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LOCAL AND REGIONAL SCALE DETERMINANTS OF BIODIVERSITY PATTERNS IN BOREAL AGRICULTURAL LANDSCAPES

by

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ABSTRACT

This thesis examines the local and regional scale determinants of biodiversity patterns using existing species and environmental data. The research focuses on agricultural environments that have experienced rapid declines of biodiversity during past decades. Existing digital databases provide vast opportunities for habitat mapping, predictive mapping of species occurrences and richness and understanding the species-environment relationships. The applicability of these databases depends on the required accuracy and quality of the data needed to answer the landscape ecological and biogeographical questions in hand. Patterns of biodiversity arise from confounded effects of different factors, such as climate, land cover and geographical location. Complementary statistical approaches that can show the relative effects of different factors are needed in biodiversity analyses in addition to classical multivariate models. Better understanding of the key factors underlying the variation in diversity requires the analyses of multiple taxonomic groups from different perspectives, such as richness, occurrence, threat status and population trends. The geographical coincidence of species richness of different taxonomic groups can be rather limited. This implies that multiple geographical regions should be taken into account in order to preserve various groups of species. Boreal agricultural biodiversity and in particular, distribution and richness of threatened species is strongly associated with various grasslands. Further, heterogeneous agricultural landscapes characterized by moderate field size, forest patches and non-crop agricultural habitats enhance the biodiversity of rural environments. From the landscape ecological perspective, the major threats to Finnish agricultural biodiversity are the decline of connected grassland habitat networks, and general homogenization of landscape structure resulting from both intensification and marginalization of agriculture. The maintenance of key habitats, such as meadows and pastures is an essential task in conservation of agricultural biodiversity. Furthermore, a larger landscape context should be incorporated in conservation planning and decision making processes in order to respond to the needs of different species and to maintain heterogeneous rural landscapes and viable agricultural diversity in the future.

This thesis is a summary of the following articles, which are referred to in the text by their Roman numerals:

I Kivinen, S. (2005). Regional distribution and biodiversity perspectives of Finnish grasslands. *Fennia* 183, 37–56.

II Kivinen, S., M. Luoto, M. Kuussaari & J. Helenius (2006). Multi-species richness of boreal agricultural landscapes: effects of climate, biotope, soil and geographical location. *Journal of Biogeography* 33, 862–875.

III Kivinen, S., M. Luoto, M. Kuussaari & K. Saarinen (2007). Effects of land cover and climate on species richness of butterflies in boreal agricultural landscapes. *Agriculture, Ecosystems and Environment* 122, 453–460.

IV Kivinen, S., M. Luoto, R.K. Heikkinen, K. Saarinen & T. Ryttäri. Threat spots and environmental determinants of red-listed plant, butterfly and bird species in boreal agricultural environments (submitted manuscript).

CONTENTS

1. INTRODUCTION

Biological diversity, the variety of life, is essential for the normal functioning of ecological processes and plays a critical role in sustainable development (Purvis & Hector 2000). The widely recognized decline in biodiversity resulting from human activities requires urgent strategies towards reducing and preventing further losses (Sala et al. 2000). Biological diversity is unevenly distributed across space (Gaston 2000). The essence of maintenance of diversity is greater understanding of the factors and processes that create this variation from place to place. The achievement of this understanding requires efficient techniques for collecting, analyzing and modelling biodiversity information. These challenges can be approached through the concepts and methods of modern biogeographical and landscape ecological research, that provide versatile tools for studying and explaining patterns of biodiversity on multiple spatial scales.

1.1 Concepts of biogeography and landscape ecology

Biogeography is the study of past and present geographic patterns of species distributions and the processes underlying these patterns (Lomolino et al. 2006). The development of biogeographical theories traces back to von Humboldt's notable pioneering studies of geographic distributions of plants in the early 19th century (e.g. von Humboldt 1849–58). Further, e.g. Wallace's interdisciplinary writings explaining geographical distributions and diversification of taxa and biotas have contributed considerably to the major principles of biogeography (e.g. Wallace 1876). Biogeography started to develop from early descriptive studies into a quantitative science under the impact of the equilibrium theory of island biogeography presented by MacArthur and Wilson (1967). The theory proposes that the number of species in islands depends on the size and isolation of the islands and reflects a balance between the rates of immigration and extinction. This new perspective brought a theoretical and population dynamical aspect to biogeography and increased interest in studies of landscape mosaics in space and time (Spellerberg & Sawyer 1999).

Nowadays, the theory of island biogeography has been challenged and modified and the field of biogeography in general has been broadened (Lomolino 2000). Modern biogeography includes studies of all patterns of geographic variation in nature. The research encompasses biological features from the level of genes to entire communities and ecosystems varying across geographic gradients, including those of area, isolation, latitude, depth and elevation (Lomolino et al. 2006). Quantitative biogeography has several applications in the fields of conservation, sustainable use of living resources and environmental change (Spellerberg & Sawyer 1999).

The early interest in large-scale patterns of diversity has shifted towards finer scales during recent decades. Spatial considerations have played an important role in the development of theories of regional and local diversity (Ricklefs 2004). Innovations in this field have included e.g. metapopulation dynamics, focused on the persistence of spatially distributed populations (Levins 1969; Hanski 1998), source-sink relationships, in which 'sink' populations in poor habitats are sustained by immigration from 'source' populations in good-quality habitats (Pulliam 1988), and landscape ecology, particularly in the Anglo-Saxon world (Turner 1989).

Landscape ecology is a study of interactions of spatial patterns in landscapes on various scales and includes the biophysical and societal causes of landscape heterogeneity (Turner 2005). The theory and concepts of landscape ecology are based on the theory of island biogeography. The original idea of the factors affecting the patterns of species diversity in physical islands surrounded by ocean was transferred to the abstract level of heterogeneous landscape mosaics (Haila 2002). Landscape mosaics consist of distinct habitat patches embedded in a more or less hostile matrix, and corridors that link the patches together. In landscape ecological studies, spatial heterogeneity is approached through the concepts of composition, structure and patterns. The number and relative abundance of different types of patches forms the composition of landscape. Landscape structure refers to the components of landscape and their spatial configuration, whereas function involves different abiotic and biotic processes (Forman 1995). The landscape ecological approach provides tools e.g. for analyzing fragmentation and its effects on populations. Fragmentation results in habitat loss and habitat isolation, as connectivity between habitat patches decreases. In an ecological context, landscape connectivity depends both on the landscape structural characteristics, i.e. the distance between suitable habitat patches, and on species-specific dispersal ability. Fragmentation can have a major effect on the movement and persistence of species in the landscape (Turner 1989; Hanski 1999a; Opdam et al. 2003).

Scale is one of the main concepts of biogeographical and landscape ecological studies (Wiens 1989; Whittaker et al. 2001). The scale of study consists of two attributes: the unit of sampling and the extent, the geographical space over which comparisons are made. The unit of sampling can be defined in terms of 'grain or resolution' that is the size of the common analytical unit and 'focus' that is the area represented by each data point. Focus can e.g. represent the scale at which a mean is calculated (Scheiner 2003; Rahbek 2005). Because observations are always scale-dependent, different scales of study reveal different kinds of information concerning the distribution patterns (Rahbek 2005). For example, increasing scale of study may indicate more the ranges of species and the factors controlling large-scale distribution patterns, whereas a smaller scale of study can elicit local population patterns and their determinants. In the case of species richness, increasing scale of study results in a higher number of observed species per data point and in the study region as a whole (Rahbek and Graves 2000; Nogués-Bravo & Araújo 2006). Thus, the choice of scale can have a notable influence on the results of the study and its comparability to other works.

