Biodiversity patterns and the importance of landscape-level land-use intensity and fragmentation of forest habitats in Europe

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Abstract

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Changes have been taking place in the landscapes of Europe for thousands of years. The aim of the studies presented in this thesis was to contribute to the understanding of the relation between human landscape changes and some aspects of forest-related biodiversity. A wide variety of spatially explicit data was used for the analysis and assessment of biodiversity, land cover and land use, together with climatic variables and topography. Differences in national economic conditions were found to affect landscapes with a common ancestry in the Carpathian Mountains, resulting in different trajectories of landscape development. These results highlight the importance of human land use on landscape composition. The method of comparing landscapes with different histories can be used to develop benchmarks for landscape change studies and policy evaluation. Clear relationships were found between land use parameters and functional diversity, species richness and species richness within functional groups. The usefulness of a meta-population model was evaluated by comparison with an area-based model for predicting the occurrence of the White-backed Woodpecker (*Dendrocopos leucotos*) in Poland. The meta-population model predicted the occurrence of the species better than the area-based model. The area-based model overestimated the occurrence of White-backed Woodpeckers, especially in areas with fragmented forests. The main conclusions of this study are that economic incentives shape landscapes; biodiversity patterns in Europe reflect the history of human landscape changes; and that land use intensity and spatial configuration, and the connectivity of suitable habitats are of importance for the predictive ability of landscape suitability models.

Keywords: macroecology, biogeography, land use, distribution patterns, functional diversity, biodiversity, meta-population dynamics, cultural landscapes, modelling

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Contents

Papers

This thesis is based on the following four papers:

I. Edman, T. and Angelstam, P.
Change in forest cover and open land since 1870 in four Carpathian landscapes and their current differences in landscape characteristics
Manuscript

II. Angelstam, P., Edman, T., Dönz-Breuss, M. and Wallis DeVries, M. F. 2004
Land management data and terrestrial vertebrates as indicators of forest biodiversity at the landscape scale
Ecological Bulletin 51: 333-349

III. Edman, T. and Angelstam, P.
Relationships between functional diversity of large forest vertebrates, climatic conditions, land cover areas and geographic position of European landscapes
Manuscript

IV. Edman T., Angelstam, P., Mikusinski, G., Roberge, J-M., Carlson A. and Gromadzki M.
Assessment of forest landscapes' conservation value using umbrella species requirements: Spatial evaluation of a meta-population model in Poland
Manuscript

Introduction

Large-scale assessments of biodiversity patterns are of importance in international efforts to reduce the loss of biodiversity (EEC, 1979, 1992; UN, 1992; Ceballos & Ehrlich, 2002; UN, 2002; EEA, 2004d). Knowledge about the driving forces and processes that shape biodiversity patterns is essential to achieve policy targets. On the global level, biodiversity, expressed as species richness, is highest near the equator and lowest at the poles (Mace *et al.*, 2005). Elevation influences biodiversity, with higher species richness in lowlands than in highlands and mountain ranges (Rahbek, 1997). The species richness is also higher in humid areas than in more arid regions (Diniz-Filho, Bini & Hawkins, 2003). Human land use changes these patterns both locally and globally (Ceballos & Ehrlich, 2002, 2006), as is evident from the distribution of threatened vertebrates, as well as in records of past extinctions, e.g. the North American Bison (*Bison bison*) in large parts of North America (Hornaday, 1889), aurochs (*Bos primigenius*) in Europe (Vuure, 2005) and wolves (*Canis lupus*) and the brown bear (*Ursus arctos*) in large parts of Europe (Breitenmoser, 1998) and North America (Mech, 1974; Pasitschniak-Arts, 1993).

Human land use often involves resource exploitation or the claiming of land for agricultural purposes, settlements or infrastructure. These activities cause many different changes in the global environment, at several levels. Agricultural practices lead to forest clearing and the eutrophication of inland and coastal waters, as well as the destruction of wetland and grassland habitats (Engström, Wadeskog & Finnveden, 2007). Animal husbandry competes with large herbivores for grazing (Herve, de Garine-Wichatitsky & Letessier, 1996), while forestry degrades the structure, composition and function of forest habitats (Angelstam & Dönz-Breuss, 2004). Infrastructure creates movement barriers (Kuehn *et al.*, 2007) and the emission of pollutants, and pollution in general reduces the carrying capacity of ecosystems, as well as the viability of individual species (Smith, 1974). Hunting and persecution affect distribution ranges, population sizes as well as sex and age composition (Milner, Nilsen & Andreassen, 2007). One of the most severely affected areas of the world regarding human land use is western Europe, where only a fraction of the original broadleaved forest remains (Mayer, 1984), the human population is largely urbanised, and the infrastructure is highly developed (Sanderson *et al.*, 2002).

In order to study biodiversity patterns at landscape, regional and continental levels in relation to human land use in Europe, the studies described in this thesis vary in geographical extent. In addition, data with different spatial and temporal resolution were used and several spatial and temporal methods of data analysis were applied.

Objectives and Scope

The aim of the studies presented in this thesis was to investigate biodiversity patterns in Europe in relation to human land use. Human landscape alteration and land use history are regularly considered important for biodiversity patterns at patch- and local levels, but are often neglected at regional and continental levels. Similarly, the legacy of past extinctions is often ignored in studies of biodiversity patterns at continental level. Biodiversity related to forests and forest-living vertebrates was studied, and structural, compositional and functional aspects of biodiversity were considered. This was performed at various levels, exploring both spatial and temporal dimensions of species distribution patterns and land use change.

Paper I investigates the land use change in four landscapes in the Carpathian Mountains, in Poland, Ukraine and Romania. The aim was to establish a common benchmark regarding landscape composition and to describe their different trajectories of land cover development. Historical maps, satellite imagery and field data were used to analyse the development of landscape composition and structure. This study illustrates the importance of historical sources of information for landscape assessment and the importance of land use history for the understanding of biodiversity patterns.

Paper II describes the biodiversity pattern in Europe regarding occurrences of larger vertebrate species requiring forest or woodland habitats. The focus of the study was on the influence of land use intensity and history at landscape level on the biodiversity patterns in Europe. Functional diversity and species richness in different functional groups were used as biodiversity proxies. Local knowledge on forest composition, land use history and species occurrences were evaluated. This paper illustrates the importance of the history and composition of landscapes for specialised species.

Paper III presents a study on the importance of climatic and geographic features for the biodiversity pattern in Europe, on the one hand, and the importance of features related to human landscape change and land use intensity, on the other. The focus of the study was on large vertebrate species living in forest or woodland habitats. Functional diversity and species richness in functional groups were used as biodiversity proxies. This study illustrates how land use intensity and land cover affect large-or-specialised-species differently from medium-sized-and-generalist species.

Paper IV describes the evaluation of a meta-population model for the assessment of forest landscapes with high conservation value at regional level. The meta-population model was compared with an area-based population model regarding the prediction of landscape suitability for the White-backed Woodpecker *(Dendrocopos leucotos)*, which is an umbrella species for deciduous forests in temperate Europe. This study contributes to the development of tools for biodiversity management and planning at regional level.

Background

Biodiversity

Structure, composition and processes are central attributes of biodiversity at all levels of organisation, from genes to biogeographic regions (Noss, 1990). Structure refers to the physical attributes of landscapes and habitats, i.e. rivers, forest types, coarse woody debris, snags and the spatial arrangement of these attributes. Composition is related to the richness and frequency of habitats, species and alleles. Processes include ecosystem function and disturbance regimes, ecosystem services like decomposition and genetic processes e.g. inbreeding or the evolution of genetic traits. Several approaches have been proposed to describe the complex differences in biodiversity between sites, regions and even biomes (Shmida & Wilson, 1985; Landres, Verner & Thomas, 1988; Noss, 1990; Ceballos & Ehrlich, 2006). Remote sensing techniques can be used to reveal the differences in structural components and landscape patterns (McGarigal & Marks, 1995) and, together with inventories of habitats and population censuses, provide measures of structural diversity at several levels. The most commonly used index of biodiversity is species richness (Magurran, 2004). Species richness relates to composition and recognises the occurrence of each species as being of equal importance to the complexity or diversity of the ecosystem. In order to reveal aspects of biodiversity related to processes, ecosystem integrity or ecosystem services can be considered. From this point of view, the number of species provides an incomplete estimate (Brian H, 1992; Walker, 1992; Petchey & Gaston, 2002; Reynolds, 2002). Since each species has a specific niche (Hutchinson, 1957) and these niches may overlap to varying degrees, it has been suggested that biodiversity indices based on the differences in niche exploitation or species richness within ecological groups, could be used as an alternative diversity measure, focusing on ecosystem processes rather than its composition (Petchey & Gaston, 2002). Structural, compositional and process-related aspects of biodiversity were analysed in the work described in this thesis. This was carried out at several levels of organisation, i.e. at the continental, regional, landscape and patch levels (Table 1).

Table 1. *The four papers and their relation to biodiversity aspects of structure, composition and process, as well as to different levels of organisation*

	Structure	Composition	Process
Continental	Paper II	Paper II Paper III	Paper II Paper III
Regional	Paper II Paper IV	Paper I Paper II Paper III Paper IV	Paper I Paper II Paper III
Landscape	Paper I Paper IV	Paper I Paper II Paper III Paper IV	Paper I Paper II Paper III Paper IV
Patch	Paper I	Paper I	

Macroecology

The concept of macroecology, e.g. distribution ranges, body mass variation and species richness patterns, has been applied to the study of large-scale ecological patterns on several scales (Brown & Maurer, 1989; Gaston & Blackburn, 2000). The size and shape of distribution ranges differ between species of different sizes and with different degrees of habitat specialisation. Brown & Maurer (1989) found that North American species differed significantly regarding distribution ranges, depending on body size. Large species showed distribution ranges following climatic gradients and latitudes, while the distribution of smaller species followed the larger rivers and mountain ranges. This pattern can be explained by the higher degree of habitat specialisation of smaller species due to energy constraints (*ibid.*). Two other generally observed patterns are that widespread species tend to occur at higher population densities (Hanski, 1982; Brown, 1984), and that large areas host more species than small areas (MacArthur, 1957). Hanski & Gyllenberg (1997) showed that these patterns are interconnected and could be explained by the same processes of local extinction and colonisation rates.

Biodiversity patterns in Europe have been investigated in relation to macroecological theories. Body mass variation in relation to climatic, geographic and vegetation index data has been investigated by e.g. Rodríguez, López-Sanudo, & Hawkins (2006) and Diniz-Filho *et al.* (2007), who found that larger species were confined to the northern and eastern parts of the European study area. Baquero & Tellería (2001) concluded that the gradient in species richness from western to eastern Europe could be related to a peninsular effect (Taylor & Regal, 1978). Several authors have analysed the patterns of species richness in relation to climate, e.g. (Diniz-Filho, Bini & Hawkins, 2003), while others have considered the importance of land cover in determining species richness patterns. Thuiller, Araujo & Lavorel (2004) reported that the descriptive but not predictive ability of bioclimatic models of species distribution was improved when land cover variables were used to describe residual patterns of the bioclimatic models.

European land use history

Thousands of years of agricultural practices and hunting activities have had a profound affect on the flora and fauna of Europe (Peterken & Game, 1984; Breitenmoser, 1998; Ceballos & Ehrlich, 2002, 2006). The development of agricultural practices led to deforestation for arable land, hay meadows and grazing grounds for cattle and sheep (Mayer, 1984). Trees were, however, kept as an important component of the archaic landscape, providing leaf-fodder during winter, important material for tools, building materials and fuel (Fritzbøger, 1994). The agricultural revolution, starting in the 18th century rapidly changed the composition and structure of pre-industrial cultural landscapes, and became a threat to biodiversity (Antrop, 2004). The demand for grain in the industrialised countries reached Eastern Europe in the 19thcentury (Powelson, 1994). The exploitation of these markets was dependent on the development of the railway system and other infrastructure for bulk transportation. Areas of Europe far from the rivers that drained into the North Sea and the Baltic remained less developed than the rest of Europe. This pattern is also evident in the distribution of cities in the 19th century (Bairoch, Batou & Chèvre, 1988) (Figure 1). Similarly, the demands for timber for shipbuilding and house construction grew in the 18th century and led to the exploitation of forests, starting at the shores of the North Sea and eventually spreading into Russia and the interior of Northern Scandinavia in the late 19th century (Bunte, Borgegård & Gaunitz, 1982; Bladh, 1995).

