothesis, some evidence found for detritivore increase related to the extensive crop rotations on long duration farms (Smeding *et al.*, 2001b), and for predator increases associated with detrital subweb on the more extensive farms (Smeding *et al.*, 2001a). In this latter case, a broader definition of 'extensive' was applied, involving both crop rotation and farming practices. Predator abundance in the crop canopy was particularly related to high K-herbivore numbers on recently converted farms; however the highest species diversity was found on long duration farms which had an intensive crop rotation (Smeding *et al.*, 2001b). The farms which had an extensive crop rotation compared with the other farms had a low predator number in the crop canopy, whereas the parasitoids had intermediate numbers. The density of birds' territories seemed to be enhanced by the crop areas of long duration organic farms with an intensive crop rotation. This was possibly related to increased herbivory (Smeding & Booij, 2001).

1.1.3. Observations in the ecological infrastructure

Increased arthropod abundance was found in the vegetation of the improved E.I. (Smeding *et al.*, 2001b). The increased functional groups included both predators and detritivores. However K-herbivore numbers did not increase in the improved E.I. when they were compared to the traditionally managed E.I.; perhaps because the prolonged vegetative development of frequently mown vegetation might extend the availability of nutritive grass tissue. Also, the abundance of epigeic predators, in particular of the quantitatively important group of predacious beetles, was not related to an improved E.I. (Smeding & Booij, 2001). Observations suggested that their numbers were related to the crop area conditions. Open, frequently mown E.I. vegetation enhanced the more specific ground dwelling functional groups compared to improved E.I. The territorial density of insectivorous birds was positively related to the high arthropod abundance in the E.I. (Smeding & Booij, 2001).

1.1.4. Observations on the interactions between the E.I. and the crop area

Field studies provided no convincing evidence for the dispersal of functional groups, abundant in the E.I., into the crop area. The effects of crop conditions on the arthropod functional group abundance in the crop area seemed to offset the influence of the E.I. (Smeding *et al.*, 2001b). Contrary to expectations, observations suggested the effects were reversed regarding epigeic predacious beetles (Smeding *et al.*, 2001a), and flying insects that were possibly transported into the E.I. (Smeding *et al.*, 2001b; Smeding & Booij, 2001).

Bird studies revealed positive correlation between bird functional groups and a combination of crop area and E.I. characteristics (Smeding & Booij, 2001). This may suggest that both the crop area and the E.I. habitats are important to these birds. This may also hold true for birds that typically live in the E.I., because a certain proportion of their prey could originate in the crop area.

1.2. Observations related to the food web theory

1.2.1. Top down and bottom up determination of abundance

The initial set of hypotheses was based on the generalisation that an increased food web base, due to an enlarged resource supply, relates to the subsequently increased trophic layers ('bottom up control', *cf.* Oksanen *et al.*, 1996). Our findings largely confirm the importance of 'bottom up' determination on detritivores, K-herbivores, r-herbivores, invertebrate predators and insectivorous birds. However, the place of the resources was different than expected: long duration organic farms did not provide a large food resource to K-herbivores and in case of an intensive crop rotation also not to detritivores. In the E.I., contrary to expectation detritivorous arthropod numbers were enhanced by late mowing and not particularly K-herbivore numbers.

Additional to indications for 'bottom up' determination, indications were found for 'top down' effects (*cf.* Wise *et al.*, 1999; Tscharntke, 1997; Power *et al.*, 1996). Observations of both the K- and r-herbivore abundance suggested that the explanation of herbivore abundance might, next to the herbivore susceptibility of the crop, also involve herbivore control by predators. An increase of predation pressure on farms, along an intensity-gradient beginning with recently converted farms, may first depress K-herbivore numbers (on intensive farms of long duration) and then also the more vigorous r-herbivores (on extensive farms of long duration). This presumed predation pressure could be due to epigeic predators that are supported by subsidised detrital food chains (Wise *et al.*, 1999; Polis & Hurd, 1996). The potential strength of such pressure is suggested by several reports on food shortages for epigeic predators (Sunderland *et al.*, 1996; Booij *et al.*, 1996; Wise *et al.*, 1999). These 'top down' effects may modify to a certain extent the generally 'bottom up' determined farm food web structure. However, much more research is required to find conclusive answers.