1.2 Spatial and statistical approaches to producing and analyzing biodiversity data

Comparison of diversity patterns in space and time promotes understanding of the underlying factors generating diversity and helps to select the best actions to maintain it. Biological diversity is a complex concept that in its broadest sense includes all biotic variation from the level of genes to ecosystems (Purvis and Hector 2000). This implies that no single parameter is capable of capturing all biological features of interest. Thus, the first theoretical problem in biodiversity analysis concerns what is actually to be measured. The second, more practical question is whether the preferred data are realistically obtainable (Sarkar & Margules 2002).

Biodiversity can be approached using surrogates that serve as indicators of the variation of diversity. At the species level, species richness (the number of species) is a widely used composite variable to describe communal and regional diversity (Gaston 1996; Gotelli & Colwell 2001). Furthermore, concentrations of rare species are often used in assessing the conservation value of a particular area (Eyre & Rushton 1989; Prendergast et al. 1993; Gaston 1994). Biodiversity hot spots, geographical regions with high numbers of species, have been adopted as an important concept in conservation strategies (Myers et al. 2000).

Unfortunately, spatial data on species distributions are often sparse. Furthermore, environmental factors determining patterns of species richness and the occurrence of rare species are insufficiently known. Acquiring data at the species level involves several practical and financial limitations, as it is impossible to carry out taxonomically, spatially and temporally exhaustive surveys in the study region. One intriguing, less data-demanding approach to obtain information of diversity patterns is the estimation of the species richness of a given taxon based on the species richness of another taxon (Sauberer et al. 2004). A growing number of studies have examined the coincidence of hotspots of different taxonomic groups, as well as of rarity hotspots, endemic hotspots and threat spots with rather inconsistent results (Prendergast et al. 1993; Dobson et al. 1997; Maes et al. 2005; Oertli et al. 2005).

The use of environmental surrogate measures and modelling techniques provide important tools to produce new information on distribution patterns (McCullagh & Nelder 1989; Yee & Mitchell 1991; Austin 2002; Luoto & Heikkinen 2003). In simple terms, models relate field observations of species to selected environmental explanatory variables. Quantification of species–environment relationships provides valuable information concerning the environmental determinants of distribution patterns. Furthermore, predictive modelling enables mapping of the potential distribution of species or habitats in unsurveyed sites, if spatially covering data of environmental explanatory variables are available (for review, see Franklin 1995; Guisan & Zimmermann 2000). These predictions can be utilized in conservation planning and selection of protected areas (Guisan & Thuiller 2005). In addition to serving as a tool in current biodiversity management, models can be used to assess the impact of climate, land cover and other environmental changes on species distributions.

The possibilities for the study of spatial patterns of biological diversity have increased tremendously during recent decades (Balram et al. 2004). Geographic information systems (GIS) have had a central role in the production, exploration, visualization and storage of spatially referenced data. GIS has developed from a computer cartography oriented basis into a powerful tool performing virtually any conceivable operation on data derived from maps (Burrough 2001; Goodchild 2004; Goodchild & Haining 2004). The benefit of GIS in analyzing spatial data is its ability to combine data from various sources on different spatial and temporal scales (e.g. Vuorela 2000). This has brought new perspectives to the examination of biogeographical and landscape ecological questions about how the patterns of different variables are related (Turner 1990)

Digital databases that can be analyzed using GIS methods have been produced at an increasing rate. Georeferenced data of the occurrences of species have been created from museum and herbarium collections, various registers and field observations (Krishtalka & Humphrey 2000; Saarinen et al. 2003). Such large-scale digitizing of data, creation of open access databases and the development of biodiversity informatics in general have made increasing amounts of baseline biodiversity data available for research communities (Soberón & Peterson 2004; Guralnick & Neufeld 2005; Neelakandan et al. 2006).

Similarly, advances in the field of remote sensing have enabled examination of the Earth's surface from different perspectives, resolutions and spectral dimensions. Remotely sensed data have been used to produce numerous land cover data sets describing physiographical characteristics of the surface environment from local to regional and global scales (Defries & Townshend 1999). For example, the first spatially consistent high resolution land cover database was created on the European level in the CORINE land cover 2000 project (Härmä et al. 2004). Space-born and air-borne remote sensing data have numerous applications e.g. in habitat mapping and production of environmental surrogates for biodiversity analyses. Operational production of remote sensing data provides opportunities to update environmental databases regularly and thus creates the basis for temporal continuity of biodiversity monitoring (Kerr & Ostrovsky 2003; Turner et al. 2003; Groom et al. 2006).

1.3 Characteristics of biodiversity in boreal agricultural environments

Habitat loss resulting from land use changes is one of the most significant causes of population extinctions (Hanski 1999b). As agriculture affects notable portions of overall terrestrial area, it has a significant effect on the availability of habitats and on biodiversity in general (Tscharntke et al. 2005). Agricultural practices have had a tremendous impact on landscape structure, habitat diversity and species distributions in the boreal vegetation zone. Cultivation and grazing originally opened up forest-dominated landscape that was otherwise altered mainly by natural disturbances, and created heterogeneous landscape mosaics consisting of various habitat types with a wide assembly of associated species (Ihse 1995). Today, the loss of agricultural biodiversity both on the species and habitat level is a major concern throughout Europe (Krebs et al. 1999). Negative changes in diversity derive from the major changes in agricultural practices and land use during recent decades (e.g. Benton et al. 2002; Robinson & Sutherland 2002). Agricultural land use has been traditionally dictated by biophysical factors. Nowadays, social-economical and political factors together with environmental restrictions are the most important determinants for agricultural developments and changing landscape diversity (Hietala-Koivu 2002; Jongman 2002).

Firstly, adoption of modern agriculture has resulted in intensification of agricultural land use particularly in favourable regions (Stoate et al. 2001). The effects of intensified farming practices include e.g. increasing size of arable fields, shortened crop rotation cycles and decreased crop diversity, increasing agro-chemical use, sub-surface drainage and machine-driven farming. Agricultural intensification results in a declining area of non-crop agricultural land, such as grasslands, fallow land and edge habitats, e.g. field margins. Further, landscape homogeneity increases as landscapes are simplified with a spatially and temporally limited number of land-use types (Matson et al. 1997; Tilman et al. 2002; Hietala-Koivu et al. 2004; Tscharntke et al. 2005). These changes have been widely reported to have a negative effect on farmland animal communities, such as plants (Weibull et al. 2003; Zechmeister et al. 2003), insects (Feber et al. 1997; Hutton and Giller 2003; Pekkarinen 2001; Pitkänen et al. 2001), birds (Krebs et al. 1999; Tiainen & Pakkala 2000; Donald et al. 2001) and amphibians (Bishop et al. 1999; Beja & Alcazar 2003). Secondly, marginalization and abandonment of agricultural land, particularly in remote areas, have also resulted in unfavourable changes in biodiversity (Fjellstad & Dramstad 1999; MacDonald et al. 2000). Like intensification, marginalization results in homogenization of landscape structure and vanishing habitat heterogeneity, as agricultural landscapes revert back to enclosed forested landscape (Ihse 1995; Jongman 2002).

