Regional distribution and biodiversity perspectives of Finnish grasslands

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The preservation of viable agricultural landscapes is essential in Finland and throughout Europe, because a considerable proportion of threatened species are associated with rural habitats, particularly various grasslands. In this study, the regional distribution of Finnish grasslands was studied using an existing nationwide digital land-use database. Further, the occurrence of traditional rural biotopes and selected butterfly and bird species living in different grassland habitats was investigated in relation to agricultural landscape mosaic. The results showed that grasslands were typically abundant in versatile agricultural regions, land uplift shores as well as in agriculturally marginal landscapes experiencing decrease of agricultural activities. Grasslands were generally scarce in intensively cultivated agricultural landscapes. The occurrence and siting of traditional rural biotopes in grassland networks vary greatly regionally, abundant and well-connected traditional rural biotopes being found e.g. in river valleys and few isolated biotopes in intensively cultivated or agriculturally marginal, forested regions. Furthermore, the nationwide occurrence of selected butterfly and bird species was positively related to the abundance of grasslands. Overall, grasslands enrich the Finnish agricultural landscape both at the habitat and species level. In addition to species-rich semi-natural grasslands, other low-productive grasslands also hold significant potential in the maintenance of diverse agricultural environments.

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Introduction

Agricultural practices and land use have changed rapidly during recent decades throughout Europe. Intensification and marginalization introduce imbalance to the agriculture-environment relationship and diminishing diversity in agricultural environments has been widely reported (Matson et al. 1997; Krebs et al. 1999; Robinson & Sutherland 2002). Species diversity is threatened mainly by habitat loss, increasing isolation of remaining habitat fragments and decline of habitat quality (e.g. Waldhart 2003).

Species-rich semi-natural grasslands were widespread in Europe at the time of low-intensity farming systems. These non-cultivated communities result from forest clearances and their persistence requires human management by grazing, mowing or burning (Briggs & Courtney 1989). Natural disturbances, such as fires and floods also creating grassland habitats in the forested landscape, are nowadays largely suppressed by humans (Pykälä 2000). Today, only remnants of semi-natural grasslands are found in Europe owing to fertilization, cultivation, abandonment and afforestation of these habitats. Artificially planted and fertilized cultivated grasslands have largely replaced semi-natural grasslands in agricultural landscapes (Alanen 1997; Pärtel et al. 1999; Ihse & Lindahl 2000; Poschlod & WallisDeVries 2002).

Because a significant part of European biodiversity is associated with semi-natural grasslands, their rapid decline is recognized as a serious threat to high numbers of rare or decreasing plant and animal species (Norderhaug et al. 2000; Luoto et al. 2001; Söderström et al. 2001; Kiviniemi & Eriksson 2002; van Swaay 2002; Cousins et al. 2003; Duelli & Obrist 2003). In Finland, one quarter of all known species live in agricultural environments (Pykälä & Lappalainen 1998). A considerable proportion, 28% of endangered species live primarily in traditional rural biotopes or other cultural environments and 39% of disappeared species used primarily these habitats (Rassi et al. 2001). Traditional rural biotopes are habitats created by traditional practices of animal husbandry, including the most valuable species-rich grasslands in Finnish agricultural landscapes. The area of these semi-natural grasslands has decreased to less than 1% of that registered one century ago (Vainio et al. 2001).

Nowadays it is also essential to identify other rural habitats that may increase the capacity of agricultural landscapes to sustain biodiversity, in addition to semi-natural grasslands (Krebs et al. 1999; Fahrig 2001; Robinson & Sutherland 2002; Benton et al. 2003). Different kinds of non-cropped habitats, such as old cultivated fields and pastures, set-aside land as well as field margins and grassy edge zones between fields and forests have been found to have significant value for plants (Corbet 1995; Freemark et al. 2002; Waldhart et al. 2003), butterflies and other invertebrates (di Giulio et al. 2001; Lee et al. 2001; Steffan-Dewenter & Tscharntke 2001; Jeanneret et al. 2003b; Haysom et al. 2004; Pöyry et al. 2004; Pywell et al. 2004), birds (Pain et al. 1997; Vickery et al. 2001; Peach et al. 2004; Virkkala et al. 2004), and small mammals (de la Peña et al. 2003). These habitats can be considered as an intermediate, biodiversity-supporting level between intensively managed, species-poor arable land and species-rich, but scarce semi-natural grasslands.

The quality of an individual grassland patch is mainly determined by its size, management history and physical conditions (e.g. climate, bedrock and soil properties) as well as its relation to the surrounding landscape mosaic (Dauber et al. 2003; Opdam et al. 2003). Small and isolated patches are expected to have an increased risk of population extinction (MacArthur & Wilson 1967; Levins 1969; Hanski & Gilpin 1991). In other words, a comprehensive network of habitat patches of sufficient size enables species dispersal and reduces the local extinction risk (Saunders et al. 1991; Bender et al. 2003; Jordán et al. 2003).

A prerequisite for monitoring and conservation of biodiversity is widespread and up-to-date information concerning the distribution of habitats and species. During recent decades new nationwide databases containing information of land use, land cover and species occurrences have been created both on the national and EU level (Mikkola et al. 1999; FEI 2003; Weiers et al. 2004). These digital datasets provide new possibilities for biogeographical research and maintenance of diversity.

Here, the distribution of Finnish grasslands was studied and grassland patterns were further examined from the biodiversity viewpoint by means of case studies. A database containing grassland habitats in 10 m resolution was created using digital land use data and the nationwide abundance of grasslands was studied in 100 km^2 grid squares. The occurrence of traditional rural biotopes in the regional grassland networks and their relation to general land cover was studied within six drainage basins. Using species atlas data recorded in the 100 km^2 grid system, the relationships between the nationwide occurrences of two butterfly and four bird species and agricultural land use were examined.

The main questions of the study were: (1) How are grassland habitats distributed in Finland and what factors are correlated with the observed patterns? (2) What is the occurrence and spatial location of traditional rural biotopes in regional grassland networks in various agricultural landscapes? (3) Is there a spatial relationship between the occurrences of the studied species and the abundance of grasslands and arable land?

Background

Characteristics of the Finnish landscape

Although Finland is generally a low-lying region, the topography varies widely in a small scale. The main part of the relief results directly from the crystalline ancient bedrock (Seppälä 1986; Simonen 1990). The most common deposit type is compact basal till that often forms a basis for other deposits. Hummocky moraines, eskers, deltas, and ice marginal and interlobate formations impart unique characteristics to the landscapes. Extensive fine-sediment deposits are found mainly in southern and western Finland (Fig. 1). Peat deposits are abundant particularly in western and northern Finland. Land uplift continually exposes new land in coastal areas, especially in the Bothnian Bay (Kujansuu & Niemelä 1990).

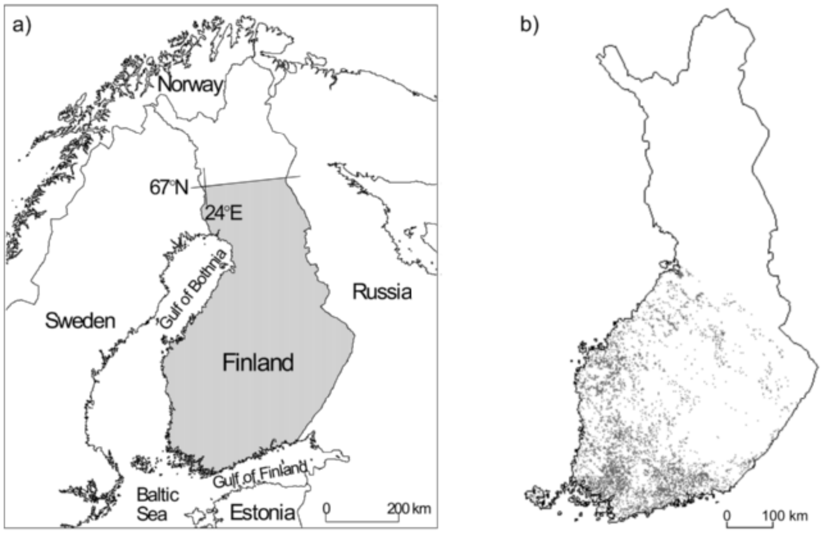

Fig. 1. a) The location of the study area in Finland (shaded in grey) and b) the distribution of fine sediment soils (silt and clay).