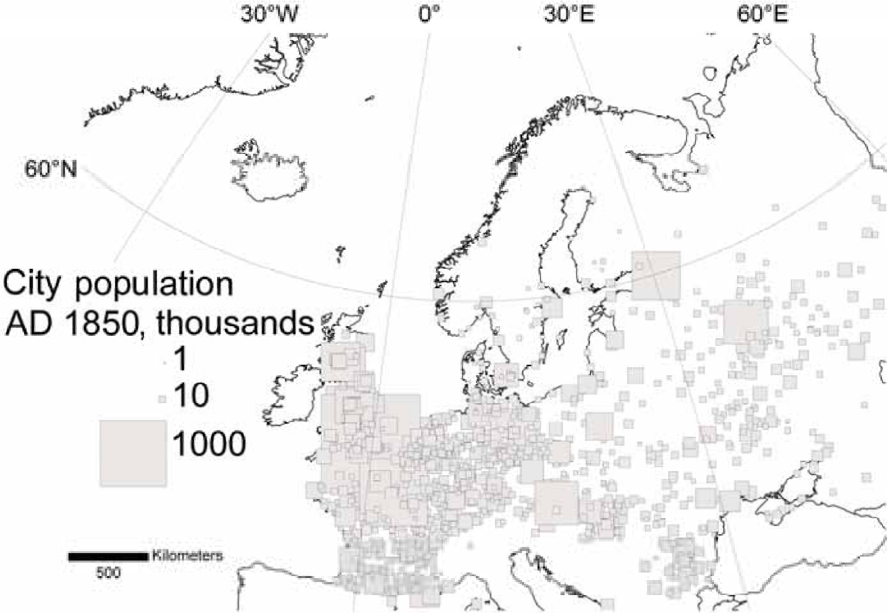


Figure 1. Urban population in various parts of Europe in 1850 illustrating the industrialisation and urbanisation process in Europe (Bairoch, Batou & Chèvre, 1988).

Study Areas

The Carpathian Mountains

The Carpathian Mountains were chosen for the study described in Paper I because of their unique landscape composition and diverse history of emerging nations, with fluctuating boundaries over the past centuries, although all with a common ancestry within the Habsburg Empire. The Carpathian Mountains are situated in central Europe and reach 2500 m above sea level.

Europe

The European continent was chosen for studies of large-scale biodiversity patterns and their relation to human land use intensity. The area described in Paper II comprises Europe from the Alps in the south, the Pyrenees in the west, to the Ural Mountains in the east (Figure 2). The study area described in Paper III encompasses the European Union (EU) from the Pyrenees to the Gulf of Finland, including the northern arc of the Carpathian Mountains and Hungary. Most of the area studied, especially the Atlantic and lowland broad-leaved forest regions and the Scandinavian boreal forest region, has been severely affected by recent and historical human land use (Mayer, 1984; Hannah, Carr & Lankerani, 1996).

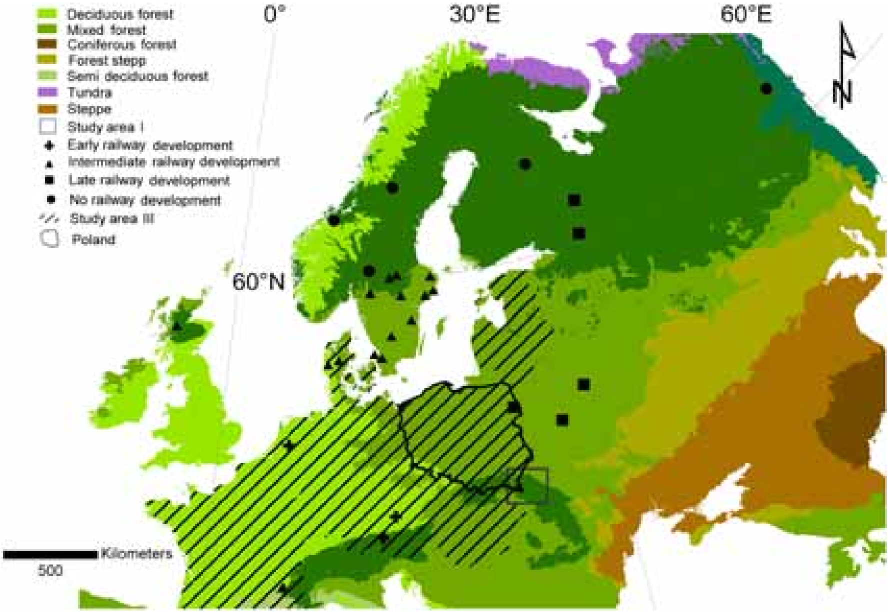


Figure 2. Biogeographic zones in Europe and the study areas described in Paper I (in the Carpathian Mountains), Paper II (northern Europe), Paper III (north central Europe) and Paper IV (Poland).

Poland

Poland was chosen for the study described in Paper IV due to the large differences between local landscapes, ranging from agricultural plains and fragmented and isolated forest patches, to large forest tracts in the peripheral and mountainous parts of the country. The forests range from extensive post-war plantations of Scots Pine (*Pinus sylvestris*) to landscapes where the abandonment of villages has led to large areas of young succession deciduous forest (Angelstam *et al.*, 2003). In addition, some remnants of forests with almost natural dynamics can be found in the eastern and southern parts of the country.

Materials and Methods

A wide variety of spatially explicit data was used for the analysis and assessment of biodiversity, land cover and land use, climatic variables and topography.

In the study presented in Paper I, 39 transects in the form of four equal squares of 500 x 500 m^2, arranged in a line, were placed so as to cover the areas from the bottom of the valleys (i.e. the villages) to the forest at the valley rim. Transects were arranged so as to give representative data from the different landscapes, and were surveyed with regards to semi-natural and cultural landscape features, in May 2003. Historical maps from ~1870, ~1910, ~1940 and ~1980, with scales from 1:50 000 to 1:288 000, and Landsat TM imagery were interpreted to assess the differences in composition of the landscapes through time.

For the biodiversity assessment described in Paper II, a questionnaire was sent to managers and scientists working in forest landscapes in different parts of Europe. The questionnaire focussed on the occurrence of large forest-dwelling vertebrate species and on the age and tree species composition of the landscape, as well as historical land use and land use change.

A biodiversity assessment is described in Paper III, based on the presence and absence of species according to the European Atlas of Breeding Birds (Hagemeijer & Blair, 1997) and the Atlas of European Mammals (Mitchell-Jones *et al.*, 1999). The species records were presented in Universal Transverse Mercator (UTM) grid cells, with sides of approximately 50 km. The geographic position, range in elevation (USGS, 1997), land cover variables (EEA, 2004c) and climate data retrieved at [http://www.grid.unep.ch/data/grid] and [http://www.cru.uea.ac.uk/cru/data/], were used as explanatory variables.

Paper IV describes the use of the European Forest Map (EFM) (Schuck, 2002) and the CORINE land cover map (EEA, 2004c) to predict the occurrence of the White-backed Woodpecker in Poland. The two databases have different characteristics: the EFM has a low spatial but high thematic resolution, while CORINE has a high spatial but low thematic resolution regarding the proportion of deciduous trees in the forest. Information on the breeding status of the White-backed Woodpecker in Poland (Figure 3) was obtained from the Polish Ornithological Database, which contains information on the presence of bird species in squares of approximately 100 km^2.

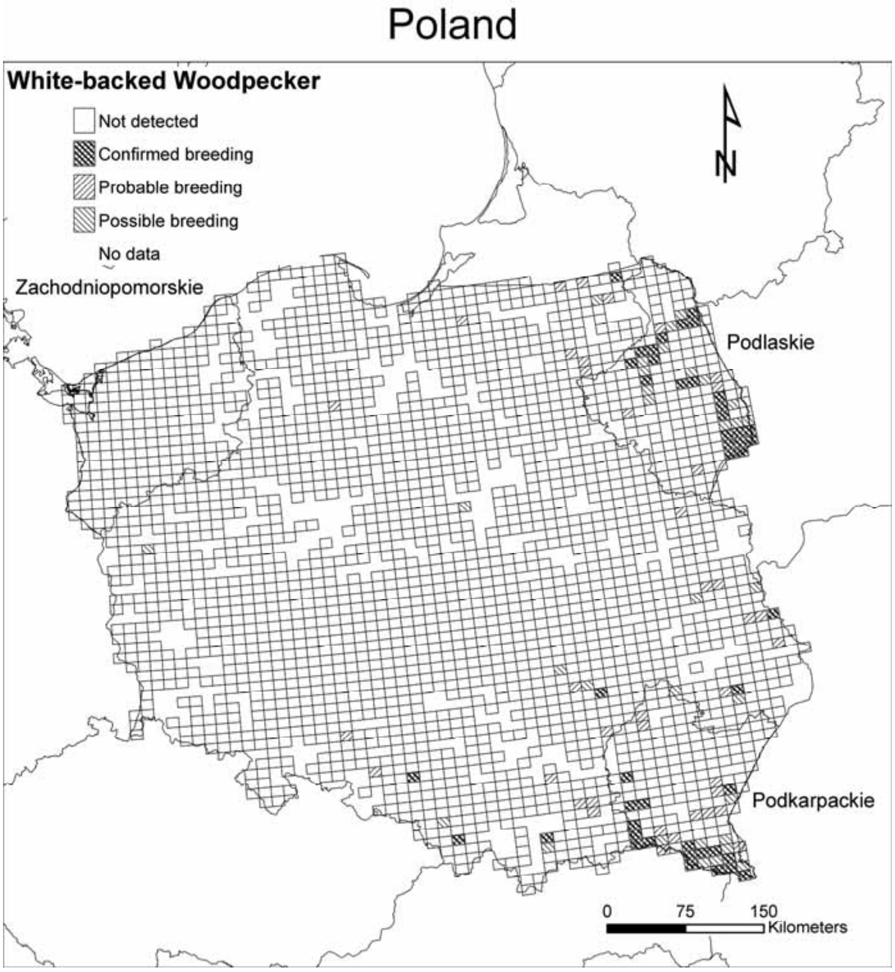


Figure 3. Occurrence of the White-backed Woodpecker in Poland, according to the Polish Ornithological Atlas Database. Squares without data on presence or absence are distinguished from squares with absence of the species

Spatial and temporal analysis

In order to interpret differences between landscapes with similar physical conditions but with different land use history in the Carpathian study area, the landscape was classified based on field inventories and interpretation of Landsat TM imagery. Classification was performed in accordance with the system of Vos & Meekes (1999) with five landscapes classes: i) industrial production landscapes, ii) overstressed multifunctional landscapes, iii) archaic traditional landscapes, (iv) marginalized vanishing landscapes and v) natural relict landscapes. The rate of change in open areas between the different historical maps was calculated according to the compound interest law, as suggested by Puyravaud (2003).

$$r = (t_2 - t_1)^{-1} \times \ln\left(\frac{A_1}{A_2}\right)$$

r is the annual rate of change, and A_1 and A_2 are the land cover areas at times t_1 and t_2, respectively.

A functional diversity index (FDI) was developed (Paper II) and used in the studies described in Papers II and III. The equation gives a high functional diversity index if many ecological groups are present in a landscape or if each ecological group has high species richness in relation to the mean species richness for that ecological group in all landscapes. The approach is similar to the measure of diversity used by Hapaanen (1965; 1966) and by Wilson & Shmida (1984), where the mean number of species in all plots is used to compare the numbers of species between plots. Functional diversity (FD) gives a measure of the completeness and diversity of life history traits in the ecosystem, which is an important complement to values of e.g. species richness (Petchey & Gaston, 2002).

$$FDI_j = \sum_{i=1}^{n} \left[\frac{a_{ij}}{\bar{a}_{i\bullet}} \right]$$

i = ecological group, a_{ij} = number of species of an ecological group in a specific landscape, j = landscape and $\bar{a}_{i\bullet}$ = mean number of species of a specific ecological group in all landscapes. FDI_j is high if there are many ecological groups in the landscape or if each group has species richness in relation to the same group in the other landscapes investigated.

The predictive ability of three statistical stepwise regression models, based on different parameters, was evaluated with an algorithm by testing the predictions on 1000 different subsets. The models were based on land cover, geographical data and a combination of the parameters in the land cover and geographical data models. Half of the sample were randomly chosen for each analysis and tested against the other half as controls, this procedure was repeated 1000 times. The root mean square (RMS) of the residuals between the predicted values and the controls was calculated. The RMS distributions were compared with regard to the land cover, geographical and combined models. In addition, the study described in Paper III explores the relationship between i) functional diversity, ii) species richness and iii) the species richness of each functional group and land cover, climatic and geographic variables. The analysis was conducted with forward selection; backward elimination stepwise regression minimising the Akaike information criterion (AIC) (Akaike, 1974). The stepwise regression includes and excludes parameters based on their contributions to minimising the AIC of the final model.

Functional diversity and species richness within the functional groups were tested for spatial autocorrelation with the local and global G-tests for autocorrelation, as suggested by Ord and Getis (2001). The local G-test identifies clusters of high and low values, and can be used to map hotspots and areas with low values (Premo, 2004). Local and regional hotspots can be identified by selecting differently sized neighbourhood areas for the local analysis. Global G statistics is used to test for spatial autocorrelation, identifying the distances between sample points when they can be considered to be independent of each other. The variables obtained from the stepwise regression analyses of functional diversity and species richness were tested with a spatial autoregressive (SAR) model, incorporating the spatial dependencies of the data in the model. The neighbourhood distance for which the spatial dependencies were low was used to calculate the weight tables that compensate for the spatial dependencies in the data.