The predominance of a particular predator functional group may affect other predator groups by means of predation as well as competition (*e.g.* Tscharntke, 1997). For example, an abundance of carabids or linyphiid spiders might affect syrphid fly larvae (oligophagous predator) and parasitoids, which also interact with each other. Consequently parasitoid distribution might to a certain extent, be determined by the occurrence of predators competing with or preying on parasitoids. These interactions (*i.e.* 'top down' and 'horizontal effects' in the food web) defined as 'predator interference' or 'intraguild predation' may influence arthropod

functional group compositions.
The abundance of insectivorous birds might be negatively affected by the 'multi-channel' omnivory of epigeic predators, since herbivores, especially K-herbivores are the preferred food items for insectivorous birds (Poulsen *et al.*, 1998). The birds feed, to a certain extent, on a higher trophic level than arthropod predators; a reduction of bird density therefore implies a shortening of the functional chain length of the farm food web. Accordingly, Power *et al.* (1996) argued that food chain length will get shorter in a succession from the pioneer stage to the secondary stage because the grazers or secondary consumers possess armoured traits protecting against predation. This viewpoint would be the reverse of the commonly held view by ecologists that there is a succession towards an increased complexity.

The highest bird densities were observed on farms that combined intensive crop production with improved E.I. This observation suggested, according to the hypothesis, that the broadening of the food web base may facilitate ('bottom up') higher trophic levels. The negative indirect ('top down') effect of detrital subsidy on the food availability to birds at the farm level, might be compensated by food availability to birds in other habitats on the farm (*e.g.* in E.I.) and around the farm.

1.3. Extrapolation of Flevoland observations to other landscapes

The comparative study of arthropod communities and birds on four organic arable farms in Flevoland and the river region (Smeding & Booij, 1999; Den Nijs *et al.*, 1998) demonstrated mainly contrasts between the landscapes. The relation of most invertebrate functional groups to E.I. seemed to be ambiguous. However, the farm type with increased E.I. in each landscape was associated with high densities of specialist insectivorous birds.

Observations suggested that wheat crops in the river region compared to wheat crops in Flevoland included a much higher species diversity, involving for example an apparent abundance and diversity of weeds. Abundant flowering weeds like camomile, attracted large numbers of anthophiles and also for example large-sized predacious Diptera (asilid flies) that did not occur in Flevoland; the territory of a stonechat (*Saxicola torquata*) on farm 'O-', an insectivorous bird, and the weed Venus' looking-glass (*Legousia speculum-veneris*) on farm 'O+' represented high nature conservation values (Smeding, unpublished data). The observed increase in species richness and associated complexity of farmland communities on organic farms in old culture landscape may require a more detailed assessment of functional group assemblages in the farm food web.

The increased food availability to birds in the river region was suggested by the total songbird territory density: 10-12 territories/10 ha, which was two to six times more than on ten selected Flevoland farms in the 1997-1999 observations. In one of both river region farms, skylarks had a density of 2.7 territories/10 ha, which was higher than the highest observed density (2.4 territories/10 ha) in Flevoland. In farm food webs in old culture landscape compared to polders, resources supplied by weeds, both directly (seeds) and indirectly (herbivores), might have particular importance. Also contributions of the E.I. to the farm food web in old culture landscape, may not only include organisms from herbaceous vegetation but also from habitats (*e.g.* woody, aquatic) that are more contrasting to farmland communities.

It can be argued that it would be more difficult to assess (*i.e.* isolate) the effects of farm management (*e.g.* involving detritis input in the crop area) in old culture landscape than in polders. More complex systems may involve more extensive ecosystem services and nature conservation contributions that do not (yet) occur in simpler agroecosystems (Brown, 1999a;

Altieri, 1994). Studies should, therefore, sooner or later, also address the more complex farmland communities in more biodiverse landscapes (Stobbelaar & Van Mansvelt, 2000; Edwards *et al.*, 1999; Vandermeer *et al.*, 1998).

1.4. Implications

1.4.1. Implications for improvement of ecosystem service and nature conservation aims

With regard to improving the utilisation of ecosystem services (Altieri, 1999), our results imply that enhancing the prey availability for epigeic predators, by subsidising the detrital subweb, might contribute to pest control on organic arable farms. This mechanism may already be an influence on long duration organic farms with extensive crop rotation (including a ley pasture). However, further research on this topic is necessary and promising. Increasing the abundance of vegetation dwelling (oligophagous) predators in the crop canopy, might not be an appropriate aim, because the great abundance of crop herbivores would be needed to increase these predators. This is in agreement with reports on the limited predation capacity of oligophagous predators (*e.g.* Coccinellidae in Hemptinne & Dixon, 1997).

With reference to the nature conservation goals, results suggest that improvement of E.I. enhances the density of insectivorous birds, which are the main conservation-worthy species on arable farms. The crop areas of intensive organic arable farms supported relatively high densities of insectivorous birds (when compared with recently converted farms), possibly related to the occurrence of r-herbivores.