Grasslands, mainly various meadows and pastures originating from traditional agricultural practices, are considered as key habitats of European agricultural environments. They are typically characterized by high species richness and a great number of specialized species (Kull & Zobel 1991; Pärtel et al. 1999; Norderhaug et al. 2000; Cousins and Eriksson 2002; Poschlod & WallisDeVries 2002; Pöyry et al. 2004; Pykälä et al. 2005). The cover of grassland habitats has largely diminished in Europe, resulting in significant losses of species (Fischer & Stöcklin 1997). The amount of grassland habitats has also declined dramatically in Finland during the past hundred years, due to the rapid decrease of small-scale dairy farming and associated grazing (Pykälä 2001; Luoto et al. 2003; Tiainen et al. 2004).

Approximately one fourth of all known species as well as red-listed species in Finland are associated with agricultural environments (Pykälä & Lappalainen 1998; Rassi et al. 2001). Thus, the recent negative developments observed in rural environments (Tiainen et al. 2004) call for examination of the main drivers of agricultural diversity and a search for efficient actions to maintain it. There is a great need for more information on the relative importance of different rural landscape elements for diversity and better understanding of the factors affecting variation in species richness in agricultural environments. Such knowledge will facilitate the development of agri-environmental schemes towards better and more cost-effective promotion of agricultural biodiversity in the future.

1.4 Aims of the thesis

This thesis contributes understanding of the production of new biogeographical and landscape ecological information and provides knowledge of the determinants of geographical patterns of diversity for multiple taxa (see Fig. 1). The main focus was on examination of biodiversity patterns and their determinants in agricultural environments. Specifically, the main objectives were:

1) To examine the production of new biogeographical information on distributions of habitats and species using existing digital databases.

2) To study the effects of different environmental and geographical factors on species richness and occurrences on various spatial scales.

3) To examine the regional variation of agricultural biodiversity in Finland and to determine the main environmental factors enhancing boreal agricultural biodiversity.

In the first paper, the nationwide distribution of grassland habitats in Finland was mapped in 10 km grid squares using existing land use data. Observed grassland patterns were examined in the light of historical and current agricultural practices and land use. The occurrence and spatial location of the most valuable grasslands, traditional rural biotopes in regional grassland networks, were studied on the level of drainage basins. Further, the relationship between the occurrence of butterfly and bird species of agricultural environments and agricultural land use was examined.

The second paper explored factors affecting species richness of multiple taxonomic groups in boreal agricultural landscapes. The study units consisted of landscapes of 0.25 km^2 in size, located in different agricultural regions in Finland. The relationships between species richness of plants, butterflies, day-active macromoths and wild bees and climate, biotope, soil and geographical location were analyzed using generalized linear mixed models (GLMMs) that can account for spatial correlations in data. The relative importance of environmental factors and geographical location were further assessed using the variation partitioning procedure.

The third paper dealt with the differing effects of land cover and climate on species richness of butterflies of agricultural environments with differing population trends. Generalized linear models (GLM) with land cover, climate and geographical location as explanatory variables were built for species richness of declining, stable and increasing butterflies recorded in 10 km grid squares. The relative importance of the explanatory variable groups and the explanatory power of individual variables were assessed using variation partitioning and hierarchical partitioning methods that are capable of tackling the collinearity problems of multiple regression models.

The fourth paper examined the geographical distribution and environmental determinants of red-listed plant, butterfly and bird species living in agricultural environments. Generalized additive models (GAM) that allow examination of complex response shapes were constructed for species richness of each group of species and for individual species with climate and land cover as explanatory variables in 10 km grid squares. Predictive modelling was used to create spatially covering information concerning the potential distributions of species and threat spots, concentrations of red-listed species, were determined using these predicted probabilities of occurrences.

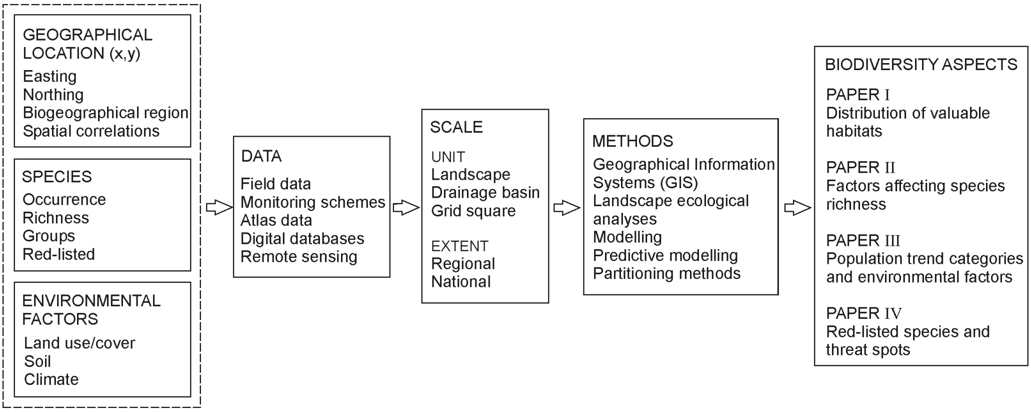


Figure 1. *A schematic illustration of the process for examining and explaining patterns of diversity.*

2. STUDIED AREAS

All analyses were carried out in Finland, located between 60° and 70° latitudes in northern Europe. The extent of the study area (Fig. 2) varied from agricultural regions in southern Finland (II) to the whole of Finland south of 67° latitude (I, III; excluding Åland in I) and the whole of the country (IV). The analytical units consisted of landscapes of 0.25 km (II), drainage basins (873–4923 km^2), 1 km^2 grid squares (I) and 100 km^2 grid squares (I, III, IV).

Finland belongs to the cold temperate climate with cool summers (Tuhkanen 1984). The mean temperature gradient runs from south to north. 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. Maritime influences balance the variation in temperature in coastal areas and the continentality of climate grows eastwards. Rainfall is rather evenly distributed throughout the seasons. The mean annual precipitation varies from 400–500 mm in the western coast and northern parts of the country to 700–750 mm in parts of southern and eastern Finland (Atlas of Finland 1988b).

Finland is located mainly in the boreal vegetation zone, although the most south-western part of the country belongs to the hemi-boreal zone (Atlas of Finland 1988a). The landscape is largely dominated by forests and mires. Arable land covers circa 7% of the total area (Tiainen et al. 2004). The most intense agricultural production and land use is concentrated in southern and western Finland on extensive fine-sediment deposits. The proportion of dairy farming grows northwards and eastwards. Excluding the most productive agricultural areas characterized by extensive field plains, agricultural landscapes in Finland often consist of patches of cultivated fields surrounded by coniferous and mixed forests (Alalammi 1994).