The AMOEBA algorithm, proposed by Estivill-Castro and Lee (1999) as a less computing intensive cluster algorithm, was used to establish clusters of mixed forests in Poland. CORINE 2000 was used with a resolution of 100 m to provide land cover data (EEA, 2004b). A centre position, area, perimeter, land cover type, minor and major axes of the smallest ellipse that can be fitted over the polygon, as well as the angle of the axis in relation to the x- and y-axes of the EUREF 99 coordinate system, were attributed to each delineable polygon. A Delaunay triangulation table was established, allowing the distances between all ellipses that are used as proxies for the actual land cover polygons, local mean (Lm) and global mean (Gm), as well as global standard deviation (Gstd) of segment length, to be calculated. If a segment is shorter than Gm+Gstd*(Gm/Lm), it is considered to connect two patches that are part of a cluster, otherwise the patches are considered to be disconnected. Clusters of suitable habitat are important for species as the individuals inhabiting the cluster may constitute a meta-population, which increases the overall viability and occupation rate of territories compared to situations when the distance between patches is too long for a meta-population to develop (Hanski, 1985).

Paper IV describes the evaluation of two different habitat models as predictors of species occurrence: a meta-population model (Lande, 1987; Lande, 1988) and an area-based population model. The meta-population model was parameterised using data on the White-backed Woodpecker population of the Białowieża forest in eastern Poland (Carlson, 2000). The model (Equation 3) incorporates the dynamics with individual territories subject to extinction and colonisation. This is a modification of the original meta-population model. The earlier models considered the populations that constitute the meta-population as being subject to extinction and colonisation, not the individual territories (Levins, 1969; Hanski, 1985). The meta-population model (Carlson, 2000) was applied to both CORINE and EFM land cover data. The area-based population model was based on the area requirements of the White-backed Woodpecker. The home range for a breeding female was set to 1 km^2 (Carlson, 2000). The potential population size within an atlas square (100 km^2) was calculated by dividing the total area of the habitat by the area requirements of a breeding female. In the case of the White-backed Woodpecker, the habitat can be summarised as deciduous or deciduous-rich forests with large amounts of dead wood compared to the situation in managed forests (Aulén, 1988; Wesołowski, 1995; Martikainen, Kaila & Haila, 1998; Carlson, 2000).

$$p = \begin{cases} 1-(1-k)/h & \mathit{for}\, h > 1-k \\ 0 & \mathit{for}\, h \leq 1-k \end{cases}$$

The equilibrium occupancy of a suitable habitat (p) is based on the proportion of suitable habitats in the surrounding landscape (h) and the demographic potential of the population (k). The demographic potential reflects the ability to produce offspring and the ability of these offspring to find new territories (Lande, 1987; Lande, 1988; Carlson, 2000)

Results and Discussion

Regional differences in land use intensity

The landscapes described in Paper I (Figure 4) displayed clear regional differences due to differences in land use history. Landscape classification according to Vos and Meekes (1999) was found to be suitable for the case study landscapes, and revealed the regional differences in land use intensity. The area around San was classified ass an industrial landscape with signs of abandonment due to transition effects since 1990 (Swinnen, 1999). Turka is also to a large extent an industrial landscape, including some forest and treeless agricultural fields, but partly an archaic traditional landscape, with old settlements and some semi-natural grassland. The Bieszczady National Park has, to a large extent, been abandoned since the 1950s and can be classified as a marginalized vanishing relict landscape in the non-forested areas and areas encroached upon by forest, and as a natural relict landscape in most areas with continuous forest cover. Maramures is largely an archaic traditional landscape in the non-forested areas and a natural relict landscape in the forested part. The distribution of the different landscape types was closely related to the land cover of the case study landscapes (Figure 5).

Figure 4. The case study landscapes San, Turka, Bieszczady NP and Maramures described in Paper I.

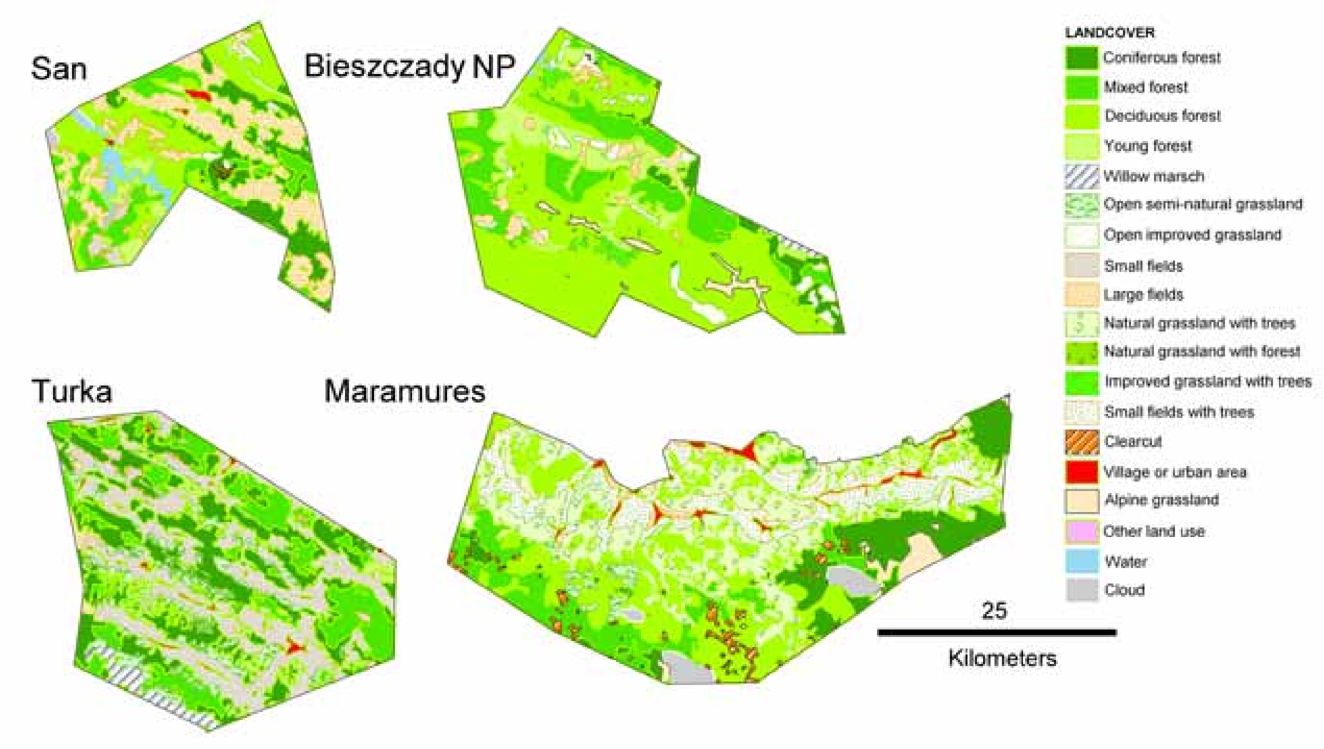


Figure 5. Present land cover composition in the case study landscapes.

The European Environmental Agency (2004a) has identified development scenarios for the intensification of land use and the abandonment of arable land in Europe. Landscapes are likely to be affected differently depending on their geographic position and historical background. Intensification of land use in landscapes that still support attributes of archaic cultural landscapes, may lead to a reduction in the biodiversity (Ihse, 1995; Skånes & Bunce, 1997; Petit & Lambin, 2002). Abandonment was seen to lead to afforestation of primarily semi-natural grasslands and peripheral agricultural fields (Ihse, 1995). Intensification and abandonment may affect semi-natural grasslands and mosaic agricultural land negatively, leading to loss of structures, composition and processes supporting species diversity (Ihse, 1995; Bürgi, 1999; Olsson, Austrheim & Grenne, 2000).

Functional diversity

The relationship between the FDI and the species richness of forest-dwelling vertebrates displayed a curvilinear shape (Figure 6). The increase in the FDI was lower for each species added if species richness was below 30 species per area unit. For species richness above 30, the increase in the FDI was higher for each species added. This could be interpreted as being the consequence of the exclusion of certain groups, e.g. large predators and eagles, from large parts of the European study area. Randomised distribution of species gives a linear relation between species richness and the FDI. The curvilinear relationship observed here could thus be interpreted as reflecting human interference with the natural distribution patterns.

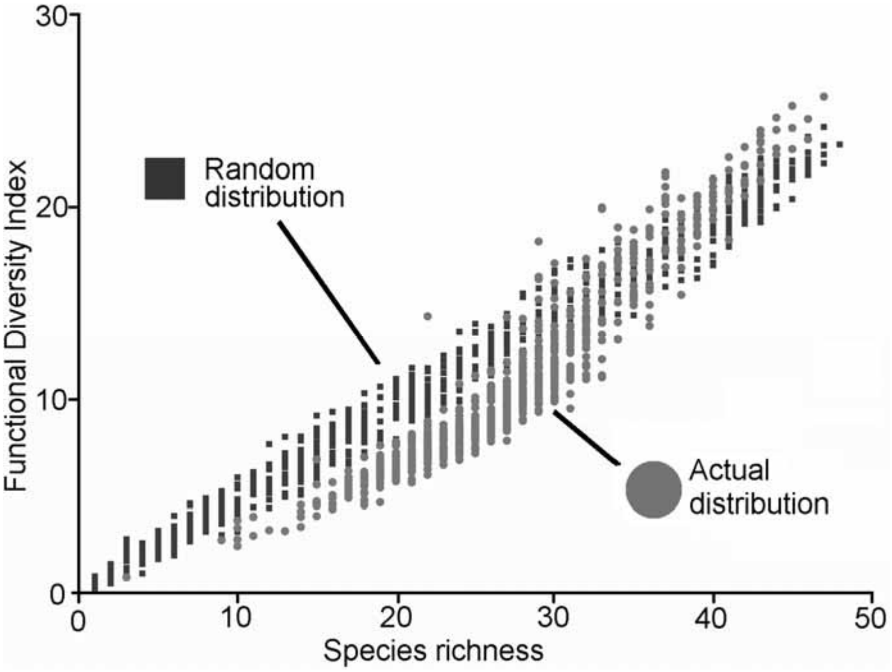


Figure 6. The atlas data on species occurrences (in grey) show a curvilinear relationship between species richness and functional diversity index, whereas random species occurrences (in black) exhibit a linear relationship.

The importance of land use for biodiversity

The results presented in Papers II and III demonstrate that functional diversity and species richness in functional groups in a landscape are related to regional human impact, land use intensity and the extent of suitable habitats in that landscape. The differences in land use intensity in Europe thus affect biodiversity throughout the continent, with a clear pattern of high functional diversity in the eastern parts of Europe (Figures 7-9). The relation between species that need holes for nesting and the proportion of forest plantations on former arable land (Figure 10) shows that even simple estimates of habitat quality can be used to make assessments of the human footprint (Sanderson, *et al.*, 2002) in a landscape or region. Landscape data concerning forest age and land cover at management unit level together with data on regional exploitation, i.e. railway development, largely explained the distribution of functional diversity and the occurrence of specialised species in the landscapes described in Paper II. The CORINE land cover data (EEA, 1999) contributed significantly to explaining the differences in functional diversity between the 50x50 km^2 grid cells of the European study area described in Paper III. A combination of geographic and land cover variables gave a significantly better prediction than those based on either the geographic or land-cover variables (Figure 11).

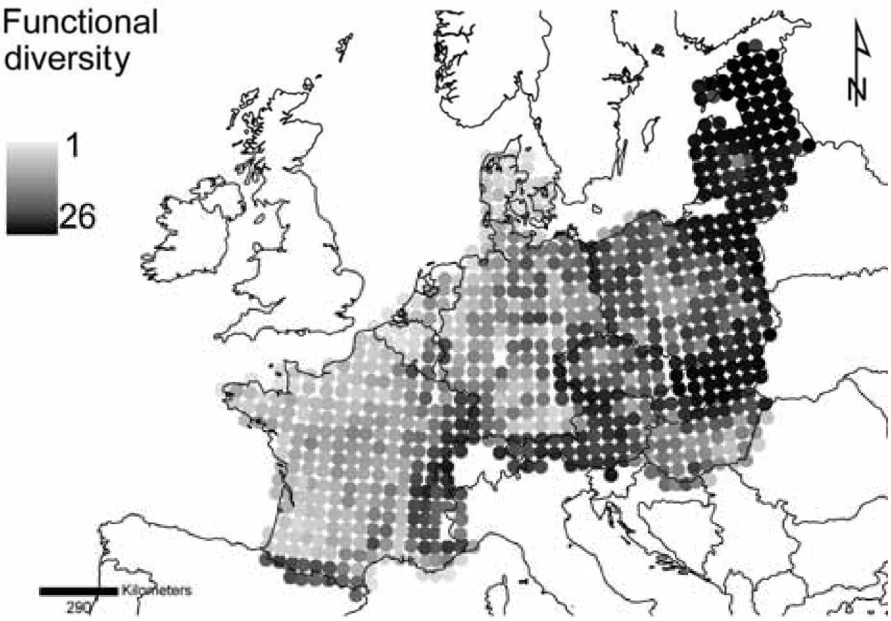


Figure 7. Large-scale pattern of functional diversity, showing higher functional diversity in the eastern and mountainous areas and lower diversity in Western Europe, with the lowest values in Belgium.