However, if these systems were to be optimised, in accordance with the principles outlined above, the increased employment of epigeic beneficials might run counter to high bird densities *i.e.* nature conservation values. An increased efficacy of weed control in the future, might further diminish the food resources in the crop area available for these birds. It might appear curious that current organic farming systems in Flevoland with an intensive cropping system (and particularly when there is also an improved E.I.) combine together, to a reasonable degree, both aims of providing ecosystem services and nature conservation, but that further improvement of organic farming systems might reduce this integration.

1.4.2. Further agroecological implications of food web management

The importance of K-herbivores as prey for insectivorous birds as well as the importance of herbivorous vertebrates for top predators suggests the relevance, from an energy point of view, of relatively small food chains ('flows') in the farm food web. Probably most consumption by herbivores is carried out by small organisms like r-herbivores (*i.e.* aphids) (Smeding & De Snoo, 2001). Because 90% of energy is lost in each transfer in the food chain (Polis & Winemiller, 1996), food chains that start from small primary organisms, dissipate more energy, before tissues are assimilated into the larger organism-'meat'; primary consumption by large herbivores (*e.g.* leather jackets, chafers, grasshoppers, sawfly larvae, caterpillars, mice) might be more effective for the higher trophic levels of the farm food web. In the detrital food web a similar arbitrary division between the small primary organism chains and large primary organism chains could be made: micro-organism based chains (De Ruiter *et al.*, 1995) versus saprovorous arthropods (*e.g.* flies, large springtails) and earthworms based chains, which connect to vertebrates, for example, lapwing and insectivorous mammals.

Food web management, which is aimed at nature conservation goals, may address, in particular, the large organism chains. This could be done by increasing the amount of less nutritive and more complex plant tissues, as well as the detritus that does not decompose easily in both the crop area and the E.I.; these resources require the employment of the larger organisms mentioned above. Accordingly, Ryszkowski *et al.* (1993) found more large species in arable crops in mosaic landscapes (*i.e.* including a high amount of 'E.I.') than in arable crops in uniform landscapes.

Cousins (1996), who was a source of inspiration for the chapter on food web structure, stressed the importance of weighting the food 'value' in a food web. From this viewpoint, for example seeds and flower products, although principally belonging to primary production, may be put on the same trophic level as aphids. Accordingly, detritus with a higher fibre content, may have a higher 'value' than easily decomposable material which is immediately decomposed by the micropredator system..However, these principles should not be applied too rigorously; for example, Steffan-Dewenter & Tscharntke (1997) found more large sized catterpillars in pioneer successional fields than in late successional fields. Another aspect is that larger organisms often have longer life cycles; therefore also physical disturbance and shelter possiblities, on both field and farm level, should be considered (*e.g.* Ryszkowski *et al.*, 1993; Brown, 1999b).

The management of components that are not harvested (NHC) (Vandermeer *et al.*, 1998), included in the concept of multi-species farms, provides a conceptual basis for a food web management that specifically addresses the 'large primary organism chains'. Central to the management of NHC is the recognition of the importance of crop residues, hay from the canal banks, and other non-harvested materials (including the standing crop of wild vegetation and trees) for the farming system and its food web. Primary production capacity, which does not feature in the economic returns of the farm (*e.g.* green manure, E.I. vegetation) might be used as a life support for the non-pest herbivore subweb and subsequently support the detritivore subweb macrofauna. Better habitat conditions for these herbivores may compensate to some extent for the predation pressure by epigeic predators, due to detrital subsidy. In such an extended food web structure, ecosystem services and nature conservation might again be integrated. However, the question whether complex food webs are better *i.e.* more stable than simple food webs is a perennial topic for discussion among ecologists (Polis & Winemiller, 1996), and might be more difficult to approach than other questions raised by this paragraph.

Swift & Anderson (1993) as well as Wardle (1999) argued that the detrital subweb on arable farms is more developed and less depleted than the herbivore subweb. Our studies, however, suggest, in reference to the above ground community, that there is an equal significance for both the herbivore subweb and the detrital subweb (Smeding & De Snoo, 2001): agroecosystems in which all the NHC enter the detritivorous food chains may not support high densities of vertebrates. From a food web perspective it might therefore be a challenge to incorporate controlled herbivory in multi-species farming systems (*e.g.* Theunissen, 1994, 1997; Andow, 1988; Altieri, 1994; Holland & Fahrig, 2000).

2. Recommendations

2.1 Improvement of topological web

The assemblage of functional groups and the identification of interactions between these functional groups are the empirical foundation of food web studies (Winemiller & Polis, 1996). Peculiarities of species may, in some cases, determine food web structure. Therefore it is important to elaborate on this foundation by extracting information on diet, habitat preferences and life history shifts from the vast amount of available literature (*e.g.* Paoletti, 1999). This information is currently being collected in a database AURYN (Booij, Lock and

Smeding, unpublished data), and will be used to update the topological food webs presented in this thesis.