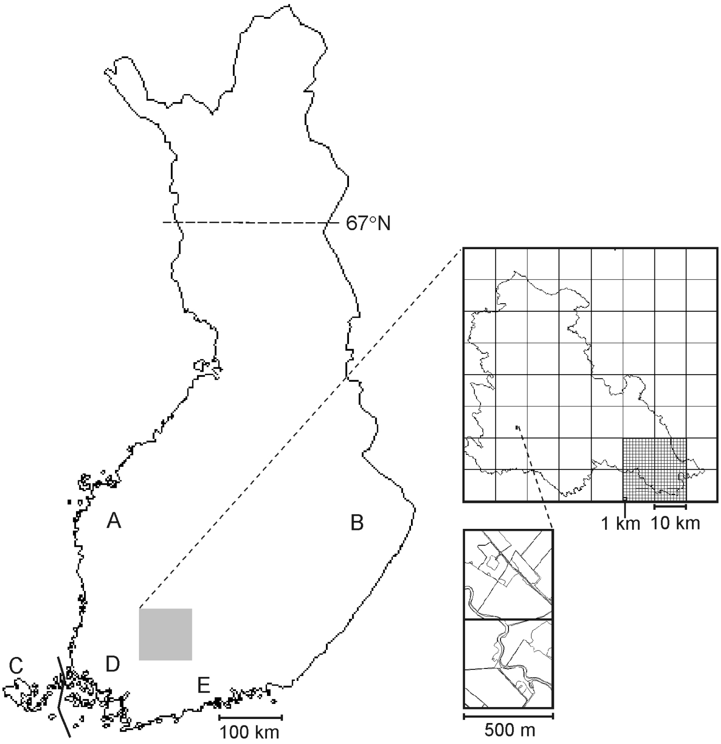


Figure 2. *The spatial scales of the studies. The grey-shaded area exemplifies the scales of the various analytical units: paired landscapes of 0.25 km^2 (II), drainage basins (I), squares of 1 km^2 (I) and 100 km^2 (I, III, IV). Agricultural areas studied in II: A = western Finland, B = eastern Finland, C = Åland, D = south-western Finland, E = southern Finland.*

The location of Finland in Fennoscandia and on the north-western edge of the Eurasian continent offers unique characteristics from the biogeographical point of view. Quaternary cold periods have had a major impact on the geographical distribution of species. The present-day species have recolonized Finland during the past 11 000 years after glaciation, and postglacial migration of species is still continuing (Atlas of Finland 1988a; Hewitt 1996; Hewitt 1999).

3. MATERIALS AND METHODS

3.1 Environmental data

Grassland data in paper I was derived from a SLICES (Separated Land Use/Land Cover Information System) database in 10 m resolution (Mikkola et al. 1999). I carried a field check of the validity of grassland data in the summer of 2004. Additional grassland data was based on digitized results of the nationwide inventory of traditional rural biotopes (Vainio et al. 2001).

Detailed information on local-level habitats (II) was derived from interpretation and digitization of aerial photography. Black-and-white aerial orthophotographs with 32 and 62 cm resolution from the period 1995–2001 were used in continental Finland and false colour aerial orthophotographs with 50 cm resolution from the year 2000 in Åland.

CORINE land cover 2000 data was used in the analysis in all the papers. An early version of CORINE data with 100 m resolution was employed in papers I and II. The analyses in papers III and VI were performed using the completed national CORINE database with 25 m resolution (Härmä et al. 2004).

Climate data (II–IV) was derived from a 10 km resolution grid based on interpolations of the Finnish Meteorological Institute (Venäläinen & Heikinheimo 2002). Soil data (II) were based on a database of Quaternary deposits with a resolution of 85 m (Geological Survey of Finland).

3.2 Species data

Species data in paper II was based on species censuses of plants, butterflies, day-active macromoths and wild bees carried out in continental Finland in 2001 (Kuussaari et al. 2004) and in Åland in 2002 (Schulman et al. 2005). Species were recorded along 50 m transect lines that were placed in uncultivated, open biotopes, mainly on different kinds of field margins and patches of semi-natural grassland. This data covered a total of 136 paired squares of 0.25 km^2.

Butterfly data in papers III and IV was derived from the National Butterfly Monitoring Scheme in Finland (NAFI) for the years 1991–2003. Field data in NAFI is based on observations of voluntary amateur and professional lepidopterists using a uniform questionnaire for the whole country (Saarinen et al. 2003).

Butterfly data in paper I were derived from the Atlas of Finnish Macrolepidoptera (Huldén et al. 2000). Plant data in paper IV were based on the atlas of threatened plant species (Ryttäri & Kettunen 1997). Bird data in papers I and IV were derived from the second bird atlas survey in Finland in 1986–89 (Väisänen et al. 1998). All atlas datasets and data in NAFI were recorded in a 10 km grid system.

3.3 Spatial and statistical analyses

All spatial analyses including digitization of species and environmental data, combining of spatial databases and calculations of habitat composition were performed using ArcView 3.2 and ArcInfo 8.1 software packages. The connectivity index for grassland patches (I) was calculated using the Si program (Moilanen 2000; Fig. 3).

The Mann-Whitney U-test was used to study the statistical significance of the relationship between species occurrences and land cover (I, IV; Fig. 3). Composite explanatory variables were created using principal component analysis (PCA) with Varimax normalized rotation in order to reduce multicollinearity among explanatory variables (II; Quinn & Keough 2002). The degree of spatial autocorrelation in the model residuals (III) was estimated by calculating Moran's I statistics and the significances of autocorrelation were estimated using Monte Carlo permutation tests using the program ROOKCASE (Sawada 1999).

The relationship between studied measures of biodiversity and environmental and geographical variables was quantified using multivariate modelling approaches (Fig. 3). Modelling was performed with the statistical software package R (R Development Core Team 2004) and S-plus (Version 6.1 for Windows, Insightful Corp.). Generalized linear mixed models (GLMM) were employed in II, generalized linear models (GLM) were used in III and generalized additive models (GAM) in IV. In IV, nationwide spatial predictions were generated and the accuracy of predictions was assessed using cross-validation methods. The advantage of GLMs compared to ordinary linear regression models is their flexibility. They allow non-normal response distributions and non-constant variance functions to be modelled. GLMs also allow transformations to linearity relating a combination of predictors to the mean of the response variable through a link function (Austin et al. 1984; McCullagh & Nelder 1989). GLMMs extend the GLM approach being able to control the spatial dependency in data arising from grouped observations (Pinheiro & Bates 2000). GAMs are non-parametric extensions of GLMs that estimate response curves with a non-parametric smoothing function and allow flexible description of complex species responses to explanatory variables (Hastie and Tibshirani 1990; Guisan et al. 2002).

Complementary statistical approaches were carried out in addition to general modelling in order to estimate the independent effects of (more or less) correlated explanatory variables (Fig. 3). Variation partitioning, i.e. partial regression analysis (Borcard et al. 1992; Heikkinen et al. 2004), was performed in order to examine the relative effects of groups of environmental and geographical variables (II, III). Hierarchical partitioning (Chevan & Sutherland 1991; Walsh & MacNally 2003) was carried out to study the explanatory power of individual variables (III). The alone and drop contributions of explanatory variables to the models (a single predictor in a univariate model and the removal of a predictor from the final model, respectively) were calculated in IV using the GRASP package (Lehmann et al. 2003).