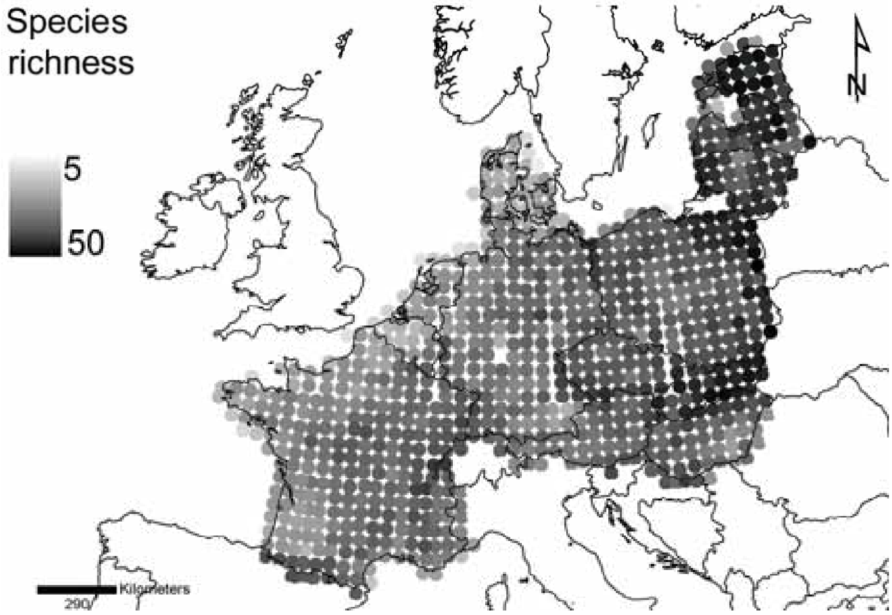


Figure 8. Species richness of larger forest-dwelling vertebrates.

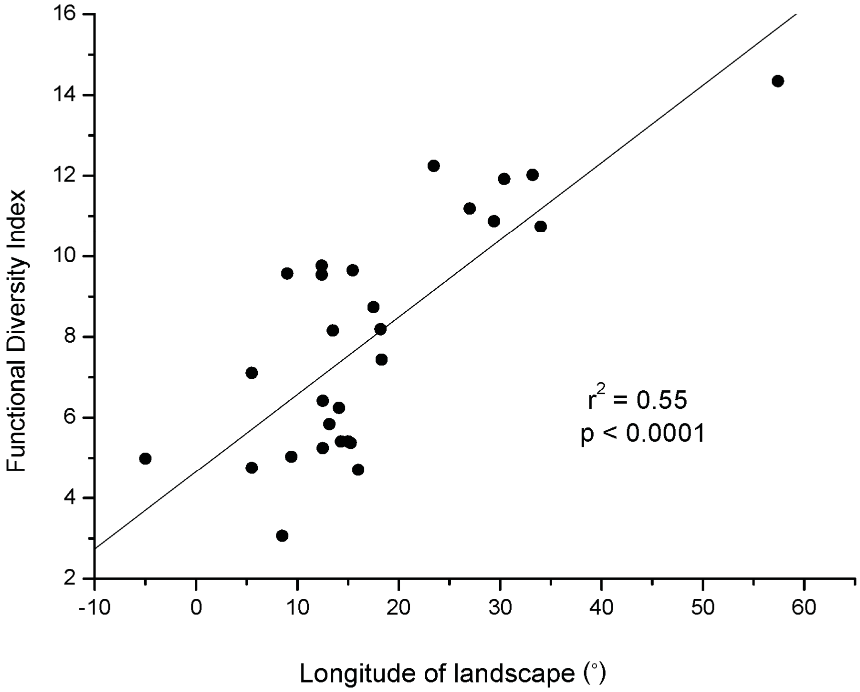


Figure 9. Diversity of ecological and taxonomic groups in the case study landscapes in relation to longitude.

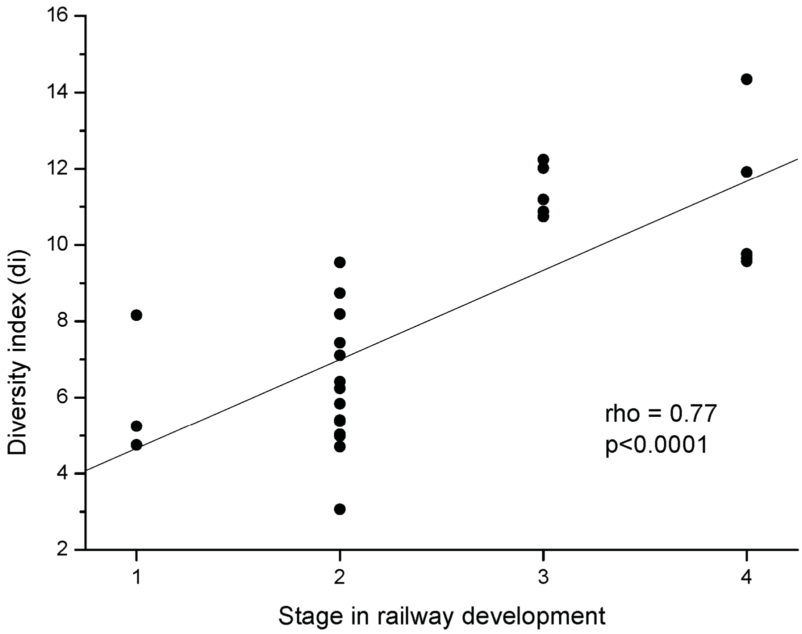


Figure 10. Relationship between the number of species in the ecological group of species requiring large trees and the history of railway development.

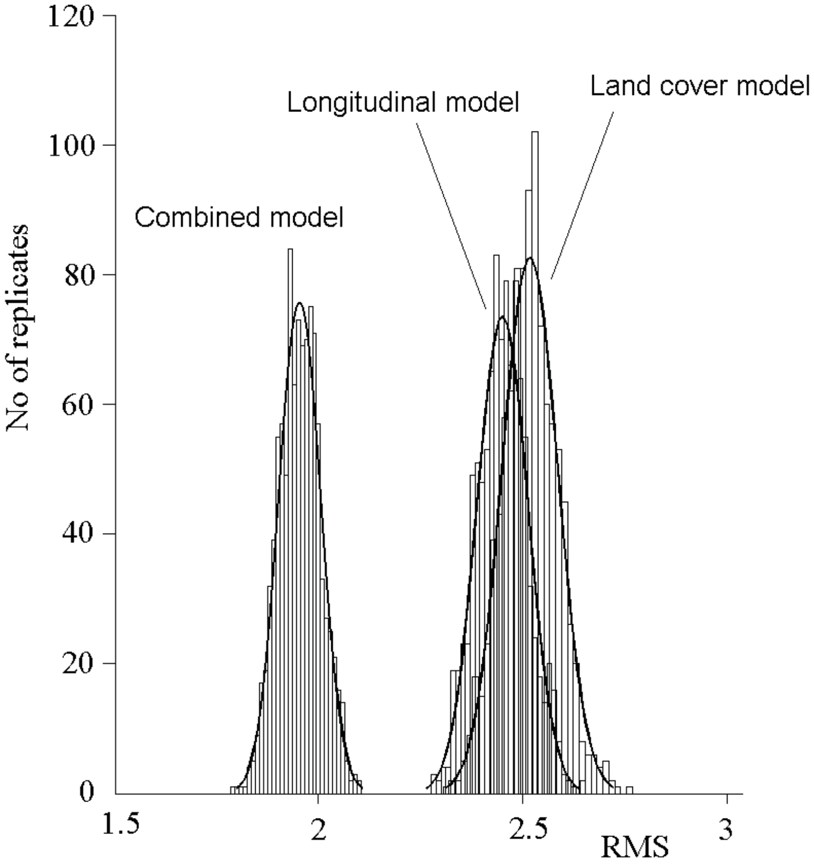


Figure 11. Histogram of the RMS of predictive models based on 1000 repeated stepwise regressions. The combined land cover and geographic model performs better than the two separate models.

The environmental variables explained the differences in the functional diversity index better than the differences in species richness, according to the stepwise regression analyses (Table 2). The functional groups were primarily explained by different combinations of land cover variables. Area of broadleaved forest showed a positive relation to species richness for the functional groups investigated except for riverine species and grouse (Paper III). The land cover with the most negative impact on species richness in this study was discontinuous urban fabric, exhibiting six negative values out of eight. Other variables had both negative and positive effects depending on the functional group analysed, e.g. non-irrigated farmland, pastures, moors and heath land. As the FDI was better explained by the different variables it seems to be more closely connected with processes related to human land use than the measure of species richness. The processes considered were, e.g. persecution of large predators (Breitenmoser, 1998), habitat destruction of grazing grounds for large herbivores (Wallis De Vries, 1995) and habitat degradation regarding natural forest components, such as dead wood (Angelstam & Dönz-Breuss, 2004).

Table 2. *Results from the stepwise regression models exploring the relation between climatic, geographic and land cover variables and the species richness within taxonomic and functional groups, overall species richness of large forest dwelling vertebrates and the functional diversity within this group. (n=796, Significance codes: '***' <0.001; '**' < 0.01; '*' < 0.05, † not significant if spatial autocorrelation is considered (Functional Diversity and Species Richness)).*

	Grouse	Woodpeckers	Owls	Harriers	Eagles	Riverine species	Falcons	Hawks and buzzards	Small predators	Large predators	Omnivores	Large herbivores	FDI	Species richness
Intercept	3.7 ***	8.6 ***	7.4 ***		0.55 ***	-3.7 ***	1.2 ***	2.4 ***	2.27 ***	1.9 ***		1.2 ***	8.8 ***	23 ***
Mean temperature in the coldest month				-0.34 ***		-0.28 ***	-0.14 ***		-8.8×10^{-2} ***		-8.6×10^{-2} ***		-0.38 **	-0.90 ***
Actual annual evapotranspiration	-9.6×10^{-4} **					1.2×10^{-3} *		9.4×10^{-4} ***						4.6×10^{-3} **
Potential annual evapotranspiration		1.2×10^{-3} *							7.0×10^{-4} *			9.9×10^{-4} ***		
Mean temperature	-0.24 ***	-0.4 ***	-0.32 ***	0.27 ***		0.52 ***	8.5×10^{-2} **	-1.7×10^{-2} **		-6.70×10^{-2} **	8.8×10^{-2} ***			
East-West position?	8.1×10^{-7} ***	1.6×10^{-6} ***		-1.1×10^{-6} ***	7.9×10^{-7} ***	7.5×10^{-7} **	-3.9×10^{-7} ***			7.80×10^{-7} ***		5.6×10^{-7} ***	2.2×10^{-6} ***	3.0×10^{-6} **
North-South position?		-2.2×10^{-6} ***	-1.6×10^{-6} ***	5.2×10^{-7} **	4.5×10^{-7} ***	2.9×10^{-6} ***		1.1×10^{-7} ***		2.20×10^{-7} ***		5.8×10^{-7} ***	1.8×10^{-6} ***	
Range in elevation	2.9×10^{-4} *	-5.7×10^{-4} ***		-2.5×10^{-4} *	5.4×10^{-4} ***		1.3×10^{-4} *				6.5×10^{-5} *		5.8×10^{-4} *	
Broadleaved forest		2.0×10^{-5} ***	1.0×10^{-5} ***	5.4×10^{-6} ***	8.8×10^{-6} ***		3.9×10^{-6} ***	1.4×10^{-6} **	1.2×10^{-5} ***	3.40×10^{-6} ***	4.3×10^{-6} ***	5.8×10^{-6} ***	4.2×10^{-5} ***	7.9×10^{-5} ***
Complex cultivation patterns	5.1×10^{-6} **	8.4×10^{-6} ***	-5.7×10^{-6} **		-4.9×10^{-6} **			1.3×10^{-6} **						
Coniferous forest	2.9×10^{-6}***	6.1×10^{-6} ***			4.0×10^{-6} ***	8.2×10^{-6} ***		1.4×10^{-6} ***			1.7×10^{-6} ***	5.0×10^{-6} ***	1.4×10^{-5} ***	2.3×10^{-5} ***
Continuous urban fabric			-4.2×10-5 *	-3.1×10^{-5} *		-5.9×10^{-5} **		1.4×10^{-5} **			-1.5×10^{-5} *			
Discontinuous urban fabric	-8.1×10^{-6} *	1.6×10^{-5} **		-2.5×10^{-5} ***	-8.4×10^{-6} ***	-3.3×10^{-5} ***		5.8×10^{-6} ***		-7.2×10^{-6} **	-6.4×10^{-6} ***		-5.8×10^{-5} ***	-7.4×10^{-5} ***
LPOA				1.2×10^{-5} **		-1.9×10^{-5} ***	-4.5×10^{-6} *			8.5×10^{-6} ***			5.0×10^{-5} ***	5.1×10^{-5} **
Mixed forest	1.2×10-5 ***	1.7×10-5 ***	9.7×10-6 ***	-1.1×10-5 ***			3.5×10-6 **				6.7×10-6 ***		2.1×10-5 **	4.0×10-5 ***