2.2. Linking food webs to farm models

The changes of farm food web structure related to farm and E.I. characteristics (Smeding & De Snoo, 2001) could be described by a mathematical model. In the exploratory phase of food web management, simple models may help to explore the hypotheses and to detect theoretical inconsistency. A preliminary model is being developed using Fuzzy Cognitive Mapping (Wolfert, in prep), which can calculate, based on certain farm and E.I. traits, relative sizes of the functional groups in the farm food web.

Food web analysis may in the future profit from extensive farm models that calculate the availability of resources for the primary functional groups in the farm food web (*e.g.* Oomen & Habets, 1998; Wolfert, 1998; Wolfert *et al.*, 1997). These models could estimate, based on data of the crop rotation and manure strategy, the amounts of various types of primary production and crop residues (NHC) that are needed to support the primary consumption in the food web. Such models could be used to design realistic experimental and commercial farms, with for example optimised detrital subsidy.

The subject of this thesis was explorative research describing arthropod and bird communities that gave an indication of food web structure. However, in the future more quantitative data sets and better understanding of processes in farm food webs are expected to deliver useful simulation models.

2.3 Spatial approaches

The spatial approach (*e.g.* Opdam, 1986; Wratten & Thomas, 1990; Den Belder *et al.*, in prep.) and the food web approach are both useful as a conceptual framework for agroecological studies at the community level (Van Wingerden & Booij, 1999). Authorities of the food web approach (Polis *et al.*, 1996; Winemiller & Polis, 1996) argue that both approaches should be combined, but also note that the resulting complexity could be a serious constraint. Accordingly, connecting spatial models to important functional groups in the food web model will pose great problems, both in technical and methodological respect. However, it might be a challenge for both food web and spatial approaches to experiment with rather simple comprehensive models (*e.g.* Kreuss & Tscharntke, 1994). The effect on the farm food web structure of the E.I. arthropod community, and also of crop mosaics, exemplify spatial heterogeneity. Accounting for the mobility of functional groups is necessary for the successful application of food web management.

The spatial approach, based on the dispersal of individuals and populations (*e.g.* Topping, 1997) is essentially a 'bottom up' approach. However, characteristics on a higher integration level should also be approached with the appropriate methods for this higher level (Almekinders *et al.*, 1995; Cousins, 1996). Examples of a spatial approach that addresses higher integration levels are provided by the work of Oldeman (1990), analysing spatial patterns based on the distinction of 'eco-units'.

2.4. Field experiments

Field research and experimentation are required to investigate the preliminary conclusions provided by this thesis. A study area might include both commercial farms as well as experimental farms. The experimental farms could represent extreme regimes of management which are not yet acceptable for farming practice. Care should be taken with experiments that involve plots where there are many small fields, which may represent a mosaic from a farm level perspective. The context and scale of a (farming) system may in some cases be a precondition for the occurrence of particular effects (*e.g.* Pimm, 1991; Brown, 1999a).

Comprehensive field studies with indiscriminate assessment of many taxa, as done by Potts & Vickerman (1974), may model field research that could optimally support food web studies.

2.5. Practical recommendations

Procedures for farm-nature plans were recently elaborated by Van Almenkerk & Van Koesveld (1997), Visser (2000) and Daemen (2000). Protocols or procedures for such combined agricultural and ecological plans might be supported by a restricted food web assessment based on simple assumptions. For example, a simple model that applies data from the farm map (areas of crops and habitats), coarse manuring strategy, and E.I. management, may provide estimates of resource availability for several functional groups on the farm. These outcomes may help the farmer or adviser to set priorities, with regard to habitats or species groups that could be and are to be enhanced.

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Summary

Species diversity of indigenous plants and animals on farmland is declining dramatically due to agricultural intensification. Biodiversity loss in agriculture affects both economic and nature conservation values. One important solution for the reversal of biodiversity loss in the agriculture of industrialised countries could be the development of farming systems that are economically based on utilisation of biodiversity and that also harbour conservation worthy species. This idea is compatible with the concept of multi-species agroecosystems. Development of organic farming systems is a possible implementation of this concept; crop areas managed according to this concept may be complemented by an adjacent ecological infrastructure (E.I.). A food web approach is an appropriate method for investigations into the higher integration levels of ecosystems and may therefore contribute to research on multi-species farming systems. Progress in scientific understanding of food webs is currently expanding into agroecology. A food web approach also provides a framework for ordering the scattered information on farmland species and habitats.