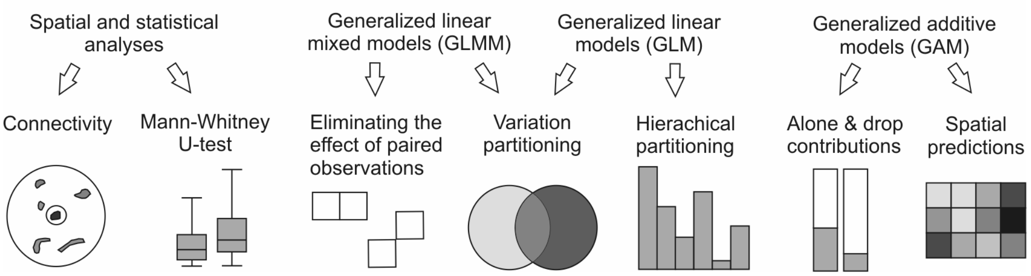


Figure 3. *Spatial and statistical methods employed in papers I–IV.*

4. RESULTS AND DISCUSSION

4.1 Opportunities and limitations in compiling new biodiversity information from existing data

The fundamental issue in biodiversity analysis is the ability to extract relevant information from the large quantities of data and to synthesize this information to create new knowledge. The applied use of existing databases is now becoming more common in landscape ecological and biogeographical research (Soberón & Peterson 2004; Groom et al. 2006; Luoto et al. 2006). These spatial data combined with modelling techniques provide new insights into studying the distribution and determinants of biodiversity.

Environmental data exist generally in a more consistent form than species data and have a crucial role in biodiversity analysis, as all biological features are directly or indirectly related to environmental conditions (Chapman et al. 2005). A new spatial database describing the distribution of grasslands in Finland was created on the basis of SLICES land use data (I). Sufficient spatial resolution, here 10 m, is essential in the examination of land use patches, such as grasslands, that are relatively small in size and often narrow-shaped. The spatially comprehensive grassland data enabled the nationwide mapping of habitats closely related to the maintenance of biodiversity (I). In addition, this database also made possible landscape ecological analyses of spatial relationships between the patches. The CORINE land cover 2000 database had a central role in papers II, III and IV providing explanatory habitat variables for modelling approaches. With its total coverage of the whole country and pan-European context, relatively high spatial resolution and free access, the CORINE land cover 2000 dataset has opened enormous opportunities to biogeographical and landscape ecological studies. Most importantly, it harmonises the study designs and improves the comparability of the results between different studies.

It should be noted that applicability of these datasets depends on the user's requirements concerning the accuracy and quality of data. More detailed habitat data are often needed in local-level landscape ecological analyses (e.g. linear features) and acquiring this data often requires interpretation and digitizing aerial photos (II). Land use and land cover classes in databases are always based on compromises in classifications (Mikkola et al. 1999). Moreover, classification criteria do not always correspond with desired habitat characteristics. Here, grassland classes derived from the SLICES database were suitable for examination of non-crop open agricultural land in general, but did not provide information on the quality of these habitats (I). Thus, it was necessary to complement grassland database with another existing database containing spatially accurate information on the occurrence of traditional rural biotopes, the ecologically most valuable grasslands found in a nationwide field inventory. This implies that field investigations are still indispensable in the production of detailed habitat data.

Continuous updating of land use and land cover databases is essential in terms of accuracy and usefulness of the data. Some land cover types are more prone to land use pressures and areal changes than other types. For example, the area of grassland habitats has experienced historically rapid changes as they have been largely converted to arable land or afforested (Cousins 2001; Luoto et al. 2003). Furthermore, grasslands are continually threatened by bush encroachment and will eventually revert back to forest if they are not adequately managed. Clear signs of bush encroachment were observed in a field check of grassland data derived from the SLICES database (I). The updating of land cover databases is greatly facilitated by remote sensing techniques (Weiers et al. 2004). However, the changes in ecological value of grassland habitats (e.g. eutrophication) can be naturally evaluated only through field work.

Species represent true targets of biodiversity conservation and as much information of species distribution as possible should be compiled for representative descriptions of diversity patterns (Hortal & Lobo 2006). Analyses here were based on species data recorded in different surveys and monitoring schemes. These primary data collected over different spatial and temporal extents enabled examination of biological diversity from multiple perspectives. In addition to the analysis on the level of individual species and taxonomic groups (II, IV), species data gathered over long periods of time also made it possible to study species groups with different population trends (III; Kuussaari et al. 2007b).

All biological data sets are based on samples of the geographical space and are generally far from ideal (Williams et al. 2002). Systematic species censuses can be carried out only in relatively small scales of study (II), whereas species data covering large geographical regions are often based on volunteer observations not collected using standardized methods. Such occurrence data derived from non-systematic sampling (III, IV) are often geographically biased (Dennis et al. 1999; Dennis & Thomas 2000). Study effort, the time spent for observing species, can explain a notable amount of the variation in observed distribution patterns, as the total number of species recorded in the study unit increases with increasing number of visits (III). Moreover, the atlas data used here contained gaps in species observations, particularly in remote regions (III, IV).

The results showed that predictive modelling is an efficient tool for complementing existing datasets with spatially non-continuous information of species distributions (IV). Evaluation of models built for species richness and occurrence of red-listed species showed that their predictive accuracy was generally good. Red-listed species are often rare species that have low probabilities of detection in field surveys. In addition to filling the gaps in datasets, predictive modelling can also help to target more intensive field work as well as conservation strategies to regions with high predicted probabilities of occurrences of species (Guisan & Thuiller 2005; Araújo & Guisan 2006).

It should be noted that in addition to the selection of modelling scale (Wiens 1989; Guisan & Thuiller 2005), the performance of predictive modelling is partially affected by the geographical distributions (prevalence, latitudinal range and spatial autocorrelation) of modelled species (Luoto et al. 2005). Species richness data compiled from the occurrence data of relatively rare species with restricted/and or scattered distributions does not necessarily show clear spatial trends (IV: red-listed plants and butterflies). As a consequence, these patterns are more difficult to capture and predict compared to well-defined regions of species richness resulting from rather wide, overlapping geographical distributions of individual species (IV: red-listed birds). In contrast, the occurrence of individual species with geographically restricted distributions and high habitat specificity can be potentially modelled and predicted more accurately by certain environmental (habitat) variables than species with wide distributions along environmental gradients (Maggini et al. 2006; cf. Pearce et al. 2001; Luoto et al. 2005).

4.2 Patterns of diversity: the interplay of environmental and geographical determinants

Identification of factors underlying distribution of diversity has been under intense research during the past decade (e.g. Gaston 2000 and references therein). The results here (II–IV) showed that distribution of diversity is an outcome of various environmental and geographical determinants. The relative importance of different explanatory variables varies between the different scales of examination and between groups of species (II–IV). The effects of explanatory variables were often confounded, which can potentially hamper the detection of key factors driving the distributions. This calls for examination of the unique contributions of climate, habitat and geographical location to distribution patterns. From a methodological point of view, the results emphasize the importance of using additional statistical analyses (e.g. partitioning methods) that can handle correlated data, in addition to classical modelling approaches (Heikkinen et al. 2005).