Finland belongs to the cold temperate climate zone with cool summers (Tuhkanen 1984). The mean annual temperature is highest in south-western Finland, decreasing towards the north-east. The length of the growing season (mean daily temperature > 5 °C) varies from 180 days in south-western Finland to 100 days in northern Lapland (Helminen 1987). Rainfall is rather evenly distributed throughout the seasons. The mean annual precipitation ranges from 400–450 mm along the western coast and northern Finland to 700–750 mm in parts of southern and eastern Finland (Solantie 1987).

Finland is located mainly in the boreal coniferous vegetation zone. Only the most south-western part of the country is situated in the hemi-boreal zone. The southern boreal zone covers southern and central Finland and parts of eastern Finland and the western coast. The middle boreal zone includes most of western Finland and parts of eastern Finland, whereas northern parts of Finland are mainly situated in the northern boreal zone (Ahti et al. 1968). Finnish landscape is largely dominated by forests and mires (Hämet-Ahti 1988; Ruuhijärvi 1988). Agricultural and horticultural land cover 7.3% of the total area of Finland (MAF 2004b).

The history of grasslands in Finland

The first signs of cultivation and livestock husbandry in Finland date back to the Neolithic Stone Age (5100–1500 B.C.) (Carpelan 1999). The significance of agriculture increased during the Bronze Age (1500–500 B.C.) and slash-and-burn cultivation was practiced over wide areas of southern and western Finland in the Iron Age (500 B.C.–1300 A.D.). Arable cultivation was started probably before the end of Iron Age in south-western Finland (Huurre 1995; Vuorela 1999).

The period of old traditional agriculture in Finland extended from the historical era until the 1870s (Soininen 1974). In the beginning of the 19th century, arable cultivation was practiced generally in southern and western Finland, whereas most of eastern Finland was largely dependent on slash-and-burn cultivation. Agriculture was based on crop cultivation and livestock was kept primarily for manure to fertilize fields (Grotenfelt 1922; Soininen 1974). The availability of fodder during the long winter feeding period was a crucial factor for cattle numbers and thus also for crop cultivation. Fodder was collected on natural meadows and the meadow area was increased through forest clearances and lake drainages. In summertime, cattle grazed in forests and fallows and after mowing also in meadows (Linkola 1922; Soininen 1974).

Cultivation and grazing opened up and diversified landscape structure and created new habitat types, whereas before the establishment of agriculture the boreal landscape was altered mainly by natural disturbances, such as fires and storms. Different physical conditions regulating agricultural intensity led to varying regional landscape mosaics, ranging from more open agricultural regions to enclosed forested landscapes (Ihse 1995; Pykälä 2000). The traditional grazing system carried nutrients from meadows to arable land and created unique nutrient-scarce semi-natural grasslands associated with high species richness and a great number of specialized species (Alanen 1997).

A revolution in Finnish agriculture took place at the end of the 19th century. Resulting from the rapid population growth, continuous crop failures and the decreasing world market prices of cereals, the basis of agriculture was changed from crop production to stock-raising. As a major renewal, hay-making in arable land became common and sustained higher cattle numbers (Soininen 1974). In addition to forest clearances, new areas for fodder production were obtained by including the most productive meadows in the cultivation cycle. As a consequence, the area of semi-natural grasslands started to decrease rapidly (Linkola 1922; Valle 1951; Oksanen 2001).

The modernization of Finnish agriculture starting in the 1950s almost completely terminated traditional farming. Agricultural production intensified as a consequence of new machines, fertilizers and techniques. Agricultural policies favoured large farms specialized in crop cultivation, whereas traditional small holdings were paid compensation for fallowing and livestock slaughter. A marked change was the regional specialization of agriculture in southern and western Finland into crop production and in eastern Finland into dairy farming (Granberg 1989; Luostarinen 1997). The role of cultivated, artificially fertilized grasslands in dairy farming increased at the expense of semi-natural grasslands. Semi-natural grasslands situated in the most favourable agricultural areas were converted to arable land, and meadows of poorer regions became wooded by natural succession, or were afforested (Alanen 1997; Pykälä 2001).

In general, the total number of dairy cows and the area under hay and grasses has declined drastically since the 1960's (Tiainen 2004). Further, only the remnants of semi-natural grasslands created by traditional practices of animal husbandry are left in Finland (Vainio et al. 2001). During the time of Finland's EU membership, the agri-environmental support of EU has provided opportunities for biodiversity and landscape management on farms (Luoto et al. 2003b). Management of the remaining semi-natural grasslands is included in the national EU agri-environment program. Moreover, furthering and management of other open non-cropped rural habitats are considered as important measures sustaining agricultural biodiversity (MAF 2004a).

Material and methods

Creation of the grassland database

The grassland data was derived from the land use database of SLICES (Separated Land Use/Land Cover Information System) (Mikkola et al. 1999). SLICES is based on the joint use of geographic information of several organizations and the source data for the land use classes has been derived from various existing land use registers. The raster format SLICES land use database with 10 m resolution covering the whole of Finland was completed in 2000. The combination of various source datasets into a single database had required reclassification of data into SLICES land use classes, coordinate transformations and conversion of polygon format data into raster format (Mikkola et al. 1999). Overlapping problems of the land use classes resulting from the disagreement of different source data sets had generally been resolved so that geometrically more accurate data overrode more inaccurate data and newer data overrode older data.

The grassland database of this study was based on two SLICES classes, 'perennial grasses and meadows' and 'long-term fallows' derived from the Finnish Land Parcel Identification System and the Topographic Database, updated in 1998–1999. Perennial grasses and meadows consist of over five years old grasses, meadows and pastures used for agricultural purposes. Long-term fallows are classified in the system as arable land that has not been cultivated or utilized in other ways for at least five years and has not become wooded.

The grassland database was built using the ArcInfo 8.1 software (Esri 1992) and it covered mainland Finland and the inner archipelago south of 67° latitude (Fig. 1a). Northernmost regions and Åland were excluded from the analysis due to deficiencies in the data. In order to facilitate faster data processing, the data was generalized by eliminating all grassland patches less than 0.1 hectares. The grassland database was compared to digital 1:20,000 base maps and distinctively misclassified patches, such as forest patches classified as grassland were removed.

In order to distinguish ecologically the most valuable semi-natural grasslands, an existing spatial database containing traditional rural biotopes found in a nationwide inventory in 1992–1998 (Vainio et al. 2001) was used to complete the SLICES grassland data. Inventoried traditional rural biotopes consist mainly of various meadows, wooded pastures and grazed forests. Wooded pastures are biotopes characterized by a mosaic of tree groups and meadow patches. Grazed forests, excluded here from the analysis, were differentiated from wooded pastures in the inventory on the basis of ground vegetation characterized by forest species and denser tree cover (>35%) (Pykälä et al. 1994).

Traditional rural biotopes had been classified in the inventory on the basis of their recent status into nationally, regionally and locally valuable traditional rural biotopes (Pykälä et al. 1994) and these value classes were used in this study. In general, nationally valuable biotopes have been managed continuously mainly by mowing or grazing at least for the last 50 years and have particularly diverse species assemblages, often including nationally endangered and rare plant species. Regionally valuable biotopes are characterized by long-continued traditional or near-traditional land use, typical vegetation created by traditional agricultural practices and diverse species assemblage. In locally valuable biotopes, land use has ceased to be traditional and typical vegetation for traditional rural biotopes occurs often in small patches. National, regional and local biotopes can also include non-managed, partially overgrown areas where diverse vegetation has still been preserved.

In order to obtain a picture of the validity of SLICES grassland data, a field check of 401 grassland patches (other than inventoried traditional rural biotopes) was carried out in the summer of 2004. Grassland patches were selected randomly within southern, western, eastern and northern parts of Finland. Grasslands were checked for actual classification errors in SLICES data (for example misclassified forest and field areas). Moreover, the proportion of bush cover in grassland patches was estimated.