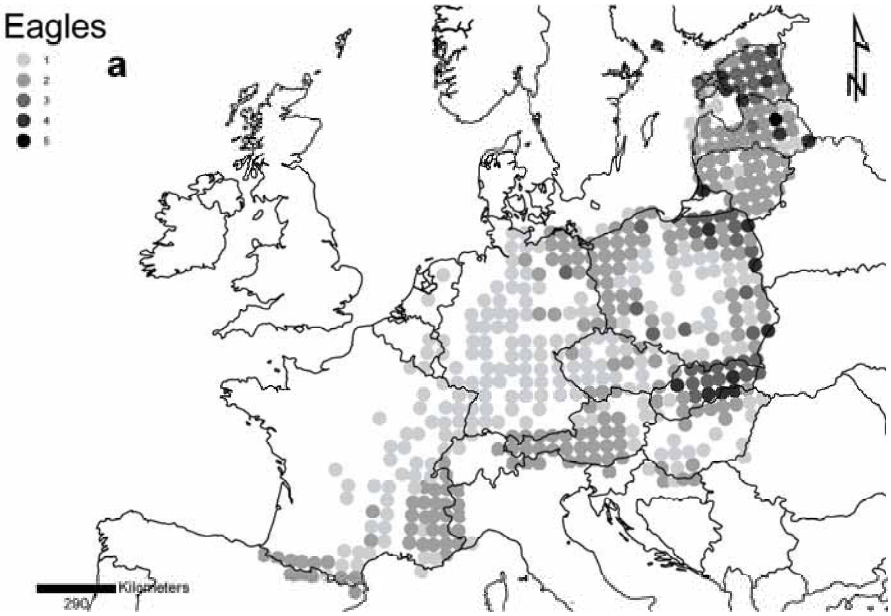
	Grouse	Woodpeckers	Owls	Harriers	Eagles	Riverine species	Falcons	Hawks and buzzards	Small predators	Large predators	Omnivores	Large herbivores	FDI	Species richness
Moors and heath land		-5.9×10^{-5} ***				2.70×10^{-5} *	1.1×10^{-5} *		-2.0×10^{-5} **	-2.1×10^{-5} ***	-9.8×10^{-6} *		-8.6×10^{-5} **	-9.0×10^{-5} * †
Natural grassland	-1.1×10^{-5} **		-1.5×10^{-5} **			1.6×10^{-5} **								
Non-irrigated farmland	-4.3×10^{-6} ***	3.5×10^{-6} ***	-2.5×10^{-5} *	4.2×10^{-6} ***	-1.8×10^{-6} ***	-2.6×10^{-6} **		1.0×10^{-6} ***	1.3×10^{-6} **	-2.5×10^{-6} ***		2.6×10^{-6} ***	-1.1×10^{-5} ***	
Pastures	$-3.0\times10^{-}6$ **	5.7×10^{-6} ***		4.9×10^{-5} ***		-3.4×10^{-6} *	1.6×10^{-6} **	7.6×10^{-7} *	1.9×10^{-6} *	-1.4×10^{-6} *	1.3×10^{-6} **			
Transitional woodland shrub	2.9×10^{-5} ***	-1.8×10^{-5} *	6.1×10^{-5} ***	4.1×10^{-5} ***			1.3×10^{-5} ***			1.1×10^{-5} ***	1.5×10^{-5} ***		1.4×10^{-5} ***	1.66×10^{-4} ***
Historical cities 1850								-8.9 ***			4.1 *	-5.8 *		
R^2	0.64	0.59	0.34	0.29	0.55	0.67	0.35	0.25	0.31	0.57	0.39	0.44	0.71	0.66

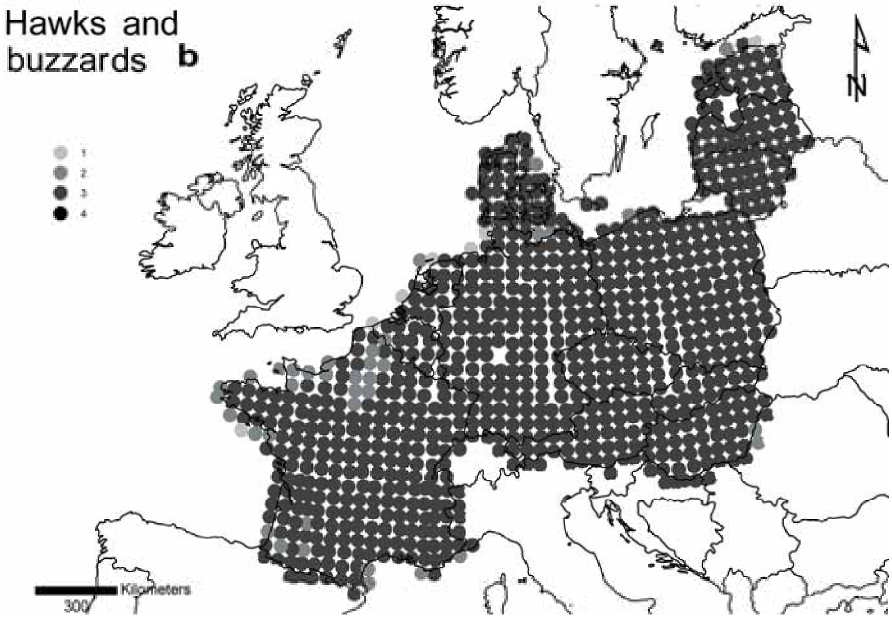
The low values of the FDI and species richness in the areas with the heaviest human footprint have several plausible explanations. As human land use leads to destruction and degradation of habitat, it has an impact on the distribution of individual species, ultimately affecting the biodiversity of whole regions. Habitat destruction lowers the population sizes as a consequence of habitat loss (Andren, 1994). Habitat degradation, on the other hand, does not lead to area loss, but to lower carrying capacity of the habitat, and consequently lower population densities. As Hanski & Gyllenberg (1997) showed, the relationships between area and species richness of a region and between population density and species distribution range are interconnected and could be explained by the same processes of local colonisation and extinction. Lower population densities due to habitat destruction or degradation over large areas consequently result in smaller distribution ranges. The gradient of functional diversity in Europe is accordingly affected by differences in habitat quality depending on land use intensity and economic history, see (Chirot, 1989; Gunst, 1989). Human impact at regional level can therefore not be neglected when biodiversity patterns in Europe are investigated, as found by e.g. (Mikusiński & Angelstam, 1998; Thuiller, Araujo & Lavorel, 2004; Verhulst, Baldi & Kleijn, 2004; Konvicka, Fric & Benes, 2006).

Distribution of medium-sized and large species

Functional and taxonomic groups that consists of medium-sized species, e.g. hawks, buzzards and small carnivores, showed more evenly distributed species richness than functional and taxonomic groups that consists of large species, e.g. eagles and large predators (Figure 12 a-d). Differences within groups were also evident, e.g. within the omnivore species, the more generalist and easily dispersed wild boar *(Sus scrofa)* occurred in most of the study area, while the large, slowly dispersing and more carnivorous brown bear only occurs in the Baltic states and the mountain ranges (Figure 12 e). Only five medium-sized species, the Great Spotted Woodpecker *(Dendrocopos major)*, goshawk *(Accipiter gentilis)*, sparrow hawk *(Accipiter nisus)*, red fox (*Vulpes vulpes)* and pine marten *(Martes martes)* were present in all the landscapes described in Paper II, and they were all among the ten most widespread species in the study area described in Paper III, apart from the pine marten. Brown &

Maurer (1989) argue that large species should be widespread as a consequence of lower habitat specialisation, and medium-sized species less widespread due to evolutionary adaptation to more specific habitats. The distributions reported in Papers II and III differ from the patterns expected for natural distribution. Similar patterns were reported by Mikusinski & Angelstam (2004), when comparing the distribution of pairs of medium-sized and large mammals in Europe. This is in accordance with the effect of landscape fragmentation on vertebrate populations (Andren, 1994) and the consequences of hunting and persecution regarding the distribution ranges of large predators (Breitenmoser, 1998). The differences in distribution between large and medium-sized species in Europe can thus be seen as a result of human land use and landscape change at continental level. Wolff (2000) reviewed the extinction of species in the south-eastern North Sea and concluded that human overexploitation was the cause of extinction for 18-22 species, habitat destruction for 9-12 species and pollution for 3-5 species, out of 31 species considered to have become permanently or temporarily extinct in the south-eastern North Sea area. The human footprint in the marine environment is thus similar to that on land.