The importance of climate in determining species distributions increases on broad biogeographical scales (Wright 1983; Turner et al. 1987; Currie 1991; White & Kerr 2007). In accordance with this, the results showed that climate is the major driver of species richness (II–IV) and the occurrence of individual species (IV) examined across relatively large geographical dimensions (400–1100 km from south to north). Growing degree days (annual temperature sum above 5 °C) and the temperature of the coldest month were the environmental variables with particularly high explanatory power. Growing degree days can be considered to represent the heat requirements of species (Skov & Svenning 2004), whereas the mean temperature of the coldest month is particularly related to low-temperature tolerance and over-wintering survival of organisms (Woodward 1990). The results here, together with earlier findings reporting climate as an important limiting factor for distributions of plants (Woodward 1987; Walther et al. 2002), insects (Hill et al. 1999; Addo-Bediako et al. 2000) and birds (Forsman & Mönkkönen 2003), suggest that on-going climatic warming is likely to have profound effects on distribution patterns in Northern Europe. Redistributions of species in their northern ranges have already been detected as they track changing climatic conditions (Parmesan et al. 1999; Thomas & Lennon 1999; Warren et al. 2001; Gian-Reto Walther et al. 2005; Davies et al. 2006).

Unlike temperature-related variables, precipitation has a minor effect on species richness and occurrence patterns (II–IV). This can result for example from the relatively weak humidity gradient in Finland. Furthermore, in previous studies precipitation has been reported to have only a minor effect on distributions of plants (Moser et al. 2005), butterflies (Turner et al. 1987; Luoto et al. 2006) and birds (Forsman & Mönkkönen 2003; Virkkala et al. 2005) in cold and wet climates. The opposite result has been obtained in regions experiencing periods of severe drought (Stefanescu et al. 2004).

As thermal conditions and general harshness of the environment determine the large-scale distribution of species, the distribution of suitable habitats further limits the occurrence of species within the region of suitable climatic conditions (Hill et al. 2002; Opdam & Wascher 2004). The results here showed that habitat (land cover as a surrogate measure) had an important role together with climate in explaining the distribution of diversity. The analysis both on the landscape level in 25 ha squares (II) and on the atlas scale in 10 km grid squares (I, III, IV) elicited three important factors related significantly to species richness and occurrences: the cover of grassland, the cover of arable land (negatively correlated with the cover of forest) and landscape heterogeneity (Shannon-Wiener diversity index in II; small-scale agricultural mosaic in III and IV; see further discussion of habitats in 3.3).

Landscape structure measured on two scales in the landscape level approach (II) had different effects on species richness. Firstly, local landscape structure (low-intensity agricultural land and/or forest-field gradient) measured within 25 ha squares had a significant effect on species richness of plants, butterflies and macromoths. This finding is in accordance with some earlier studies suggesting that the influence of landscape context on species richness extends over relatively small spatial dimensions (Weibull et al. 2000; Luoto et al. 2002; Krauss et al. 2003). Secondly, surrounding landscape structure (habitat diversity and forest-field gradient) measured within a 2-km-wide buffer zone was significantly related to the species richness of plants. This supports the increasing evidence that wider landscape structure also has an important effect on the persistence of populations (Hanski 1999b; Ouborg & Eriksson 2004; Piha et al. 2007). Unlike plants, species richness of insects was not significantly affected by surrounding landscape structure. However, it should be noted that pollinator insects vary in their mobility and habitat preferences, and the examination of individual species instead of the species richness of a whole taxonomic group could potentially reveal various effects of landscape structure on distributions (Hanski & Kuussaari 1995; Cook et al. 2001; Gathmann & Tscharntke 2002).

The results of the atlas scale studies (III, IV) emphasize the importance of examining different groups of species in order to acquire a diversified picture of the determinants of diversity. Different species perceive their environments on different scales and thus are likely to reflect different aspects of environmental determinants of diversity (Atauri & de Lucio 2001). Red-listed plant and butterfly species were mainly related to the cover of grassland (IV), whereas red-listed bird species were affected by various land cover types: small-scale agricultural mosaic, arable land and built environment. This reflects the fact that red-listed plant and butterfly species often have a relatively limited dispersal capacity and strict specialized habitat requirements. By contrast, birds as highly mobile species have notably broader use of habitat and are not dependent solely on one habitat type (Tiainen & Pakkala 2001).

In addition to various taxonomic groups, the analysis of species on the basis of population trends provides new insights into diversity studies (III). Climate is a fundamental driver of butterfly species richness in general (II–IV). This is particularly true in the case of butterflies characterized by increasing population trend, whereas species richness of declining butterflies was more significantly related to the land cover, particularly grasslands (III, IV), than that of increasing and stable butterflies. These findings indicate different ecological requirements of butterfly species. Increasing butterflies are often generalists with relatively broad habitat use, whereas many of the declining butterflies are specialists with strict habitat requirements (Kuussaari et al. 2007b). The results suggest that increasing butterflies can potentially gain the greatest advantage from improving climatic conditions. Declining species, with relatively low current habitat availability (I), have a weaker ability to expand their distributions with warming climate (Hill et al. 1999; Hill et al. 2001; Opdam & Wascher 2004).

The results of the partitioning methods revealed that geographical location plays a significant role in explaining diversity patterns (II, III). Geographic location can reflect the effects of several historical and current factors on species distributions (see e.g. Storch et al. 2003). Glaciation history, dispersal routes and barriers can have a notable impact on distribution patterns (Hewitt 1999). Here, south-eastwards and eastwards increasing trends of species richness (II, III) as well as eastern threat spots of red-listed species (IV) may be partially explained by land-connected eastern migration routes that allow dispersal from other parts of Eurasia (Taberlet et al. 1998; see also Mikkola et al. 1991). This implies that the geographical location of the studied areas should be taken into account even in landscape ecological studies.

Geographical location may also indicate the effects of habitat characteristics that explanatory variables derived from land cover databases cannot reveal. For example, more detailed information on the quality, management and spatial configuration of habitats (I) could potentially increase the explanatory power of land cover variables in comparison to the basic information of their coverage (II, III; Harrison & Bruna 1999). Further, geographical location can reflect the effect of historical land use on species distributions, which was not considered here. The effect of current and historical availability of habitat is not necessarily clear, because there is a time-lag between change in environmental conditions and change in populations (Tilman et al. 1994). Landscape must satisfy certain conditions in terms of number, size and spatial configuration of suitable patches in order to support long-term (meta)population persistence. Habitat loss and fragmentation can eventually result in the extinction of (meta)populations, but it takes some time following habitat loss before extinction finally occurs. From the conservation viewpoint, this may lead to an underestimate of the number of endangered species (Hanski & Ovaskainen 2002). In the light of this fact, many plant species, for example, may actually be remnant populations persisting from an earlier period of significantly better availability of suitable habitat, and current land use may have no relevance for their observed occurrence (Lindborg & Eriksson 2004; Helm et al. 2006).