Other datasets

A spatial database of arable land was built similarly to the grassland database from SLICES land use data with 10 m resolution. The source data for arable land was based on the Finnish Land Parcel Identification System. Arable land is defined in the SLICES system as continually cultivated ground, including fields and not more than five years old fallows and cultivated grasslands (Mikkola et al. 1999). Furthermore, general land cover information was derived from a nationwide CORINE land cover database in 100 m resolution. The CORINE land cover data is based on satellite image interpretation completed with digital databases (FEI 2003).

Studied species

The reflections of grassland and arable land abundances on species distributions were studied using two butterfly species and four bird species. The species data were derived from the butterfly atlas (Huldén et al. 2000) and the bird atlas (Väisänen et al. 1998), in which the occurrence of both species groups were presented in 100 km^2 squares. Species data were digitized using ArcView software (Version 3.2, Esri, Redlands, CA, USA).

Both studied butterflies, *Coenonympha pamphilus* (Small Heath) and *Lycaena hippothoe* (Purple-edged Copper) are meadow species. *C. pamphilus* is a grassland generalist, living in all kinds of grassland areas, such as dry and mesic meadows, road verges and clear fellings. Larvae feed on grasses (Poaceae). *L. hippothoe* occurs in forest-sheltered, especially dry flower-rich meadows and also in river shore meadows and grassy slopes in the north. Larvae feed on *Rumex acetosa* and *Rumex acetosella*. Both species are common in southern and central Finland and occur more scarcely in northern Finland. Species abundances vary annually, but *C. pamphilus* appears to have declined especially in parts of western and eastern Finland and *L. hippothoe* in parts of southern and western Finland (Marttila et al. 1990).

Acrocephalus palustris (Marsh Warbler) and *Locustella naevia* (Grasshopper Warbler) represent farmland bird species feeding and breeding in successional semi-open agricultural land. The habitat selection of *A. palustris* contains lush bush vegetation in meadows, abandoned land and neglected gardens, and particularly moist brookside bushes. *L. naevia* breeds in meadows and abandoned arable land in bushes with dense grass undergrowth and is particularly abundant in cultivated areas located near coastal bays and lakes. *A. palustris* and *L. naevia* occur in southern and central Finland. *L. naevia* has bred in Finland already since the 19th century. *A. palustris* arrived in Finland in the mid-20th century from the south and southeast and has become more abundant and spread northwards ever since (Väisänen et al. 1998).

The occurrence of two bird species, *Crex crex* (Corn crake) and *Perdix perdix* (Gray Partridge) living in open agricultural land was also studied in relation to grassland abundance. *C. crex* lives in open hay fields, fallow fields and dry shore meadows in southern and central Finland. *P. perdix* breeds in bushy and weedy edges of large field areas and midfield islets in southern Finland and along the western coast. Intensification of agriculture has led to rapid decline of the populations of both species throughout Europe. *C. crex* has been particularly affected by nest-destroying harvest machines and the decline of meadows surrounding cereal fields. *P. perdix* is also affected by modern cropping practices as well as the by the decreased habitat quality of production fields (Väisänen et al. 1998; Meyer-Aurich et al. 2003). Both species have been classified as near-threatened species in Finland (Rassi et al. 2001).

Spatial analyses on the national scale

The spatial distribution of grasslands was studied in 100 km^2 grid squares and within drainage basin units. Grid squares were created using the ArcInfo generate function. Drainage basin units were based on the first level partition of Finland's water system areas (Ekholm 1993) and this GIS data was taken from a database of the Finnish Environment Institute. The proportion of grassland in grid squares and drainage basin units was calculated using the ArcInfo intersect function. The proportion of arable land derived from the SLICES database was also calculated in the grid squares.

The amounts of grassland and arable land in 100 km^2 squares were compared to the occurrences of butterfly and bird species. The coordinates of land use grids coincided with the grids of animals observed. The quantity and quality of butterfly observations collected in different parts of Finland varied considerably and there were no proper estimates of the survey activity in atlas squares. Therefore only observations after the year 1988 and observation squares included in the Butterfly monitoring scheme (see Huldén et al. 2000) were taken into account in order to reduce inaccuracies of data. By contrast, survey activity and nesting probabilities in squares were available for the bird atlas data. Well and satisfactorily surveyed atlas squares and the squares with certain, probable, or possible nesting were chosen for analyses. The northern limits of species distributions were taken into account in the calculations. The spatial analyses were carried out using ArcInfo intersect functions and the statistical relationships between species and habitat distributions were analysed using the SPSS-program (SPSS 2002).

Spatial analyses on the regional scale

The number, connectivity and type of traditional rural biotopes as well as land cover in four grassland-rich and two grassland-poor drainage basins were studied. CORINE land cover data was reclassified as 1) grassland, 2) arable land, 3) urban area, 4) forest, 5) mire, 6) bare ground and 7) water and was further complemented by the SLICES grassland database. Land cover proportions for drainage basins were calculated using ArcInfo intersect functions.

Landscape connectivity is determined by interactions between landscape spatial structure and the movement behaviour of species (e.g. the review of Tischendorf & Fahrig 2000). For connectivity analyses, a total of 11 traditional rural biotopes (meadows and wooded pastures), including 1 nationally, 3 regionally and 7 locally valuable biotopes were selected within drainage basins. Nationally valuable biotopes were not found in grassland-poor drainage basins, and therefore the total number of biotopes was 10 in these regions. Connectivity for selected traditional rural biotopes was measured using a distance-weighting scheme, in which the amount of grassland area was calculated within a user-specified threshold distance from a biotope patch. Following Hanski (1994), connectivity S is given by the sum of contributions of all grassland patches:

$$S_i = \sum \exp(-\alpha d_{ij}) A_j$$

where A_j is the area of grassland (in ares), d_{ij} is the distance between grassland patches i and j (in km*10). Connectivity was calculated for each traditional rural biotope patch up to five kilometres from the centre point using the Si program (Moilanen 2000). Because no specific species was studied, the parameter α was given a value 1. The exponential function gives more weight for the patches, which are close to the focal patch.

Results

The validity of grassland data

Field checks showed that classification of the SLICES data was relatively accurate. Out of 401 grassland patches 1.7% turned out to be urban green cover, 1.6% grassy clear cuttings and 0.7% former grazed forests. Moreover, 2.7% of grassland patches carried planted young trees and 0.5% of patches were ploughed. Otherwise, field checked grassland patches consisted mainly of old, cultivated grasslands and long-term fallows in accordance with SLICES classification.

Over half of the visited grassland patches were open habitats. One third of the patches had bush cover up to ten percent and approximately one tenth of patches had bush cover between 11 and 60% of the total area. Bushes were often found by the side of ditches, whereas the core of the patch was typically open habitat.

The characteristics of distribution patterns of grasslands

The proportion of grassland varied noticeably in different parts of Finland, and several grassland belts could be distinguished in 100 km^2 squares (Fig. 2a). Grasslands formed an almost continuous zone running from western Lapland through coastal areas to south-eastern Finland. Another wide grassland belt extended from northern Finland southwards along the eastern border. Furthermore, a noticeable grassland zone covered parts of southern and central Finland, and a diagonal grassland belt extended from eastern Finland to the western coast.