Hawks and buzzards b
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2
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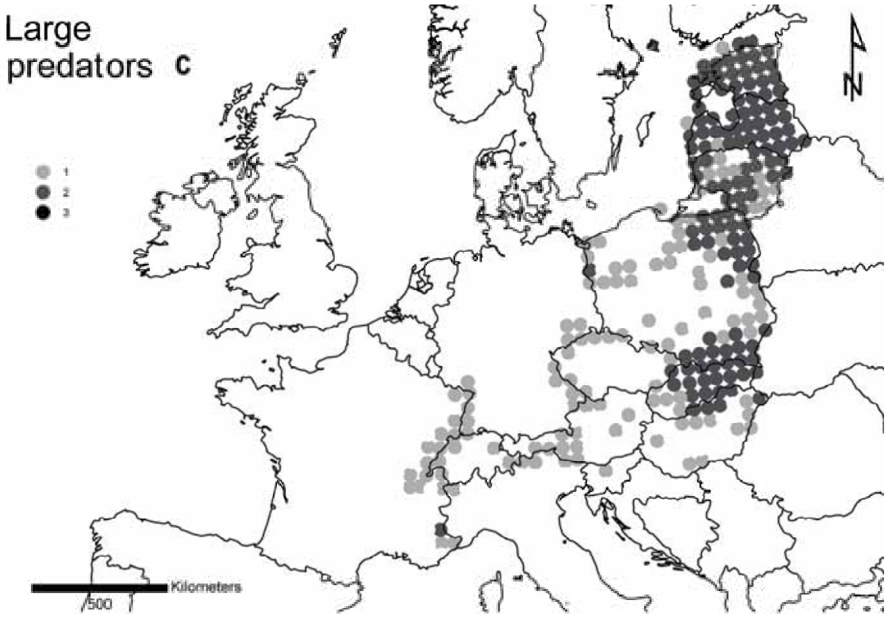
Large predators c
1
2
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Kilometers
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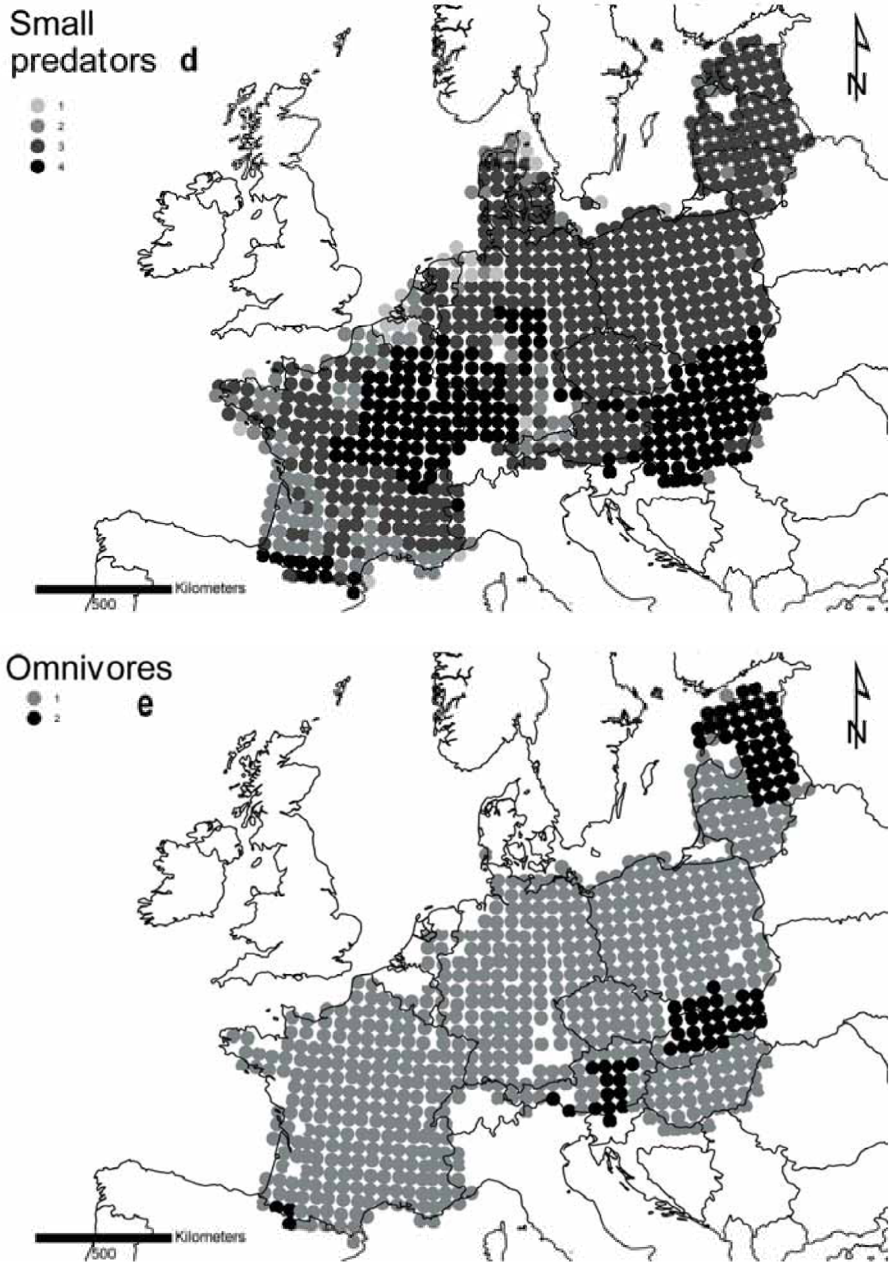
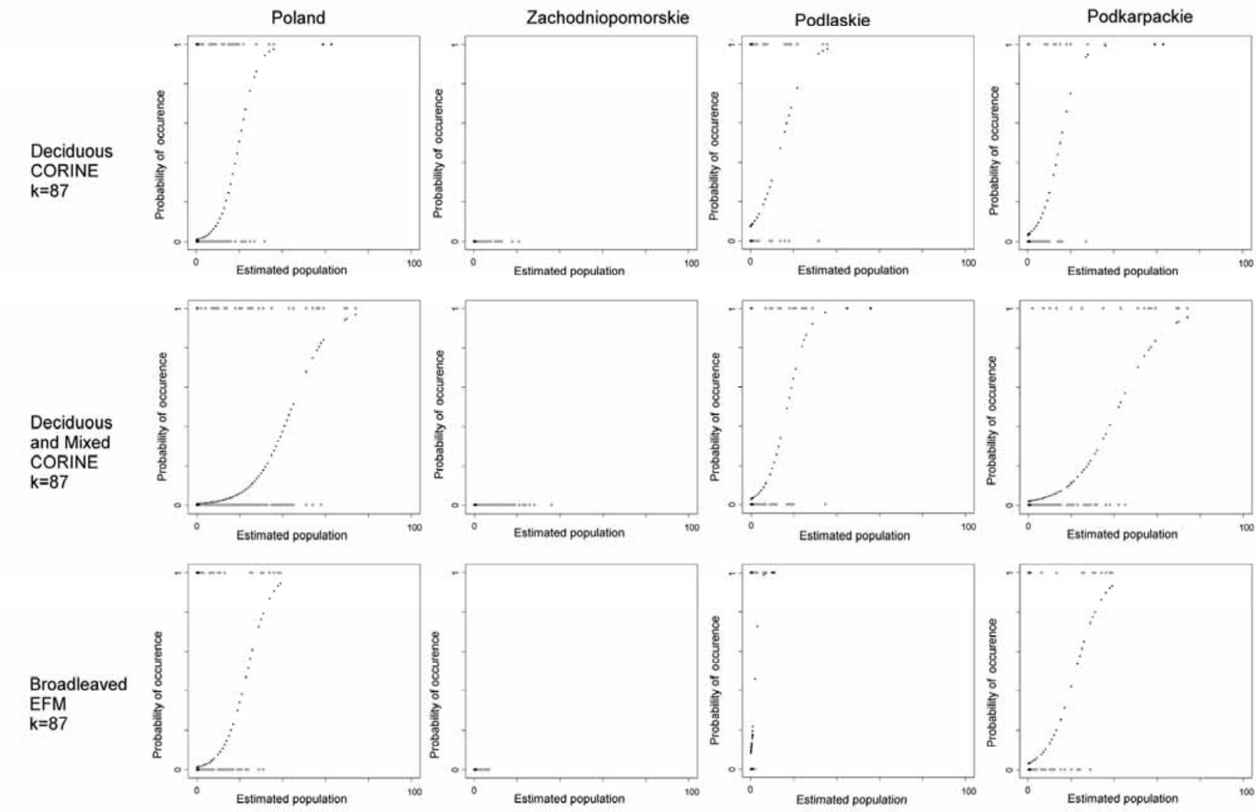


Figure 12. Distribution of: a) eagles, b) hawks and buzzards, c) large predators, d) small predators and e) omnivores in Western and central Europe.

Spatial modelling

The study described in Paper IV showed that incorporation of spatial aspects linked to meta-population dynamics improved predictions of the occurrence of reproducing individuals compared to a model based only on area requirements (Table 3, Figures 13 & 14). Nevertheless, both the meta-population and the area-based models performed well in identifying landscapes where reproducing White-backed Woodpeckers occur. There were, however, clear differences in the number of potential occurrences predicted by the meta-population and the area-based models. As the area-based model does not use any assumptions regarding the importance of the spatial arrangement of the potential habitat patches, it overestimated the habitat potential for White-backed Woodpeckers in the atlas squares. This is seen in the logistic regression curves, as they are skewed to the right for the area-based population model in relation to the meta-population model. The reason is that the meta-population model excludes areas of deciduous forest that are situated in surroundings with an insufficient fraction of habitat suitable for a White-backed Woodpecker population, hence giving fewer potential habitats than the area-based population model. The predictions of the meta-population model regarding the occurrence of at least one breeding pair of White-backed Woodpeckers were significantly better than those of the area-based population model, as the meta-population model identified atlas squares without potential for breeding White-backed Woodpeckers more accurately.


Poland
Zachodniopomorskie
Podlaskie
Podkarpackie
Deciduous
CORINE
k=87
Deciduous
and Mixed
CORINE
k=87
Broadleaved
EFM
k=87
Probability of occurence
Estimated population
0
1
100

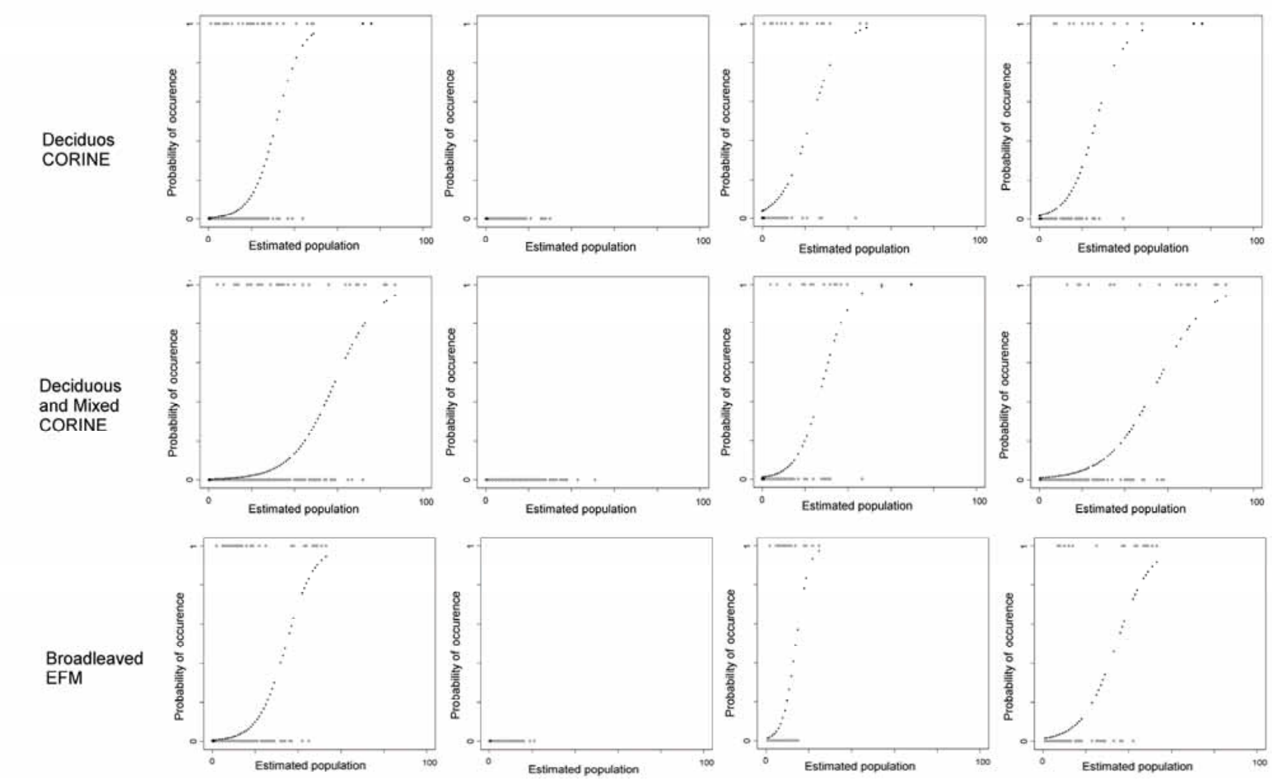


Figure 13. Logistic regression curves showing the relation between the potential for breeding of the White-backed Woodpecker according to the meta-population model and the actual breeding status of the woodpecker according to atlas data (1 = confirmed breeding, 0 = no confirmed breeding) at national and regional levels in Poland. The significance levels are < 0.001.

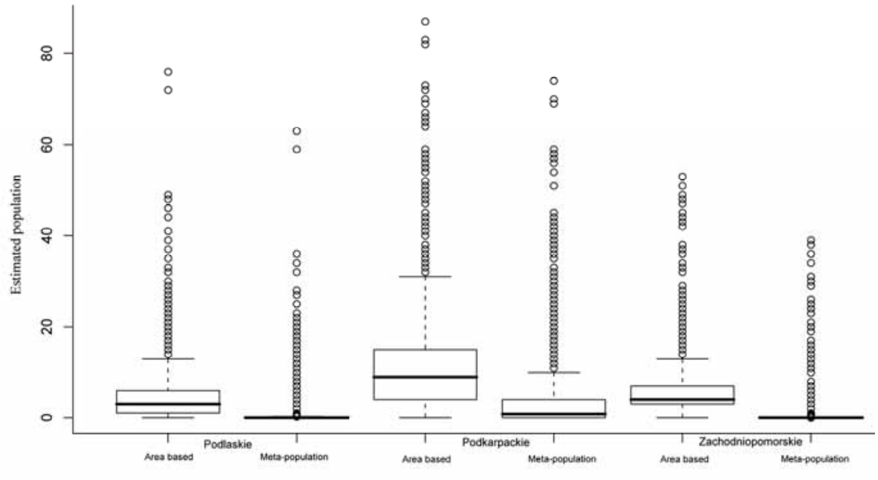


Figure 14. Box plot showing the distribution of expected population sizes in the atlas squares for the two models studied, in relation to actual occurrence and absence in Poland and EFM data.

Table 3. *Results of the logistic regression for the meta-population model based on the broadleaved (B) land cover class in CORINE, the mixed and broadleaved land cover classes (MB) in CORINE and the EFM data, as well as for the corresponding area-based population model. All results were significant ($P < 0.001$). Cohen's kappa values for the prediction of the presence of at least one breeding pair of White-backed Woodpeckers, Area Under the Relative Operating Characteristics Curve (AUC_{ROC}) and R^2 of the ordinary least squares regression are given for the different models and datasets.*

		POLAND (n=2246, occurrence=46)			Podlaskie (n=165, occurrence=22)			Podkarpackie (n=142, occurrence=17)		
		AUC_{ROC}	R^2	Kappa	AUC_{ROC}	R^2	Kappa	AUC_{ROC}	R^2	Kappa
Meta-population model	CORINE (B)	0.83	0.28	0.15	0.88	0.27	0.53	0.88	0.48	0.35
	CORINE (MB)	0.91	0.32	0.040	0.93	0.53	0.29	0.90	0.50	0.090
	EFM	0.82	0.21	0.17	0.76	0.25	0.29	0.89	0.50	0.38
Area-based population model	CORINE (B)	0.89	0.32	0.0022	0.88	0.36	0.091	0.93	0.50	0.061
	CORINE (MB)	0.90	0.32	0.012	0.92	0.54	0.017	0.90	0.49	0.0074
	EFM	0.89	0.26	0.00046	0.79	0.27	0	0.91	0.50	0

Differences were expected in predictions of White-backed Woodpecker occurrence reported in Paper IV (Table 4) by the models based on the CORINE and on the EFM data sets, since the data differ regarding both thematic and spatial resolution. The EFM has a high thematic resolution but a low spatial resolution, while the opposite is true of the CORINE land cover data (EEA, 1999; Päivinen et al., 2001). The accuracy is somewhat lower for the models based on EFM data at national level and in the Podlaskie region, than for models based on CORINE data. However, the spatial extent of the EFM data is much larger, as it covers the whole European continent (Päivinen*, et al.*, 2001). This is an important advantage from a European level perspective, and the EFM data should therefore be considered a valuable tool for regional planning and ecosystem management the eastern border of the EU.