A simplified set of hypotheses with regard to food web structure on organic farms served as the starting point for the thesis: it was expected that the duration of organic management, extensive crop rotation as well as an improved E.I. (*i.e.* enlarged area and late mowed), would relate positively to the abundance of arthropods in both non-pest herbivorous and detritivorous primary subsystems. The varied plant tissues in improved E.I. would particularly boost the non-pest herbivorous functional groups. Consequently predator and parasitoid numbers on the farm would be supported. An accumulated high invertebrate density on the farm would support insectivorous vertebrates, particularly birds. The objectives of the thesis were: to take a comprehensive food web approach in relation to the farm and E.I. management; to link component knowledge on species and farm operations to food web theories; and to point out implications for multi-species farm development. The study area involved farms that were mainly situated in the relatively uniform landscape of Flevoland. This polder has a concentration of organic arable farms, including farms with improved E.I.

Empirical investigations were concentrated on particular sections of the farmland community, namely ground dwelling arthropods, vegetation dwelling arthropods and insectivorous birds. Functional group compositions (*e.g.* detritivores, herbivores and predators) within these sections were assessed. Field studies indicated that all the factors included in the above hypothesis affected abundance and functional group composition of both arthropods and birds. However, the effects differed from what was expected.

In the crop area (*i.e.* wheat crops), K-herbivore abundance was related to farms that had been recently converted and r-herbivore abundance was related to farms of a longer duration with an intensive crop rotation. Both the observed herbivore increases might be explained by a combination of crop susceptibility to the herbivore group, and limited predation pressure (Chapter 2). There was, according to the hypothesis, some evidence for detritivore increase related to extensive crop rotation on long duration farms and for detrital subweb-connected predator increase in relation to more extensive farms (Chapters 2 and 3). Predator abundance in the crop canopy was particularly related to high K-herbivore numbers on recently converted farms. The highest species diversity was found on long duration farms which had an intensive crop rotation (Chapter 2). The farms which had an extensive crop rotation, compared with the other farms, had a low predator number in the crop canopy, whereas the parasitoids had intermediate numbers. The density of birds' territories seemed to be enhanced by the crop areas of those long duration organic farms that had an intensive crop rotation, this being possibly related to an increased herbivory (Chapter 4).

An increased arthropod abundance was found in the vegetation of the improved E.I. The increased functional groups included both predators and detritivores (Chapter 2). However, K-herbivore numbers did not increase in the improved E.I. when they were compared to the traditionally managed E.I. (Chapter 2 and 3); perhaps because the prolonged vegetative development of frequently mown vegetation might extend the availability of nutritive grass tissue. Also, the abundance of the epigeic predators, in particular of the quantitatively important group of predacious beetles, was not related to an improved E.I. (Chapter 3). Observations suggested that their numbers were related to the crop area conditions. Open, frequently mown E.I. vegetation enhanced the more specific ground dwelling functional groups, when compared to improved E.I. The territorial density of insectivorous birds was shown to be positively related to the high arthropod abundance in the E.I. (Chapter 4).

Field studies provided some evidence for the dispersal of functional groups, abundant in the E.I. into the crop area. However, the effects of crop conditions on the arthropod abundance in the crop area were observed to offset the influence of the E.I. for some groups. Contrary to expectations, observations suggested the opposite effects regarding flying arthropods, which were possibly transported into the E.I., and epigeic predacious beetles (Chapters 2 and 3). Bird studies (Chapter 4) revealed positive correlations between bird functional groups and a combination of crop area and E.I. characteristics. This may suggest that both the crop area and the E.I. habitats are important to these birds. This may also hold true for birds that typically live in the E.I., because a certain proportion of their prey could originate in the crop area.

In the discussion section of each empirical study observations were linked to theory in food web literature. Field observations provided some indications for indirect effects of subsidised detrital food chains on herbivore abundance and consequently on bird abundance, as well as possible effects of intraguild predation on arthropod functional group composition. However extrapolation of the results obtained in Flevoland to other geographical regions may require a further examination of functional group assemblages, and of primary resources related to weeds or to semi-natural habitats other than herbaceous habitat (Chapters 5 and 8).

A proposal for a descriptive or topological farm food web is drawn from field observations as well as from references in literature (Chapter 6). Important themes in the food web theory were tentatively applied to this preliminary model in explaining differences between localised farm food web structures and how they are related to the farm and/or ecological infrastructure management. Predictions are made for four different farm food web structures that express four extremes of two environmental gradients which correspond to the length of organic duration and the amount/quality of the E.I. Empirical observations are used to illustrate the different food web structures. However, further investigation is necessary to confirm the hypotheses put forward.