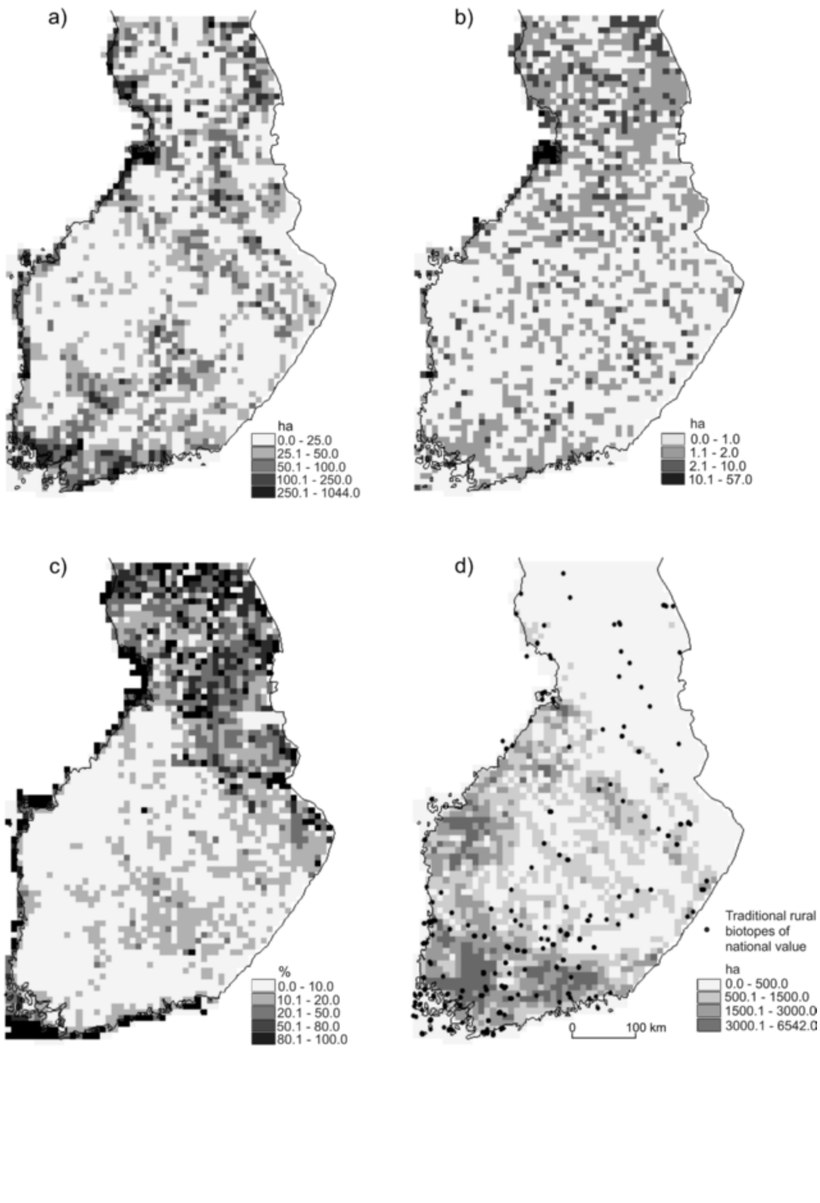

Fig. 2. The distribution of grasslands in Finland in 100 km^2 squares. a) The amount of grassland in hectares. b) The mean size of grassland patches in hectares. c) The proportion of grassland of all agricultural land in percentages. d) The occurrence of nationally valuable traditional rural biotopes (grazed forests excluded) (see Vainio et al. 2001) and the amount of arable land in hectares.

Over three quarters of the studied grid squares had 50 hectares or less grassland, and 3.5% of squares had no grassland. Grassland areas greater than 100 hectares were found in 5.7% of the squares and the maximum value was 1044 hectares in the northern Bothnian Bay region. In comparison, three quarters of the squares had arable land more than 100 hectares, and arable land was absent in 7.4% of the squares. Grassland patches were generally larger in northern Finland than in the south (Fig. 2b). Inventoried traditional rural biotopes (meadows and wooded pastures) (Vainio et al. 2001) accounted for approximately one tenth of the total grassland area.

Grasslands were found both in the main agricultural regions and in regions where agriculture has only a minor role. The Spearman rank correlation coefficient (r) between grassland area and arable land area calculated for 100 km^2 grid squares was 0.299 ($p < 0.001$). The proportion of grassland of all agricultural land was greatest in northern Finland and in coastal areas (Fig. 2c). A general absence of most valuable semi-natural grasslands (traditional rural biotopes of national value) was found in the most intensively cultivated regions of southern and western Finland (Fig. 2d).

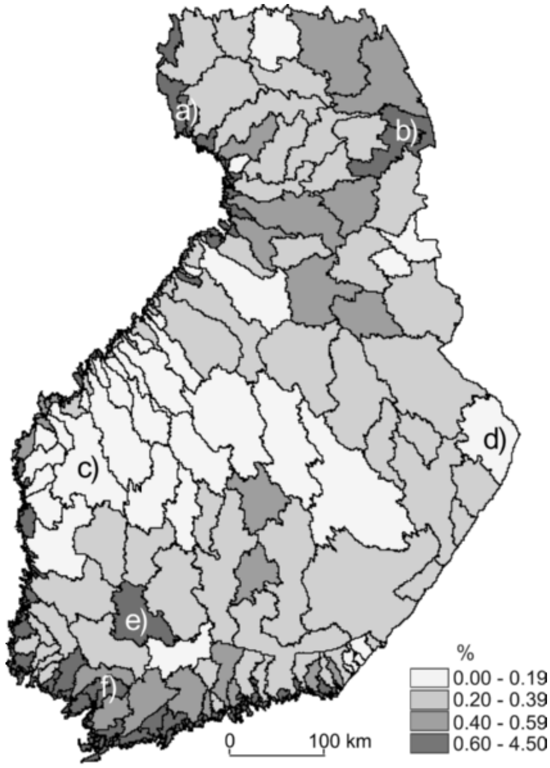

Fig. 3. The grassland proportions within drainage basins (in percentages) and the locations of six study areas. a) The lower course of Tornionjoki–Kaakamajoki, b) The upper courses of Vienan Kemi and Iijoki, c) Kyrönjoki, d) Koitajoki, e) Vanajavesi–Pyhäjärvi and f) Uskelanjoki–Halikonjoki (see Ekholm 1993).

Traditional rural biotopes and landscape properties

The grassland networks in six drainage basins located in different parts of Finland (Fig. 3) varied considerably in terms of the number and type of traditional rural biotopes, patch sizes, connectivity and surrounding land cover.

A northern drainage basin including the lower course of Tornionjoki and Kaakamajoki (Fig. 4a) was generally characterized by extensive forest areas (Table 1). Grasslands covered 1.5% of the total area and were generally found in river valleys. Traditional rural biotopes, with flood meadows as the most common type (Fig. 5a), were rather abundant, but mainly of local value. The studied traditional rural biotopes were located in the well-connected network of generally large grassland patches (Fig. 6a).

A drainage basin including the upper courses of Vienan Kemi and Iijoki, also located in northern Finland (Fig. 4b), was dominated by forests, mires and numerous watercourses and grasslands covered 0.8% of the area (Table 1). The characteristic traditional rural biotope type was fen meadows (Fig. 5b). The number of traditional rural biotopes was small compared to the area of the drainage basin. The grassland patches were large, but had a rather scattered location (Fig. 6b). Thus, traditional rural biotopes of the region were significantly isolated.

The Kyrönjoki drainage basin located in western Finland (Fig. 4c) was characterized by arable land and forested areas (Table 1). Grasslands covered 0.2% of the total area and were located mainly by rivers. Traditional rural biotopes, nearly all of local value, were rather few compared to the area of drainage basin and no nationally valuable biotopes were found in the region. The most typical biotope types were mesic meadows, shore meadows and wooded pastures (Fig. 5c). Selected traditional rural biotopes were poorly connected with the other, relatively small grassland patches (Fig. 6c).

The eastern Koitajoki drainage basin (Fig. 4d) was dominated by forests and mires and grass-