The use of surrogate taxa as indicators of biodiversity has recently attracted considerable interest (Kerr 1997; Maes et al. 2005; Oertli et al. 2005). Significant correlations between the distribution patterns of different groups of species would facilitate efficient allocation of limited management efforts to critical regions with high conservation value. Here, geographical coincidence of species richness of different taxonomic groups ranged from weak to moderate (II, IV). The most notable spatial correlations were found between species richness of plants and butterflies. In general the results suggest that species richness of one taxonomic group is not a strong indicator of species richness of other taxonomic groups. This indicates that multiple regions should be included in conservation planning of different species groups.

4.3 The crucial role of versatile agricultural landscapes in maintaining biological diversity

Land cover plays an important role in explaining regional differences in Finnish agricultural biodiversity, together with climate and geographical location. The results showed that grasslands and the arable land–forest gradient as well as general landscape heterogeneity are the key land cover determinants of distribution patterns (I–IV; Fig. 4).

Although grasslands cover rather small areas in agricultural landscapes (I), they have a crucial role in enhancing the biodiversity of boreal agricultural environments (Luoto et al. 2001; Pöyry et al. 2004; Pykälä et al. 2005; Öckinger & Smith 2007). The results showed that grasslands had a positive effect on species richness of plants and butterflies on the landscape level (II), as well as on species richness of declining butterflies (III) and richness and occurrence of red-listed plant and butterfly species (IV) on the atlas scale. In other words, grassland habitats appear to have a positive contribution to overall species richness, particularly to the distributions of less mobile, threatened species of agricultural environments (e.g. Maes & Van Dyck 2001). The significance of grasslands for red-listed birds was not observed here, but has been reported e.g. in one study conducted on a notably smaller spatial scale (Virkkala et al. 2004). Landscape composition in threat spot grid squares of 10 km further emphasizes the strong connection between grassland habitats and threatened species associated with rural habitats. Threat spot squares with one, two or three taxonomic groups of red-listed species contain 3, 5 and 6 times more grassland habitats than other squares (see Fig. 4 in IV).

The relative proportions of arable land and forest largely define the general characteristics of boreal agricultural landscapes (Ihse 1995). The negative effect of the cover of arable land on richness and occurrence of plants and insects was observed both on the landscape level (II) and in the nation-wide examination (IV). Intensively cultivated agricultural landscapes often contain few grasslands (I). Further, extensive cover of arable land can signify intensified use of agricultural inputs (chemicals, pesticides, etc.) that have negative effects on plants and pollinator insects (Matson et al. 1997). A somewhat positive effect of arable land as well as of built-up areas was found for farmland birds (IV). This is likely to result from the versatile habitat utilization of these birds. Farmland birds studied here include species feeding and breeding on fields, open and bushy verges, forests and farmyards (Tiainen & Pakkala 2001; Virkkala et al. 2004). The positive effect of forest on species richness of plants and butterflies (II) and species richness of stable butterflies (III) can indicate for example the importance of sheltered forest edge habitats for the occurrence of species in agricultural landscapes (Dover et al. 1997; Söderström et al. 2001; Pywell et al. 2004; Kuussaari et al. 2007a).

Landscape heterogeneity, indicating habitat diversity on the landscape level (II), and small-scale agricultural mosaic on the atlas scale (III, IV) had a significant positive contribution to species richness of plants (II), butterflies (III) and birds (IV). Landscape heterogeneity in general indicates lower agricultural intensity in the region. Regions with diverse land use contain a wide selection of habitats and provide multiple resources for species with various ecological requirements (Benton et al. 2003). Heterogeneous agricultural landscapes with substantial proportions of important non-crop habitats are likely to contain well-connected networks of uncultivated patches that enhance the movement of species with relatively weak dispersal capacity, such as some plants and butterflies and can lead to more persistent populations (Hanski 1999a; Duelli & Obrist 2003). Agricultural intensification and specialisation, such as the decline of livestock farming and associated habitats, loss of ditch verges, pesticide use and mechanisation have been considered to be the major reasons for the decline of farmland birds (Tiainen & Pakkala 2001). The strong positive contribution of landscape heterogeneity to the occurrence of red-listed birds, together with earlier findings (e.g. Herzon & O'Hara 2007), suggests that lower agricultural intensity and versatile land use are the key factors in the maintenance of farmland bird populations.

The abundance of grassland habitats varies widely in different parts of the country (I). The most valuable grasslands, traditional rural biotopes, have an exceedingly high cover in the Åland islands, where traditional agricultural practices have been carried out until recently (Schulman et al. 2005). In mainland Finland, various types of grasslands are typically abundant in regions with versatile agriculture and varied topography. Well-connected grassland networks containing numerous 'hotspots' of traditional rural biotopes representing high biodiversity values (Hanski 1999a; Luoto et al. 2003; Opdam et al. 2003) were found e.g. in river valleys (Fig. 4 in I). Generally, the Åland islands represent one of the main concentrations of agricultural biodiversity in Finland together with some south-western and southern (particularly coastal) regions. In addition, some regions in south-eastern and eastern Finland and along the western coast have significant biodiversity values (Fig. 3 in IV).

The results emphasize that homogenization of landscape structure is a major threat to agricultural biodiversity. Homogenization has taken place in the easily cultivated fine-sediment plains in south-western and western Finland. These regions generally have an extensive cover of arable land and few grassland habitats. In particular, the most valuable traditional rural biotopes are located outside these areas (I, Fig 2d). The remaining valuable meadows and pastures are rather isolated in the (hostile) matrix of cultivated fields (I, Fig. 4), which has an unfavourable effect on species dispersal and persistence of populations (Turner 1989; Hanski 1999a; Opdam et al. 2003). The results showed that vast regions particularly in south-western and western Finland can be considered as 'cold spots' with generally low diversity values (Table 3 in II, Fig, 3 in IV).

Homogenization through the increasing forest cover and enclosing landscape structure threatens diversity particularly in eastern and northern regions experiencing agricultural marginalization. The large areas of grasslands in eastern and northern Finland may partially reflect agricultural marginalization rather than viable agricultural landscapes (Ihse 1995). The area of non-cultivated land first increases but will eventually revert back to forest if not adequately managed. Analogously to the intensively cultivated region, the remaining traditional rural biotopes are isolated within the (hostile) matrix of forest (Fig. 4 in I).

Conservation of agricultural biodiversity is a dynamic approach, unlike the protection of wilderness areas often aiming at intactness of pristine habitats (Mittermeier et al. 2003). Agricultural biodiversity strongly depends on various grassland habitats and mosaic landscape structures that are typical for traditional agricultural environments (Jongman 2002; Tscharntke et al. 2005). As a simple 'return to the past' is not possible, the key issue in conservation of rural biodiversity is the willingness to preserve landscapes and habitats created by land-use activities that are no longer current practice (Foster 2002). This often requires the continuation or reintroduction of traditional management activities and habitat restoration (Sutherland 2002; Foster et al. 2003). Moreover, in addition to the management of individual habitat patches, the development of agri-environmental schemes that operate more on the landscape level has a major role in promoting the existence of viable agricultural environments.