The implications of both empirical as well as conceptual studies are that the organic duration and the amount/quality of the ecological infrastructure may both positively contribute to improving ecosystem services and to aims based on nature conservation. However, an optimisation of the farm food web with regard to ecosystem services may run counter to nature conservation values, as in the case of enhanced epigeic predators which would depress herbivorous food items for birds. Nevertheless an increased understanding of the farm food web and its management is likely to show more clearly the possibilities for the development of multi-species agroecosystems that integrate ecosystem services and nature conservation goals. The outcome of this kind of applied ecological research is likely to improve the basis of pragmatic protocols for farm-nature planning exemplified in Chapter 7.

Samenvatting

De soortsdiversiteit en de aantallen van wilde dieren en planten in landbouwgebieden gaan achteruit ten gevolge van intensivering van de landbouw. Dit verlies aan biodiversiteit heeft nadelen voor zowel economie als natuurbescherming. Aanwending van *ecosystem services* in verband met biodiversiteit, zou kunnen bijdragen aan een verminderde inzet van bestrijdingsmiddelen, meststoffen en fossiele brandstoffen. Deze *ecosystem services* worden mogelijk door een kleine groep van essentiële soorten verzorgd. Echter vanuit het oogpunt van natuurbescherming is brede stimulering van biodiversiteit gewenst omdat landbouw veel ruimte gebruikt en specifieke leefgemeenschappen omvat. Een mogelijke oplossing voor het geschetste probleem is het ontwikkelen van landbouwsystemen die biodiversiteit benutten en instandhouden en dus landbouw en natuurbescherming op het niveau van een landbouwbedrijf verenigen. Verschillende agroecologen hebben dit thema uitgewerkt. De Amerikaanse onderzoeker Vandermeer noemt dergelijke landbouwsystemen *'multi-species agroecosystems'* (Vandermeer *et al.*, 1998); dit begrip vat de doelstelling van deze thesis samen.

Onderzoek dienstig aan het ontwikkelen van *multi-species agroecosystems* in de praktijk verlangt een specifieke opzet. Wat betreft het object is het belangrijk dat het onderzochte systeem de gewenste specifieke complexiteit bezit omdat de gezochte processen mogelijk alleen in een dergelijke context optreden. Vanuit deze overweging is gekozen om op biologische landbouwbedrijven onderzoek te doen en met name op biologische bedrijven met rondom de percelen een ecologische infrastructuur (E.I.) die verbeterd is, d.w.z. vergroot qua oppervlak en ecologisch beheerd. Wat betreft de methode is het belangrijk dat het onderzoek kenmerken meet op het systeemniveau. Vanuit deze overweging is gekozen voor een voedselwebbenadering, overeenkomstig de aanbevelingen van Gezondheidsraad (1997) met het oog op ecosysteemanalyse. Uitgangspunten en uitwerkingen van de benadering zijn te vinden in het gezaghebbende werk van Polis & Winemiller (1996). In agroecosystemen (in de gematigde streken) verkeert voedselwebonderzoek nog in een overwegend exploratieve fase met bijvoorbeeld fundamentele studies aan het detritus web van De Ruiter *et al.* (1993, 1995) en hypothese-ontwikkelende artikelen van Wise *et al.* (1999), Brussaard (1998) en Tscharntke (1997).

Het onderzoeksdoel voor dit proefschrift was drieledig:
- het opstellen van een descriptief ('topologisch') voedselweb voor een biologisch akkerbouwbedrijf, dat zowel het onder- als bovengrondse systeem omvat en dat geschikt is voor het leggen van relaties met handelingen van de boer;
- het leggen van verbanden tussen componentkennis (diersoorten, teeltmaatregelen en biotoopbeheer), en ecologische theorie vanuit de voedselwebbenadering, om zodoende aanwijzingen te vinden voor effecten op bedrijfsniveau van voedselwebinteracties;
- zoekrichtingen aangeven voor het ontwikkelen van bedrijfssystemen die het benutten van *'ecosystem services'* en natuurbescherming combineren.

De hypothese van het onderzoek bestaat uit een serie, vanuit de literatuur onderbouwde, deelhypothesen ten aanzien van de voedselwebstructuur. Deze hypothese was dat er op lang (geleden) omgeschakelde bedrijven met een verbeterde E.I. een relatief grote dichtheid is van mesofauna en macrofauna van de primaire functionele groepen. De detritivoren worden bevorderd door een extensieve vruchtwisseling met granen en kunstweiden die veel organische stof achterlaten, en ook door organische mest. De herbivoren, en met name niet-plaagsoorten, hebben relatief hoge dichtheden door de aanwezigheid van veel verschillende gewassen en wat talrijkere onkruiden. De E.I. bevordert vooral de aantallen herbivoren vanwege haar grotere variatie aan plantenweefsels, inclusief bijvoorbeeld bloemen en zaden.