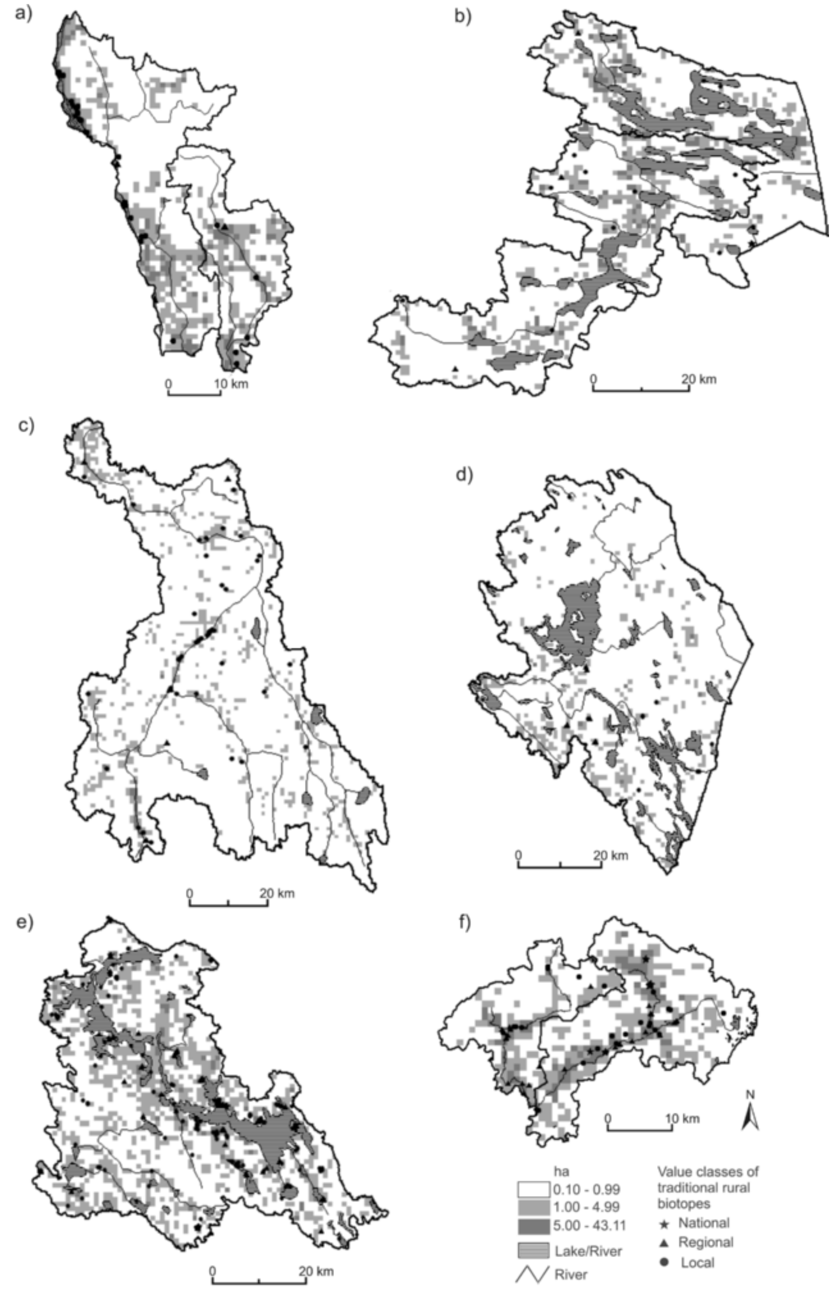

Fig. 4. The distribution of grasslands presented in 1 km² grid squares and the occurrence of traditional rural biotopes within six studied drainage basins. a) The lower course of Tornionjoki–Kaakamajoki, b) The upper courses of Vienan Kemi and Iijoki, c) Kyrönjoki, d) Koitajoki, e) Vanajavesi–Pyhäjärvi and f) Uskelanjoki–Halikonjoki.

Table 1. Land use statistics for the studied six drainage basins. MPS = mean patch size of grassland, Grass = Grassland, Arable = arable land, Urban = urban area, Bare = bare ground.

Drainage basin	Area km²	MPS ha	Grass %	Arable %	Urban %	Forest %	Mire %	Bare %	Water %	Total %
Tornionjoki–Kaakamajoki	1416	2.1	1.5	7.2	3.8	76.1	7.9	0.2	3.3	100.0
Vienan Kemi–Iijoki	3122	2.0	0.8	1.5	1.8	69.2	10.9	0.0	15.8	100.0
Kyrönjoki	4923	1.2	0.2	24.6	5.1	61.0	7.5	0.2	1.4	100.0
Koitajoki	3741	1.0	0.2	0.9	1.2	71.8	14.0	0.0	11.9	100.0
Vanajavesi–Pyhäjärvi	2759	1.1	0.8	17.7	11.2	55.2	1.2	0.1	13.8	100.0
Uskelanjoki–Halikonjoki	873	1.9	1.6	40.5	8.2	48.0	0.9	0.2	0.6	100.0

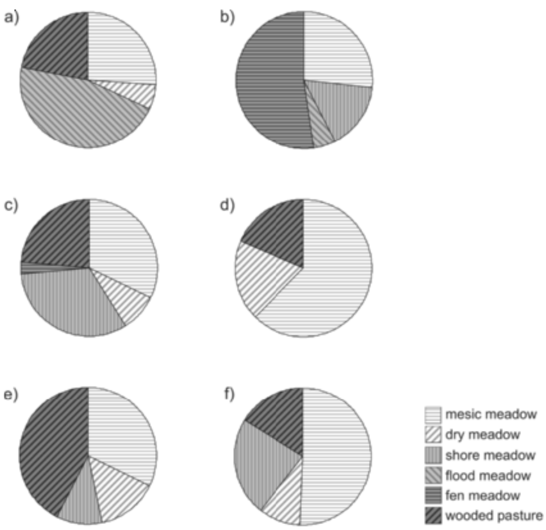

Fig. 5. The proportions of traditional rural biotope types in six studied drainage basins (grazed forests excluded). a) The lower course of Tornionjoki–Kaakamajoki, b) The upper courses of Vienan Kemi and Iijoki, c) Kyrönjoki d) Koitajoki, e) Vanajavesi–Pyhäjärvi and f) Uskelanjoki–Halikonjoki.

lands covered 0.2% of the total area (Table 1). Few traditional biotopes, with mesic meadows as the dominant type, were found in the region (Fig. 5d). Most of these biotopes were of local value and no nationally valuable traditional rural biotopes occurred in the region. The studied traditional rural biotopes were located in the disconnected network of small grassland patches (Fig. 6d).

The landscape of a southern Vanajavesi–Pyhäjärvi drainage basin (Fig. 4e) consisted of moderate amounts of arable and urban land, forests and large watercourses (Table 1). Grasslands covered 0.8% of the total area and were concentrated near to lakes. Compared to the area, the number of traditional rural biotopes was highest of all studied drainage basins and a considerable number of the biotopes were of national or regional value. The main biotope types were wooded pastures and mesic meadows (Fig. 5e). Traditional rural biotopes were located in the dense network of rather small grassland patches (Fig. 6e).

A drainage basin including Uskelanjoki and Halikonjoki (Fig. 4f) in south-western Finland was characterized by wide arable land areas (Table 1). Grasslands covered 1.6% of the total area and were located mainly by rivers. A high number of traditional rural biotopes were found in the region, over half of them classified as semi-natural grasslands of national or regional value. Mesic meadows and shore meadows were the most common biotope types (Fig. 5f). Selected traditional rural biotopes were highly connected with the other relatively large grassland patches (Fig. 6f).

The area and connectivity of traditional rural biotopes varied notably between drainage basins (Fig. 6g, Table 2), but less distinctively between value classes (national, regional, local) within drainage basins (Fig. 6). Some differences between value classes were found in Tornionjoki–Kaakamajoki and Vanajavesi–Pyhäjärvi, where the most valuable patches were the biggest ones. However, their connectivity was not generally greater than that of less valuable patches. Furthermore, in the Koitajoki drainage basin and partially in Uskelanjoki–Halikonjoki the most valuable traditional rural biotopes were either biggest in size or had the highest connectivity values.

Table 2. Connectivity statistics for the selected 10 or 11 traditional rural biotopes. FPS = focal patch size, NN = mean distance between the focal patch and the nearest neighbouring grassland patch, Conn = connectivity value of focal patches.