Table 4.*Pearson's correlation coefficients between the meta-population and area-based models, and between predictions based on CORINE land cover and the European Forest Map*.

		Meta-population model			Area-based population model		
		CORINE (B)	CORINE (MB)	EFM	CORINE (B)	CORINE (MB)	EFM
Meta-population model	CORINE (B)	1					
	CORINE (MB)	0.76	1				
	EFM	0.62	0.72	1			
Area-based population model	CORINE (B)	0.86	0.62	0.59	1		
	CORINE (MB)	0.75	0.94	0.74	0.71	1	
	EFM	0.55	0.57	0.83	0.66	0.67	1

The expected number of breeding White-backed Woodpecker pairs according to the meta-population model can be used to assess the core areas of the White-backed Woodpecker populations. The forest areas that were suitable according to the meta-population model and where the White-backed Woodpecker has been breeding according to the atlas data can be regarded as being of high conservation value, since they can be expected to harbour both natural forest attributes required by the White-backed Woodpecker and meet the area requirements of a meta-population. Many of the atlas squares with high potential for breeding of White-backed Woodpeckers according to the models but without confirmed breeding have no adjacent squares with predicted or observed occurrence, while squares with low potential for occurrence of the species but with observed breeding are adjacent to squares with both high potential and observed occurrence of the White-backed Woodpecker. These patterns could be due to larger-scale meta-population dynamics (Levins, 1969; Hanski, 1985), sink-source dynamics (Pulliam, 1988), the mass effect (Shmida & Wilson, 1985) or extinction debts (Tilman *et al.*, 1994). The areas with potential and actual occurrence of the White-backed Woodpeckers in Poland (Figures 3 and 15) are located in the border regions towards Belarus, Ukraine and Slovakia. This distribution pattern coincides with the Polish distribution of large forest vertebrates, e.g. the lynx (*Lynx lynx*) (Niedzialkowska *et al.*, 2006), wolves (Okarma, 1993), European bison (*Bison bonasus*), brown bears (Jakubiec & Buchalczyk, 1987) and capercaillie (*Tetrao urogallus*).

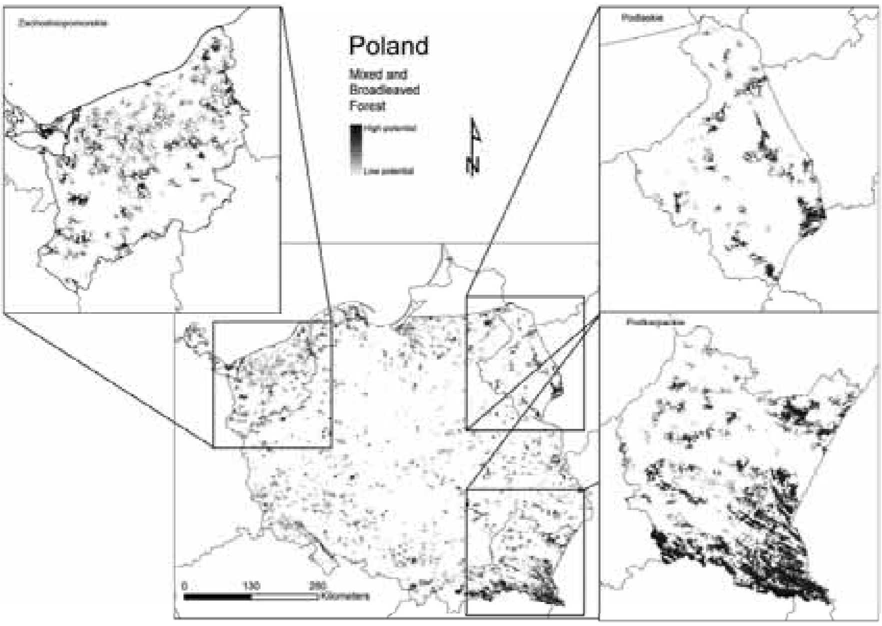


Figure 15. Potential for breeding of White-backed Woodpeckers in Poland, according to the meta-population model based on the CORINE land cover classes mixed and broadleaved forests.

A cluster analysis of mixed forest in Poland (Figure 16) using the AMOEBA algorithm (Estivill-Castro & Lee, 1999) showed that the forested areas in Poland are disconnected from each other and fragmented within themselves. CORINE 2000 data (EEA, 2004b), with a resolution of 100 m were used as land cover proxy.

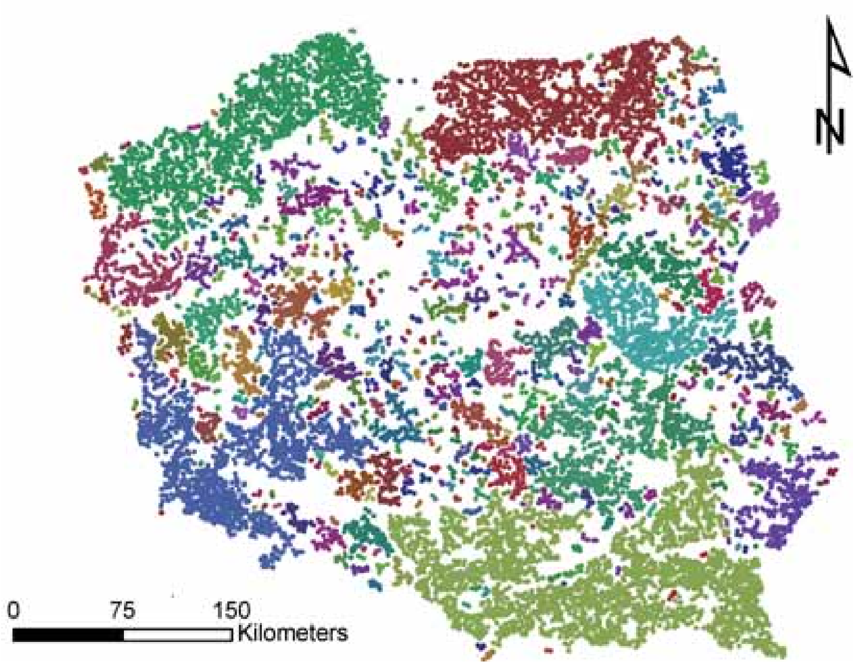


Figure 16. AMOEBA clusters of mixed forest stands in Poland according to CORINE land cover, different colours represent different clusters.

European reference areas

Studies have been made on landscape changes all over Europe to investigate the relation between land use policy and economic driving forces on the one hand, and landscape change on the other (Ihse, 1995; Antrop, 1998; Vos & Meekes, 1999; Bicik, Jelecek & Stepanek, 2001; Wood & Handley, 2001; Cousins, Eriksson & Franzen, 2002; Petit & Lambin, 2002; Schneberger, Bürgi & Kienast, 2006). These studies are generally of a local character, considering landscape changes in a village or in a couple of villages within a local landscape, examining the land use and land cover changes in the specific area, or comparing the landscape change between areas with differences in physical conditions but subject to the same regional economic drivers.

Paper I describes an alternative approach. Four landscapes (Figure 17) with similar physical characteristics, but which had been subjected to different policies and economical conditions were investigated. Most of the land cover change in the investigated landscapes took place between 1950 and 1980 (Figures 18 & 19), as in other studies of land cover change in Europe (Ihse, 1995; Bicik, Jelecek & Stepanek, 2001; Antrop, 2004; Schneberger, Bürgi & Kienast, 2006). The slow change in landscape composition up until the Second World War, in all four landscapes described in Paper I, suggests that the main driving forces of landscape change until then were internal pressures, i.e. domestic needs, management changes or population growth (Antrop, 2004). Maramures was an exception in the post-war era as a slow rate of change was seen here during the whole of the 20th century. This is probably due to the geographical remoteness of the area. Maramures can thus be regarded as a benchmark for the whole region concerning landscape level targets for structures, composition and processes.

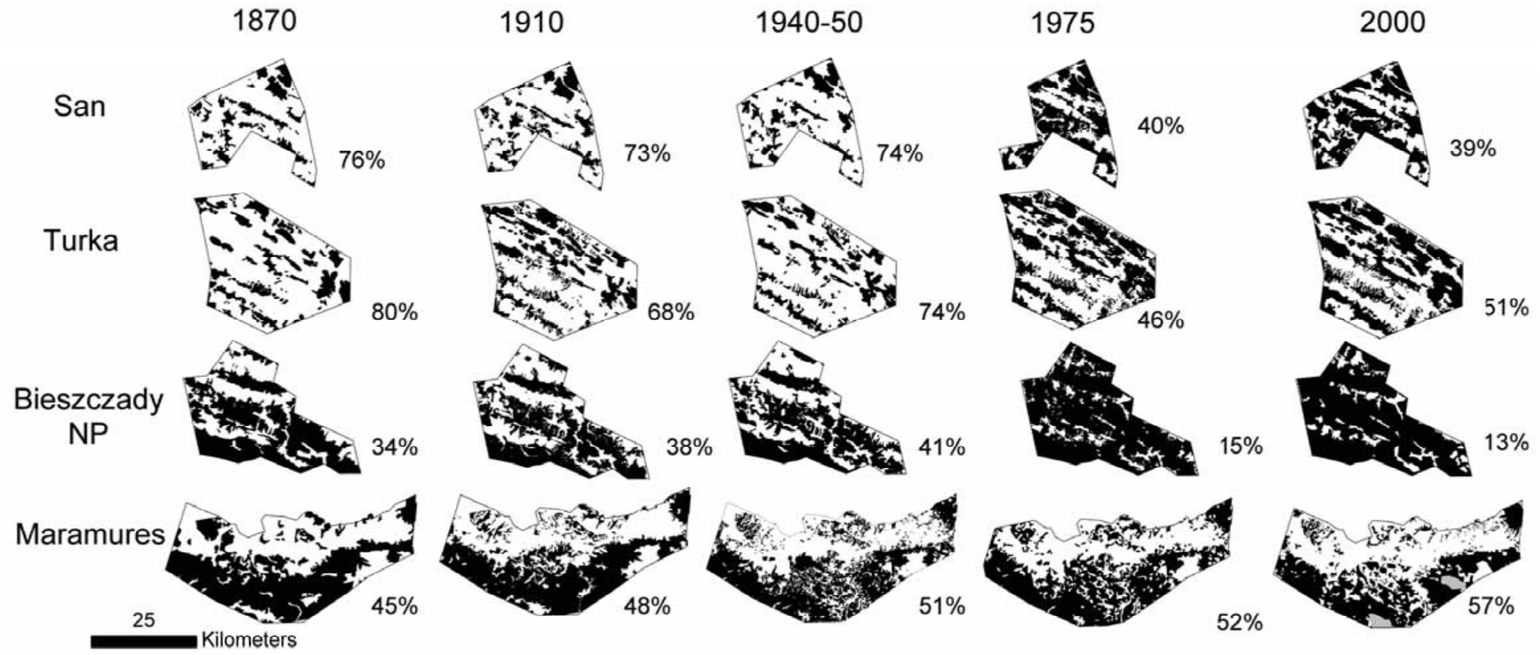


Figure 17. Forest cover in ~1870, ~1910, ~1950, ~1980 and ~2000 in the case study landscapes. The forest cover of San in 1975 is incomplete due to deficiencies in the data coverage. Black indicates forest areas, white open areas and grey denotes clouds in the Landsat images.

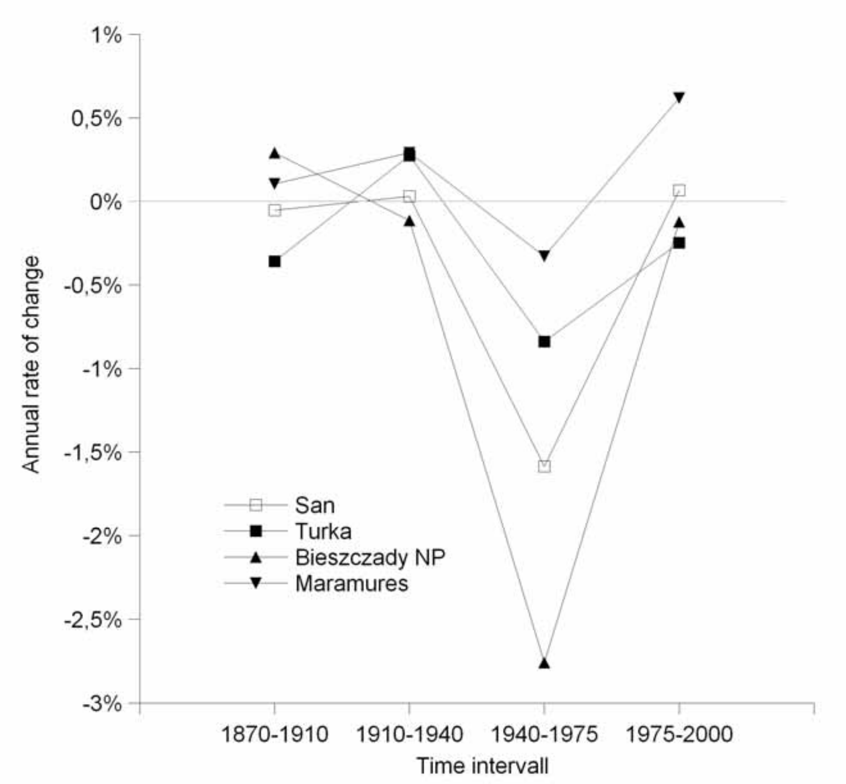


Figure 18. Change in open area of the landscapes derived from the historical map layers and satellite imagery.