Bij de toename van de primaire functionele groepen en hun voedselbronnen spelen cumulatieve effecten over de jaren mee. De toegenomen dichtheid van beide primaire subsystemen draagt het hogere trofische niveau van de ongewervelde predatoren en parasitoiden. De verhoogde dichtheden van deze groepen werken de exponentiële toename van plaagherbivoren tegen. Vervolgens is de totale dichtheid van zowel de predatoren als de primaire groepen van belang als voedsel voor insectenetende vogels op het bedrijf. De dichtheid van predatoren, parasitoïden en vogels wordt dus verondersteld toe te nemen in verband met omschakelingsduur en E.I.-kwaliteit.

Het onderzoek bestond uit veldonderzoek en literatuurstudie. Het veldonderzoek was vrijwel beperkt tot Flevoland omdat landbouwbedrijven daar een overeenkomstige topografie en historie hebben. Ook bevindt zich in Flevoland een concentratie van ongeveer 75 biologische akkerbouw- en vollegrondsgroenteteeltbedrijven, waaronder bedrijven met een verbeterde ecologische infrastructuur.

In het veldonderzoek werden waarnemingen verricht aan epigeïsche geleedpotigen door middel van vangbekers, vegetatiebewonende insecten door middel van een zuigapparaat, en insectenetende vogels door middel van territoriumkarteringen. Ongewervelden werden verzameld in tarwevelden en in de ernaast gelegen slootkanten. Vogels en omgevingsvariabelen werden gemeten op bedrijfsniveau.

De resultaten van de veldonderzoeken lieten, overeenkomstig de hypothese, effecten zien op de hoeveelheden van functionele groepen, van de duur van de biologische bedrijfsvoering, intensiteit van de vruchtwisseling en de omvang en het maaibeheer van de E.I.

In de gewassen bleken herbivoren echter het talrijkst te zijn op pas omgeschakelde bedrijven met een weelderig gewas; typische plaagherbivoren (bladluizen) hadden de hoogste dichtheden op lang omgeschakelde bedrijven met een intensieve vruchtwisseling (Hoofdstuk 2). Waarnemingen aan detritivoren wezen wel meer in de richting van de hypothese. Detritivoren (vliegjes en mugjes) waren op lang omgeschakelde bedrijven met een extensieve vruchtwisseling relatief talrijk (Hoofdstuk 2). Ook epigeïsche predatoren (o.a. loopkevers en spinnen), die waarschijnlijk vooral verbonden zijn met detritivore ketens, leken talrijker te zijn in systemen met een extensievere teeltwijze (Hoofdstuk 3). Predatoren in het bladerdek van het gewas bleken geassocieerd te zijn met herbivoren; deze waren talrijk in weelderige gewassen van pas omgeschakelde bedrijven en waren divers qua soorten op lang omgeschakelde bedrijven met een intensieve vruchtwisseling (Hoofdstuk 2).

Het verbeterde beheer in de E.I. had, overeenkomstig de hypothese een sterk positief effect op de dichtheid van arthropoden en met name predatoren in de vegetatie (Hoofdstuk 2). Detritivoren waren echter de talrijkste primaire groep; herbivoren waren weliswaar talrijk maar hadden een overeenkomstige dichtheid in E.I. met het traditionele klepelbeheer. De talrijkste epigeïsche groepen van predatore kevers en baldakijnspinnen vertoonden een gewas-affiniteit (Hoofdstuk 3). Andere, minder talrijke groepen, zoals wolfspinnen waren meer geassocieerd met klepelbeheer dan met het verbeterde beheer. Verbeterde E.I. had dus (in de zomer) voor epigeïsche soorten weinig betekenis. Waarnemingen in de gewas-E.I. gradiënt, lieten zien dat hoge dichtheden in de E.I. kunnen uitstralen in de richting van het gewas. De omstandigheden in het gewas waren echter overheersend en konden zulke effecten teniet doen of aan het zicht onttrekken, bijvoorbeeld in geval van de toename van herbivoren en predatoren in een weelderig gewas.

De dichtheid van insectivore broedvogels bleek geassocieerd te zijn met zowel bedrijfs/gewaskenmerken, als met E.I. kenmerken (Hoofdstuk 4). Wat betreft het bedrijf, suggereren de resultaten dat lang omgeschakelde biologische bedrijven met een intensieve vruchtwisseling, de hoogste vogeldichtheid hadden. Mogelijk bevordert de periodieke toename van plaagherbivoren de voedselbeschikbaarheid. Wat betreft de E.I. werden duidelijke verbanden gevonden tussen vogeldichtheid en verhoogde dichtheid van arthropodengroepen in de vegetatie van de E.I.