4.4 Themes for future research

In this thesis, the scale of the study, i.e. units of sampling and/or the extent of study area, varied between different papers. As there is no single 'correct' scale on which to examine biodiversity, different significant explanatory variables should emerge at different spatial scales (e.g. Levin 1992; Willis & Whittaker 2002). Therefore, a more detailed analysis of scale issues is an interesting theme for future research. This could be approached for example by examining (intensively) sampled species data at different grid resolutions. Modelling the relationship between species occurrence/richness and explanatory variables using finer and coarser grid cell sizes would further deepen understanding of the effect of the choice of scale on results and the relative importance of different factors at various scales of study.

Environmental variables acting on finer scales than explanatory variables included in the analyses of this research could further explain the distribution of biodiversity in agricultural landscapes. For example, there can be a large variation in the quality of agricultural habitats e.g. in terms of food resources, vegetation structure and composition. Information on agricultural practices, such as grazing, mowing and organic farming could notably improve the explanatory power of the land use data. Acquiring such data is naturally rather cost-demanding. However, detailed land use data collected over moderate spatial extents could increase the knowledge of the relative importance of local-scale factors on biodiversity patterns and support for example the development of agri-environmental schemes. Furthermore, analysing the configuration of agricultural landscapes at a more detailed level, such as taking into account the spatial arrangement of habitat patches and resistance of the matrix in the modelling could better reveal the functional effect landscape structure has on the distribution of species (e.g. Chardon 2003; Stevens et al. 2004).

In addition to examining various spatial scales, considering temporal scale in the analysis would promote the understanding of the distribution of present and future biodiversity patterns. Building models with explanatory variables gathered over multiple temporal scales could show the effect of historical environmental conditions on observed biodiversity patterns today (e.g. Lindborg & Eriksson 2004). Unfortunately, the availability of spatially comprehensive historical land use data in Finland is rather limited. Updating the land cover/use databases such as CORINE Land Cover 2000 will promote the availability of such time series in the future. Otherwise spatially comprehensive historical land use data and detailed information on habitats can be largely obtained only by digitization of old aerial photographs and maps.

It is essential to monitor the changes in species distribution in order to preserve biological diversity. For example, mapping the hot spots and threat spots are important tasks in conservation of biodiversity, but the locations of these concentrations of species are not static. Thus, it would be useful to detect changes in the spatial arrangement of the hot spots and threat spots and to assess their relative importance over time (Rutledge et al. 2001). This requires naturally continuous monitoring schemes for different taxa.

Simulation models can be used to create and examine potential land use and climate change scenarios and thus to predict the changes in biodiversity of agricultural environments (e.g. Topping et al. 2005). Different scenarios of future habitat availability and responses of different taxa on predicted changes could give an opportunity to react in time to negative land use developments in the critical areas for biodiversity. Incorporating easily measurable socioeconomic and political factors in the models would advance understanding of the dynamics of agricultural landscapes and provide useful information for land use planning and decision making processes. Furthermore, in addition to estimating the responses of species to the direct effect of improving temperature conditions, it would be beneficial to examine also indirect effects of climate warming on species distributions that act through the changes in agricultural land use, crop production and farming systems.

5. CONCLUSIONS

This study focused on the examination of local and regional scale determinants of biodiversity patterns in boreal agricultural landscapes using existing species and environmental data. In conclusion:

1) Existing digital databases provide vast opportunities for landscape ecological and biogeographical studies. Spatially consistent land cover data, in particular, have a strong potential use in habitat mapping, indirect mapping of species occurrences and understanding the species-environment relationships. Although field work has an essential role in collecting accurate ecological data, existing databases greatly enhance efficient targeting of conservation and management efforts to crucial areas. The applicability of different datasets depends on the required accuracy and quality of the data needed to answer the questions in hand.

2) Patterns of biodiversity arise from combined effects of climate, land cover and geographical factors (Fig. 4). Complementary statistical approaches that can tackle the correlated explanatory variables are needed in addition to simple multivariate modelling for deeper examination of the relative effects of variables and ultimately, key environmental determinants of distribution patterns.

3) Biodiversity analyses should be performed from various standpoints including richness, threat status and population trends of different taxonomic groups in order to provide better understanding of the factors underlying the variation in diversity. The determination of key landscape elements enhancing biodiversity should be based on the analysis of multiple taxonomic groups, because different species perceive the landscape on various scales and thus have different environmental requirements.

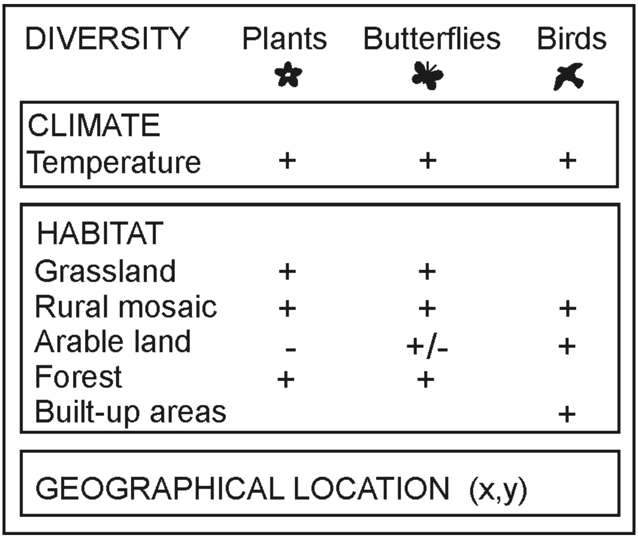
4) This study showed that the geographical coincidence of species richness of different taxonomic groups is rather limited. Thus, these results do not support the use of one taxonomic group as an indicator of species richness of other taxonomic groups in conservation planning. This further implies that multiple geographic regions should be taken into account simultaneously in order to preserve various species groups.

5) Agricultural biodiversity in boreal regions and in particular, distribution and richness of threatened species is strongly associated with various grasslands. The maintenance of grasslands, especially the most valuable meadows and pastures, is a key task in ensuring habitat availability for these species. Furthermore, heterogeneous agricultural landscapes experiencing less intense agriculture and characterized by moderate field size, forest patches and non-crop agricultural land provide multiple resources for species and greatly enhance the biodiversity of rural environments. Similarity of the results derived from various scales supports these conclusions (Fig. 4).

6) From the landscape ecological perspective, one of the major threats to Finnish agricultural diversity is the decline of connected grassland networks that sustain the movement of species and persistence of populations in the landscapes. Moreover, general homogenization of landscape structure resulting from intensification and

marginalization of agriculture poses a major threat to species associated with rural landscapes.

7) According to the results presented here, it is highly recommended to incorporate a larger landscape context in conservation planning and the development of agri-environmental schemes. In addition to maintenance and management of patches of focal key habitats such as grasslands, there should also be efforts towards increasing general heterogeneity of rural landscapes in order to respond to the needs of different species and maintain viable agricultural diversity in the future.



DIVERSITY	Plants	Butterflies	Birds
CLIMATE			
Temperature	+	+	+
HABITAT			
Grassland	+	+	
Rural mosaic	+	+	+
Arable land	-	+/-	+
Forest	+	+	
Built-up areas			+
GEOGRAPHICAL LOCATION (x,y)			

Figure 4. *Potential key determinants of agricultural biodiversity (plants, butterflies and birds). A positive contribution of the variable found in this study is marked with '+' and a negative effect with '-'.*

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