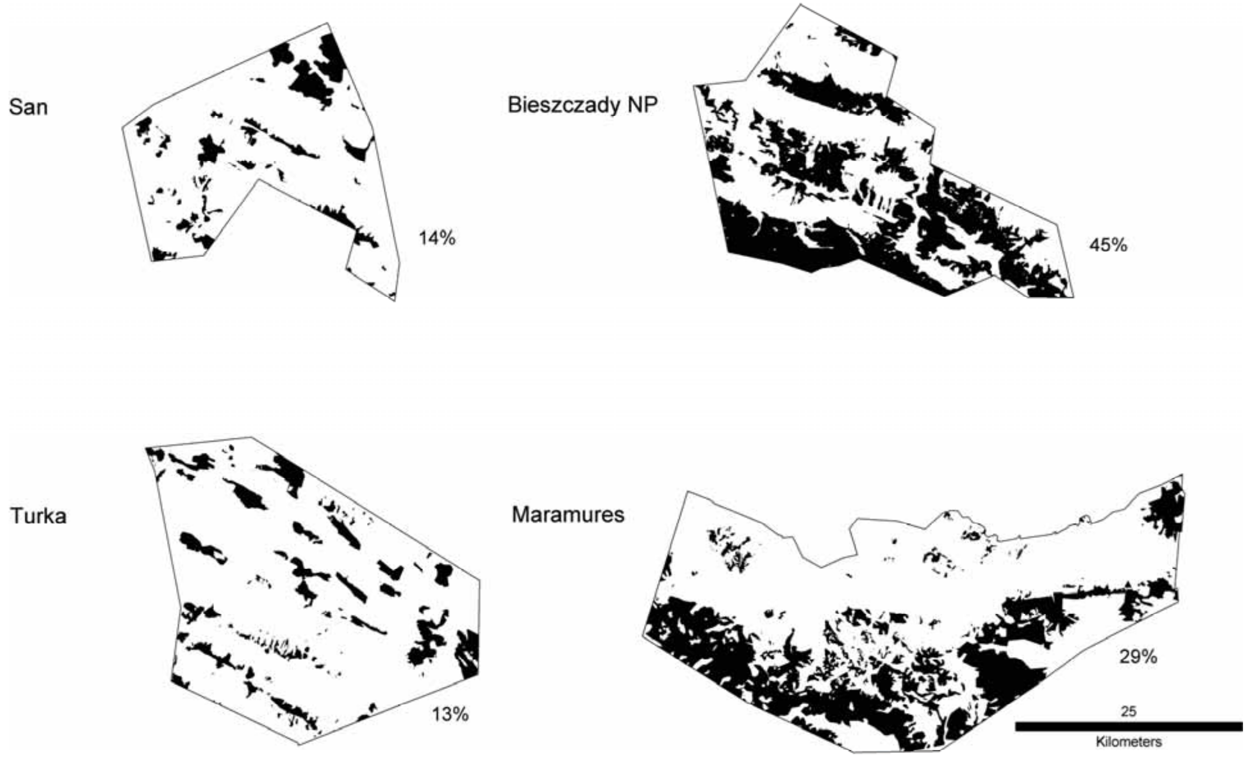


Figure 19. Areas with continuous forest cover since ~1870 according to historical maps and satellite imagery.

In many parts of Europe vertebrates occurring in the pre-industrial era have become extinct (Hagemeijer & Blair, 1997; Mikusiński & Angelstam, 1998; Mitchell-Jones, *et al.*, 1999) and the land use history is so long that it is difficult to establish a natural benchmark for many species (Ceballos & Ehrlich, 2002). The year 1980 has been set as a benchmarking year for the assessment of the state of birds in agricultural areas in Europe (EEA, 2005). However, there is no evidence that 1980 would provide good benchmarks for naturalness or cultural authenticity in European landscapes as landscape change accelerated long before this (Antrop, 2004). Population levels in 1980, therefore, do not represent a desired state for either natural or cultural landscapes in Europe. A more reasonable approach has been adopted in Alberta, Canada, where the population levels in areas resembling natural reference areas are used to set benchmarks for natural population levels. These are used to calculate a biodiversity index giving negative values for both positive and negative deviation from the benchmark (Nielsen *et al.*, 2007). To detect the loss of ecological function the species are divided into ecological groups. A similar approach was used in the studies described in Papers II and III. The pattern of functional diversity of larger forest-dwelling vertebrates in Europe (Figure 8) was assessed from atlas data, and the differences between regions are linked to land use intensity and habitat quality. Several studies have demonstrated higher species richness in the eastern parts of the EU than in the intensely managed landscapes of the western parts (Mönkkönen, 1994; Mikusiński & Angelstam, 1997; Mönkkönen & Viro, 1997; Baquero & Tellería, 2001; Diniz-Filho, Bini & Hawkins, 2003). The patterns of occurrences and predictions of the White-backed Woodpecker (Paper IV) also support the suggestion that the landscapes at the eastern border of the EU could be regarded as benchmark areas for conservation management in the EU.

Conclusions

Comparative studies of landscapes with a common ancestry regarding landscape structure and composition can be valuable for the establishment of benchmarks for policy targets and for research on the relation between landscape change and land use policy.

The differences in accumulated and recent human land use between areas must be considered in studies of biodiversity patterns. The history of human utilisation and the associated species loss are important factors influencing biodiversity patterns at local, regional and continental levels.

The spatial arrangement of habitat is important for population viability at local as well as regional level. For large-scale assessments of biodiversity, conservation potential and population viability, the spatial arrangement of suitable habitats must be considered

The eastern border region of the EU hosts high species richness and functional diversity. There is hence a need for cooperation with Ukraine, Belarus and Russia regarding joint efforts in the preservation of European ecosystems and species richness.

Populärvetenskaplig sammanfattning

Europa är präglat av kontraster, från arktisk tundra och trädlös stäpp till rika lövskogar och stora barrskogsområden. Det gör att de naturliga förutsättningarna varierar kraftigt, vilket återspeglas i olika arters utbredning. Stora delar av Europa är också präglade av mänsklig markanvändning och har varit det sedan tusentals år tillbaka. Till att börja med tog sig den mänskliga påverkan sig uttryck i fiske och jakt efter villebråd samt insamling av bär, frukter och rötter. Med jordbrukets införande för drygt 6 000 år sedan så har den mänskliga påverkan i allt högre grad inneburit förändringar av olika arters livsmiljöer. Den mänskliga påverkan har lett till att en del arter har försvunnit helt. Uroxen och den europeiska vildhästen blev utrotade i Polen 1627 respektive 1880, medan andra arter har försvunnit lokalt. I Holland finns det lämningar från uroxe fram till 400-taler, älg och björn fram till 1000-talet och varg förekom sporadiskt in mot slutet av 1800-talet. I havet utanför Holland har det tidigare funnits stora valar som gråval och nordkapare, de försvann på 400 respektive 1400-talet. Gråvalen är idag utrotad från hela Atlanten medan Nordkaparen finns kvar i ett litet bestånd (ca 400 djur) i Nordatlanten. Holland ligger i norra Europas urbana och ekonomiska centrum och har gjort det under de senaste 1000 åren. Ju längre bort från centrum desto mindre blir den mänskliga påverkan. Det är därför inte förvånande att uroxen försvann 1200 år senare från Polen jämfört med Holland.

Många har undersökt orsakerna till att det finns skillnader i artrikedom mellan olika platser och regioner. Ett flertal allmängiltiga samband har kartlagts. De kan delas in i två kategorier, där den ena utgår från möjligheten att sprida sig till ett område och den andra kategorin fokuserar på livsutrymme och mängden tillgängliga resurser. De spridningsrelaterade teorierna kan sammanfattas som att områden som ligger isolerade får färre arter eftersom de är mycket svårare att kolonisera och att stora områden är artrikare än små eftersom de kan hysa större populationer, som inte dör ut lika lätt som små, och eftersom de är lättare att kolonisera. De resursrelaterade teorierna förklarar artrikedom med att områden som har stora resurser kan härbärgera fler arter. Tillgången till vatten och näringsämnen är två faktorer som är viktiga för artrikedomen. Områden med god tillgång på bland annat vatten och näringsämnen kan därför härbärgera fler arter än områden där det råder brist på desamma. Det visar sig i att varma fuktiga områden i tropikerna, som regnskogar, har fler arter jämfört med torra eller kalla områden som öknar och tundror. Sammanfattar man båda teorierna så är artrikedomen störst i stora områden med gynnsamma förutsättningar där livsmiljöerna varit stabila under lång tid.

I artikel I undersöks hur skillnader i ekonomiska och politiska förutsättningar kan påverka i grunden väldigt lika landskap. Resultat från fältarbete och kartanalyser av fyra områden i Karpaterna kombinerades för att klarlägga hur landskapen utvecklats under 1900-talet. De fyra områdena ligger idag i Polen, Ukraina och Rumänien, men tillhörde alla under slutet av 1800-talet det Habsburgska riket. Sedan dess har gränserna ändrats efter både första och andra världskriget. Undersökningen visar att det Rumänska landskapet har ändrats i långsam takt under hela 1900-talet, medan de andra landskapen har börjat med en långsam förändringstakt för att accelerera denna mellan 1950 och 1980, vilket ligger i linje med utvecklingen i övriga Europa. I Rumänien var stora delar av den brukade marken slåttermark, vilket är ett markslag som hyser stor artrikedom av framförallt kärlväxter. I ängarna fanns det mycket träd och buskar, vilket ger förutsättningar för arter som är anpassade till att leva i skogen att också överleva i odlingslandskapet. Sammanfattningsvis så var betydelsen av den ekonomiska och politiska bakgrunden mycket viktig för hur landskapen såg ut idag. De landskap som upplevt kraftig landskapsomvandling hade endast rester av de artrika träd och buskmarkerna kvar.

Artikel II bygger på en enkätundersökning som skickades ut till forskare och skogsförvaltare i Europa. De fick besvara frågor om förekomst av större skogslevande djur, trädslagssammansättning och markanvändningshistorik. Områdena var på ca 50 000 hektar och spridda från Frankrike till Uralbergen. Analyserna visade på ett tydligt samband mellan antalet artgrupper, antalet arter inom varje grupp och mänsklig påverkan. Fåglar som häckar i bohål var negativt påverkade av skogsplanteringar och artrikedomen var generellt sett högre ju längre österut ett landskap låg.

Artikel III går vidare med resultaten från artikel II, men analyserna genomförs utifrån utbredningskartor, klimat, topografi och markanvändning. Utbredningen av såväl örnar, stora rovdjur, stora växtätare och hackspettar visar att arterna är tydligt undanträngda och att mänsklig markanvändningsintensitet har en uppenbar påverkan på deras nuvarande utbredning.

Artikel IV fokuserar på Polen och utbredningen av vitryggig hackspett i de polska landskapen. Polen är varierat, med både stora slättbygder och skogsområden. Skogarna skiljer sig från varandra avseende habitatkvalite, stora områden utgörs av efterkrigstida tallplanteringar, medan andra områden är det närmaste en europeisk lövurskog man kan komma. Två olika metoder för att förutsäga förekomsten av vitryggig hackspett testades. Den som fungerade bäst tog hänsyn till hur skogsområdena låg i förhållande till varandra. Resultaten visar att det är viktigt att ta hänsyn till hur habitat är fördelade i ett landskap och inte bara till hur stor areal av lämpligt habitat som finns.

Sammanfattningsvis så kan man säga att arter påverkas av mänsklig markanvändning och påverkan på den omkringliggande miljön och att förekomsten av arter är beroende av var ett landskap ligger i förhållande till mänskliga och ekonomiska centra. I Europa finns en tydlig gradient i artrikedom som är påverkad av mänsklig markanvändning, vilket ger skillnader i artrikedom på kontinental nivå. Fördelningen av lämpligt habitat i ett landskap har stor betydelse för förekomsten av arter och är ett bättre mått än areal när ett landskap skall utvärderas utifrån arters olika krav.

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