Drainage basin	FPS (ha)		NN (km)	Conn	
	mean	st dev	mean	mean	st dev
Tornionjoki–Kaakamajoki	11.8	23.2	0.4	20.9	25.1
Vienan Kemi–Iijoki	14.3	16.3	1.4	4.5	11.0
Kyrönjoki	2.2	1.5	0.5	7.3	7.5
Koitajoki	1.8	1.8	1.0	6.8	10.4
Vanajavesi–Pyhäjärvi	1.1	0.8	0.4	16.1	23.9
Uskelanjoki–Halikonjoki	4.3	6.5	0.3	29.6	29.3

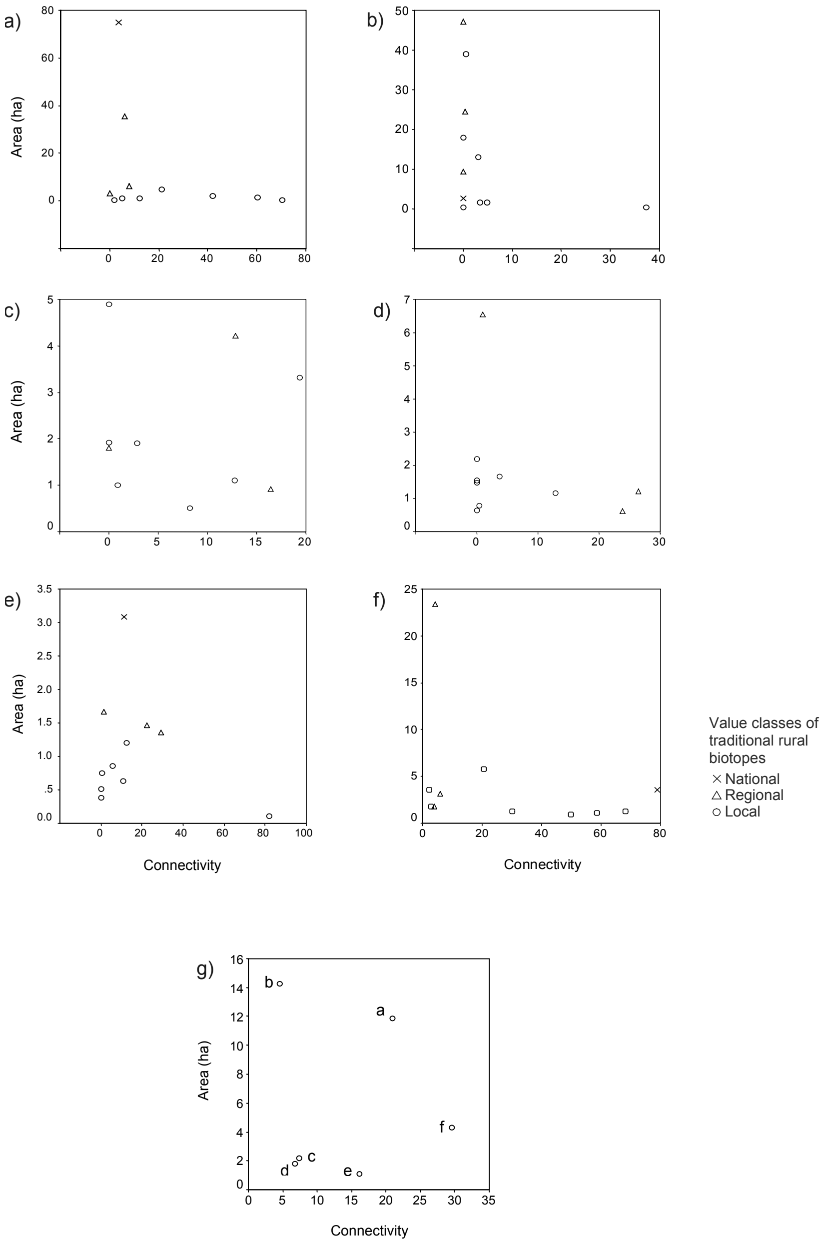

Fig. 6. The patch size and connectivity of traditional rural biotopes in six studied drainage basins. a) The lower course of Tornionjoki–Kaakamajoki, b) The upper courses of Vienan Kemi and Iijoki, c) Kyrönjoki d) Koitajoki, e) Vanajavesi–Pyhäjärvi and f) Uskelanjoki–Halikonjoki and g) the mean values of traditional rural biotopes for drainage basins. Note that the axes have different scales.

Studied species in relation to grassland and arable land

Butterflies

C. pamphilus and *L. hippothoe* were present in 32.3% and 28.4% of 776 investigated grid squares, respectively. Occupied squares had significantly higher amounts of grassland than unoccupied squares (Fig. 7a & b, Table 3). The occurrence of *L. hippothoe* was also significantly positively related with arable land area, in contrast to *C. pamphilus*. Both species occurred densely in grassland-rich areas of southern, central and eastern Finland. In the north, *C. pamphilus* occurred in the regions of Bothnian Bay with abundant grasslands. Both species were absent in several squares with high proportions of arable land in southern and western Finland (Fig. 8a, c & d).

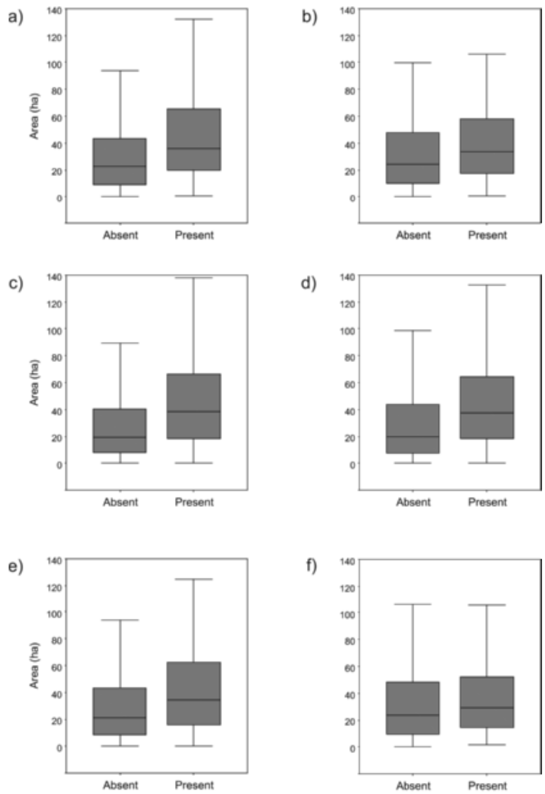

Fig. 7. The relationship between species presence and absence and grassland area in 100 km² squares. a) *C. pamphilus*, b) *L. hippothoe*, c) *A. palustris*, d) *L. naevia*, e) *C. crex* and f) *P. perdix*. The box represents the inter-quartile range, the line within the box shows the median, and the whiskers extend to the smallest and largest observations that are not suspected outliers.

Birds

The farmland edge species *A. palustris* and *L. naevia* were the most common of the studied bird species found in 30.8% and 33.1% of the grid squares, respectively. Both grassland and arable land were significantly more abundant in occupied than in unoccupied squares (Fig. 7c & d, Table 3). *A. palustris* and *L. naevia* occurred densely in southern Finland and in coastal regions with abundant grasslands. The densest occurrences of the species in central and eastern Finland coincided largely with grassland patterns. The species occurred sporadically or were absent in forest-dominated regions of western and eastern Finland. Moreover, they occurred scarcely in intensively cultivated regions of western Finland as well as in parts of agricultural areas in southern Finland. In northern Finland, species were found mainly in grassland-rich regions of the Bothnian Bay (Fig. 8b, e & f).

The distributions of *C. crex* and *P. perdix*, the species breeding in fields, differed greatly from each other. *C. crex* was present in 22.4% and *P. perdix* only in 10.1% of the studied squares. The occurrence of *C. crex* was significantly positively related to the amount of grasslands and arable land, whereas the occurrence of *P. perdix* was significantly positively associated only with arable land (Fig. 7e & f, Table 3). The spatial distribution pattern of *C. crex* in relation to grasslands and arable land resembled largely that of *A. palustris* and *L. naevia*. *P. perdix* was mainly present in squares with a great amount of arable land located in the main agricultural regions of southern and western

Table 3. Statistics for the relationship between butterfly and bird species occurrences and agricultural land use based on 100 km² grid-square analysis. p-values derived from the Mann-Whitney U-test designate the significance of the differences between presence (1) and absence (0) squares. p-values were corrected using the Bonferroni method. n.s. = not significant, ** $p < 0.01$, *** $p < 0.001$.