In de discussies van ieder empirisch onderzoek (hoofdstukken 2, 3 en 4) zijn de resultaten in verband gebracht met voedselwebtheorieën. De veldwaarnemingen gaven indicaties voor het optreden van een indirect negatief effect van toegenomen detritivore voedselketens, via bevordering van polyphage predatoren, op de dichtheid van herbivoren. En ook indicaties voor mogelijke interacties tussen predatorengroepen. Verder onderzoek is echter noodzakelijk.

In hoofdstuk 6 is op basis van literatuur en veldonderzoek een topologisch voedselweb opgesteld. De variatie in de structuur van dit voedselweb is voorspeld aan de hand van vier extreme bedrijfstypen die twee gradiënten representeren wat betreft de duur van biologische bedrijfsvoering en E.I. kwaliteit. Aanvullend is nog onderscheid gemaakt tussen lang omgeschakelde bedrijven met verbeterde E.I., wat betreft de mate van herbivorie in hun gewassen. Thema's die naar voren kwamen in de discussies van de empirische onderzoeken (hoofdstukken 2, 3 en 4) werden ondergebracht in het grotere verband van het voedselweb op bedrijfsniveau. Overeenkomstig de oorspronkelijke hypothese, is de aanvoer van voedselbronnen van onderaf in het voedselweb als bepalend aangewezen ('bottom up' processen). Mogelijk zijn echter ook terugkoppelingen van boven naar beneden in het voedselweb belangrijk ('top down' effecten). Zulke effecten treden op als epigeïsche predatoren, bevorderd door detritivore prooien, herbivore prooisoorten onderdrukken. Een complete onderdrukking van plagen en ook van andere herbivoren kan echter ongunstig zijn voor dichtheden van insectenetende vogels omdat deze groep in belangrijke mate gevoed wordt via herbivore voedselketens op het landbouwbedrijf. *Ecosystem services* en natuurbelang zijn dan tegenstrijdig.
De studie laat zien dat een voedselwebbenadering veelbelovend is; hiermee is onderzoek mogelijk aan de effecten van interacties in het voedselweb, inclusief gevolgen voor landbouw en natuurdoelen. Eventuele tegenstrijdigheid kan de aanleiding zijn te zoeken naar alternatieven ter optimalisatie van beide doelen. Verder onderzoek is echter zeer noodzakelijk.

Naast de drie hoofdstukken over veldonderzoek in Flevoland en het hoofdstuk met het conceptuele model, is er een empirisch hoofdstuk 5 dat een studie toont van diergroepen op twee biologische bedrijven in Flevoland en twee in het rivierengebied. In beide landschappen was een bedrijf met veel en een bedrijf met weinig E.I. Deze waarnemingen tonen echter vooral het contrast tussen de landschappen. Extrapolatie van de Flevolandse gegevens naar andere landschappen is mogelijk maar verlangt mogelijk uitbreiding van de functionele groepen en een beter zicht op de bijdragen aan deze functionele groepen (inclusief prooien en predatoren) van bijvoorbeeld houtige biotopen en onkruiden.

Hoofdstuk 7 beschrijft een procedure voor het opstellen van bedrijfsnatuurplannen. Dit instrument is pragmatisch en streeft naar zo goed mogelijke ontwerpen op basis van ecologische kennis, veldbiologie en praktische mogelijkheden. Door het expliciet maken van doelen en criteria is getracht om de stappen van waarneming, via waardering naar beslissing te verhelderen en ook te versnellen. De vraag in hoeverre een bedrijfsnatuurplan effectief is voor het bevorderen van predatoren of bijzondere dieren, was een aanleiding tot de voedselwebstudies. Verder onderzoek op basis van dit proefschrift kan in de toekomst bijdragen aan adviesinstrumenten ten behoeve van *multispecies farming systems*.

Curriculum Vitae

Frans Wouter Smeding was born on the 4th September 1962 in Meppel, The Netherlands. He graduated from the Athenaeum of the Stedelijk Lyceum in Zutphen, in 1981, and subsequently studied Biology at the Wageningen Agricultural University. He specialised in vegetation science, plant ecology and weed science as well as alternative methods in agriculture and horticulture. He achieved his MSc in March 1989, including a qualification for first degree education. In 1989-1990 he contributed to the setting up of unsprayed field margin research at the department of Vegetation science, Plant ecology and Weed science. In November 1990 he started to work at the department of Ecological Agriculture where he participated in ongoing research and international education programs with reference to holistic approaches. He has specialised there, since 1992, on the integration of agriculture and nature. In collaboration with the Dutch agricultural extension service, he developed in 1994-1995 a protocol for farm-nature plans. This work was followed by explorative research on farm food webs in relation to the management of crop and field margins (1996-2001). He is currently employed as lecturer by the Wageningen University and Research Centre, at the Biological Farming Systems group, Department of Plant Sciences.