Species			Grassland (ha)			Arable land (ha)		
		n	mean	st dev	p	mean	st dev	p
C. pamphilus	0	525	36.8	60.9	***	1046.6	1105.1	n.s.
	1	251	54.1	57.6		1124.1	1027.9	
L. hippothoe	0	556	40.9	65.4	**	1007.7	1080.3	***
	1	220	46.1	45.3		1233.4	1066.9	
A. palustris	0	1008	32.9	60.0	***	933.4	1117.1	***
	1	449	51.2	52.1		1389.4	1202.2	
L. naevia	0	1106	32.6	41.1	***	717.1	1029.4	***
	1	547	54.9	80.6		1446.7	1193.9	
C. crex	0	1087	35.0	59.6	***	1021.1	1163.9	***
	1	314	47.0	46.2		1428.9	1145.7	
P. perdix	0	1383	36.5	43.8	n.s.	848.2	975.5	***
	1	156	56.3	119.3		2599.4	1416.9	

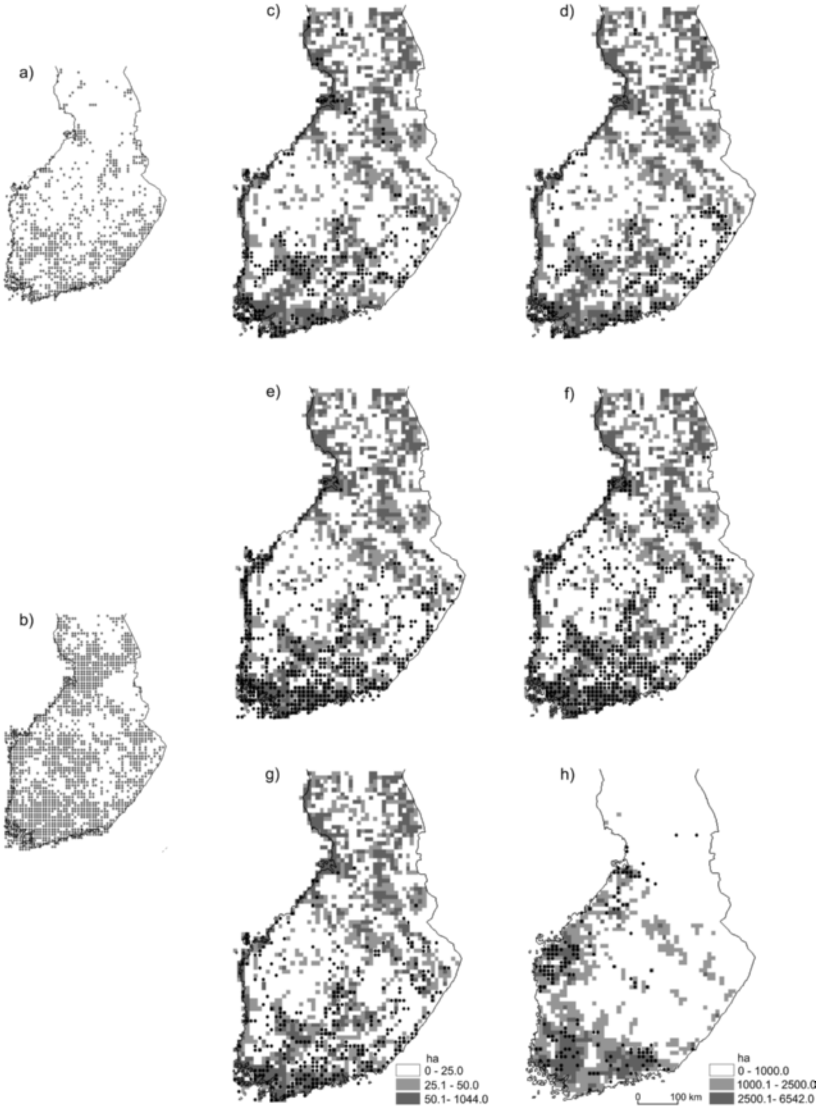

Fig. 8. The spatial relationships between studied species and agricultural land use patterns. a) Observation squares for butterfly species and b) bird species. The occurrence of c) *C. pamphilus*, d) *L. hippothoe*, e) *A. palustris*, f) *L. naevia* and g) *C. crex* in relation to grassland area (ha/100 km^2) and h) *P. perdix* in relation to arable land area (ha/100 km^2).

Finland and in the Bothnian Bay region (Fig. 8b, g & h).

Discussion

Regional distribution of grasslands in the Finnish landscape

The abundance of grasslands varied greatly in different parts of Finland. Grasslands were generally scarce in parts of southern and western Finland. In these regions, favourable physical conditions, such as mild climate, flat topography and fine-sediment soils have promoted intensification of agriculture (see Alalammi 1994; Palomäki & Mikkonen 1999). Regions with high cover of grasslands were generally characterized by varied topography, which has led to smaller field sizes and more mosaic agricultural landscapes compared to easily cultivated fine-sediment plains (e.g. Luoto 2000). As a special case, land uplift processes have created a unique grassland pattern in western coastal areas. Land uplift is particularly rapid in the Bothnian Bay region, as much as 8 mm per year (Kakkuri 1990). As the land rises, the bottoms of long, sheltered reedy bays gradually turn into coastal grasslands. However, the expansion of reeds due to eutrophication and natural succession makes these grasslands rather instable habitats (Vainio et al. 2001).

Physical conditions have traditionally determined the interactions between nature and agricultural land and have created the traditional landscape structure of Europe (Jongman 2002). However, agricultural land use today, and thus the present distribution of grasslands, is determined to a growing degree by economic conditions, cultural and social aspects and agricultural policies (Ihse 1995; Jongman 2002). Agricultural landscapes of southern and western Finland, characterized by relatively monotonous field plains, share similar biodiversity problems with Western European agricultural regions. Large crop cultivation areas often have only few grasslands. Moreover, in the western regions characterized by effective dairy farming, grasslands are continually renewed. In other words, rural habitats of different age and structure are generally lacking. Agricultural subsidies directed to such favourable cultivation regions further intensify the development (Jongman 2002; Robinson & Sutherland 2002; Waldhart & Otte 2003).

The number of dairy farms grows eastwards and northwards, which is naturally reflected in the occurrence of various grassland habitats. Further, the occurrence of non-renewed grasslands may partially reflect the decrease of agricultural activities. Small-scale dairy farming is diminishing to a growing degree as production is concentrated on economically more profitable larger farms and as the current farmer population ages (e.g. Pyykkönen 2001). For example, between 1990 and 2000 the number of dairy farms decreased by about 50% (TIKE 2002). Agricultural marginalization, affecting in a larger context mainly northern and eastern Europe, does not have a positive effect on biodiversity in the long run (Pärtel et al 1999; Norderhaug et al. 2000). Although the area of non-renewed grasslands first increases in the landscape, the grasslands will eventually revert to forest if they are not adequately managed (Luoto et al. 2003a; Waldhart et al. 2003). In other words, semi-open mixed farm landscape will become more enclosed, forested landscape at the expense of the diversity of agricultural habitats and species (Ihse 1995).

Traditional rural biotopes in the agricultural landscape mosaic

The occurrence of traditional rural biotopes as a part of grassland networks varied considerably in different parts of Finland. Traditional rural biotopes can be considered as diversity "hot spots" in the grassland network (see Vainio et al. 2001). They contribute regional biodiversity, providing essential habitats for specialised species and act as essential source populations in depleted agricultural landscapes (Duelli & Obrist 2003). Further, other grasslands enlarge the non-crop habitat selection and can provide important dispersal routes in the landscape (Steffan-Dewenter & Tscharntke 1997).

Well-connected grassland networks containing abundant traditional rural biotopes were found in three studied drainage basins located in northern and southern Finland. In Tornionjoki–Kaakamajoki previously widely mowed and grazed flood meadows, once cleared from bushes and grassy flood forests (Cajander 1909; Kalliola 1973), have been partially preserved in the landscape along with cultivated grasslands. The Vanajavesi–Pyhäjärvi region has long traditions of successful, versatile agriculture (Maisema-aluetyöryhmä 1993), and rather numerous wooded pastures and meadows are still found in the landscape. The Uskelanjoki–Halikonjoki drainage basin represents a special case in Finland. Agri-environmental support and successful restoration projects have increased the area of various semi-natural grasslands located in topographically steep, economically marginal river valleys surrounded by intensively cultivated fine sediment plains (Luoto et al. 2003b). From the metapopulation point of view, these regions represent landscape mosaics with high biodiversity values (Hanski 1998).

Disconnected grassland networks including few traditional rural biotopes occurred in three drainage basins in northern, eastern and western Finland. Vienan Kemi–Iijoki and Koitajoki were both forested, sparsely settled drainage basins affected by agricultural marginalization. In Vienan Kemi–Iijoki, half of the traditional rural biotopes were fen meadows that are typically less species-rich than drier meadows, and the relatively high proportion of grasslands in the region results from the large and scattered non-renewed cultivated grasslands (see Maisema-aluetyöryhmä 1993). In Koitajoki, scarce, but species-rich dry and mesic meadows have been preserved in the rather enclosed forested landscape. In the Kyrönjoki drainage basin the intensification of agriculture in fine-sediment river valleys has resulted in a scarcity of traditional rural biotopes and grassland habitats in general (see Alalammi 1994). On the basis of metapopulation theory (Hanski 1998) these landscapes cannot maintain a diversity of agricultural nature as high as landscapes with well-connected grassland networks including several patches of semi-natural grasslands.

The number of traditional rural biotopes is rapidly decreasing and their quality has largely declined. The most valuable semi-natural grasslands are typically located in small-holdings owned by elderly farmers and are thus threatened by the end of management in the near future (Pykälä 2001). The maintenance of biodiversity in Finland requires the management and restoring of traditional rural biotopes on a large scale. However, this is naturally cost-demanding and can be difficult to accomplish. As mosaic agricultural landscapes with diverse habitat selection are crucial for the maintenance of biodiversity, it would be more preferable to direct the limited resources to traditional rural biotopes located in well-connected grassland networks than to isolated grassland patches (e.g. Dunning et al. 1992).

Grassland patterns and the distribution of species

The distributions of the studied butterfly and bird species were generally related to the grassland patterns. Moreover, a general absence of the studied species excluding *P. perdix* favouring large field areas was observed in the most intensively cultivated regions in southern and western Finland. These results are in accordance with other studies that have pointed out the impoverishing impact of agricultural intensification on diversity (Robinson & Sutherland 2002; Jeanneret et al. 2003a; Steiner & Köhler 2003).

The location and dispersal of butterfly populations strongly depend on flowering plants, and various meadows have been found to be the richest habitats for butterflies (Kuussaari et al. 2001). Further, butterflies need an appropriate landscape structure in order to be able to move between the habitat patches, and often require several habitats to complete their life-cycles (Jeanneret et al. 2003b). In general, the widespread decline of butterfly species in Finland and throughout Europe has been associated with the decrease of open, uncultivated land (Pitkänen et al. 2001). It has been noted that old, abandoned fields may partially compensate the scarcity of meadows for butterflies (e.g. Heliölä et al. 2000).

Farmland birds have in many cases been affected by the loss of the mosaic of pastures and field in agricultural landscapes (Tiainen & Pakkala 2001). The habitat requirements of birds are wider compared to several other species groups and birds use various open and semi-open grasslands as feeding and breeding habitats (Söderström et al. 2001; Barnett et al. 2004; Peach et al. 2004; Virkkala et al. 2004). Farmland birds breeding in bushes, such as *A. palustris* and *L. naevia* studied here, have benefited from the increase of abandoned successional agricultural land (Väisänen et al. 1998). Further, *C. crex* has recently recovered slightly in Finland, possibly due to the decreased intensity of agriculture in the neighbouring Baltic countries and in Russia and the establishment of non-cropped shelter zones on Finnish fields (Tiainen & Pakkala 2001). It has also been observed that *C. crex* is nowadays found more often on low-productive grasslands than on fields (Kunttu & Laine 2002). In contrast, *P. perdix* has been noted to benefit particularly from short-term rotated set-aside (Tiainen & Pakkala 2001), which was included in arable land in the classification system of this study.

The distribution of plant species was not examined in this study. The highest diversity of plant species is generally found in traditionally managed dry and mesic meadows in boreal agricultural landscapes (Pykälä 2000). A large part of grasslands studied here had earlier been subject to a rotation cycle and the development of vegetation in these areas strongly depends on the intensity of former arable management, which in turn affects the nutrient balance and seed bank (Hansson & Fogelfors 1998; Pärtel et al. 1999; Perner & Malt 2003; Waldhart & Otte 2003). The signs of former cultivation can be seen in a grassland patch even one century after cultivation has ended (Skånes 1991; Gibson & Brown 1992). Common plant species for meadows may disperse rapidly on grassland patches, but rarer ones are often missing. The proximity of well-preserved species-rich meadows enhances species dispersal (Dunning et al. 1992; Norderhaug et al. 2000; Pykälä 2001; Duelli & Obrist 2003). Maps of the studied agricultural landscapes reflect the different dispersal potentials of plant species from species-rich "hot spots" of semi-natural grasslands in the network of grassland patches (Fig. 4).

The main limitations of the species data were the large number of uninvestigated squares of the butterfly atlas and the lack of estimation of species abundance in the atlas squares. Furthermore, species distribution is driven by multiple factors acting on multiple spatial and temporal scales (Wiens 1989; Levin 1992). For example, the impact of climate on species distribution is particularly pronounced in large scale studies (Thuiller et al. 2004). Thus, the multivariate analysis including both climatic and habitat variables, as well as species abundances instead of presence/absence data would provide interesting information concerning the relationship between species distributions and environmental factors.

Advantages and limitations in using large spatial databases

Technical advantages and recent production of nationwide spatial databases have made significant contributions to biogeographical research (Johnson 1990; Goodchild 1994; Burnett & Kalliola 2000; Weiers et al. 2004). In this study, new information on the distribution of grasslands was produced by combining large databases with relatively high spatial resolution and detailed land use information. From a biodiversity point of view, these methods can provide effective tools and new insights for management and monitoring of Finnish agricultural landscapes.

However, the use of large databases does cause some problems. Because nationwide databases are usually created by combining different kinds of source data, they can be variable by quality and age, and even include classification errors. Thus, GIS users should be aware of these potential pitfalls and their influence on the studied distributions (e.g. Berry 1987). Here, the SLICES grassland data was based on two continually updated vector databases, the Finnish Land Parcel Identification System administered by the Ministry of Agriculture and Forestry and the Topographic Database produced by the National Land Survey of Finland. These databases include the most accurate information of the Finnish agricultural land use and terrain. However, the production of SLICES database naturally required compromises in resolving spatially overlapping land use classes of source data (see Mikkola et al. 1999) and these decisions are largely out of reach of the ordinary database user.

The field check of the grassland database carried out here showed that actual classification errors (e.g. clear-cuttings classified as grassland) were rather few. Thus, the data can be considered to represent rather reliably the distribution of grasslands in Finland. A more crucial potential problem in extracting habitats from land use databases is the disagreement between the desired habitat properties and the classification criteria of land use in the database. In this study, the SLICES classification system was suitable for the mapping of low-intensity grassy habitats, i.e. old grasslands and long-term fallows. However, in order to distinguish ecologically the most valuable semi-natural grasslands from other grassland habitats, it was necessary to use the database containing inventoried traditional rural biotopes. Furthermore, low intensity grasslands habitats are continually threatened by bush encroachment if not adequately managed and the information of open grassland habitats in the database may become obsolete rather rapidly especially in agriculturally marginal regions. In this study the main part of the grasslands were open or nearly open habitats. However, clear signs of bush encroachment were also observed, and so the correspondence between the information in the database and the real state of grasslands is continuously changing.

Conclusions

The distribution of grasslands in Finland was effectively mapped using a nationwide land use database. The increased production and availability of large digital spatial databases provide powerful possibilities for research and biodiversity management. However, classification errors, the age of data and particularly classification criteria of land use classes compared to aspired habitat properties may limit the usability of the databases and must be taken into account in habitat mapping.

The results showed great variation in the regional abundance of grasslands, due to physical conditions and various social-economical and historical as well as political factors. The results also indicated the positive effect of grassland abundance and the negative effect of intensified land use on the occurrence of the studied species living in various grassland habitats. Agricultural intensification in the most advantageous farming regions and the end of dairy farming in small-holdings in the near future threaten the existence of versatile agricultural landscapes with a diverse selection of grassland habitats and associated species. Thus, the maintenance of well-connected grassland networks including diversity "hot spots" of semi-natural grasslands is an essential, but demanding challenge in the management of Finnish agricultural biodiversity.

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