

Predicting mammal species richness and distributions: testing the effectiveness of satellite-derived land cover data

Marcel Cardillo^{1,3*}, David W. Macdonald¹ & Steve P. Rushton²

¹Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK; ²Centre for Land Use & Water Resources Research, The University, Newcastle upon Tyne NE1 7RU, UK; ³Present address: School of Australian Environmental Studies, Griffith University, Nathan QLD 4111, Australia

(*author for correspondence, e-mail: M. Cardillo @ mailbox.gu.edu.au; fax: +61-7-3875 5014)

Received 11 December 1997; Revised 8 September 1998; Accepted 21 September 1998

Key words: associative models, biodiversity mapping, distributions, land cover, mammals, species richness

Abstract

Mapping species richness and distributions is an important aspect of conservation and land use planning, but the time and cost of producing maps from field surveys is prohibitive. It is useful, therefore, if mappable environmental variables, from a readily accessible source, can be used as surrogates for species attributes. We evaluated the power of satellite-derived land cover information, from the Land Cover Map of Great Britain, to predict species richness and occurrences of terrestrial mammals in one hundred 10 × 10 km quadrats, from four regions of Britain. The predictive power of the land cover data was relatively poor – with a few exceptions, land cover explained less than half of the variation in mammal species richness and occurrence in regression models. Predictive power was considerably stronger when regions were analyzed separately than when analyzed together, and best fitting models varied between regions and between mammal taxa. Predictive power was also affected (positively or negatively depending on taxon) when PCA-ordinated land cover variables were used as predictors. The predictive strength of the land cover data was probably limited mostly by the high proportion of British mammal species with geographic distributions changing rapidly and independently of land cover (and hence the non-saturation of preferred habitats), and to a lesser extent by shortcomings in the mammal and land cover data, and the influence of landscape factors other than land cover on mammal distributions. The results suggest that regional stratification is essential when attempting to predict species richness and distributions, even across relatively limited areas such as Great Britain. We conclude that caution is necessary in using results from environmental information systems such as this as a basis for conservation and land use planning decisions.

Introduction

Mapping the patterns of plant and animal distributions and diversity has become an important aspect of conservation and land use planning (Clarke 1986; Spellerberg 1991; Miller 1994). For example, maps can provide a baseline against which temporal changes in individual species' distributions can be monitored, or they can help identify areas of special biodiversity importance where conservation resources should be focused. Such areas include 'hotspots' of high species richness as well as places where vulnerable species,

or species assemblages of particular interest, occur. It is therefore important to map both species richness and the geographic distributions of individual species. In most cases, however, producing such maps by conventional field survey methods, especially for large areas, is logistically impossible. For this reason, it is valuable to be able to predict species richness and distributions, using associative models based on mappable surrogate variables. Given the importance of time- and cost-effectiveness in conservation planning and management, a system for producing maps quickly and cheaply, using easily accessible surrogate

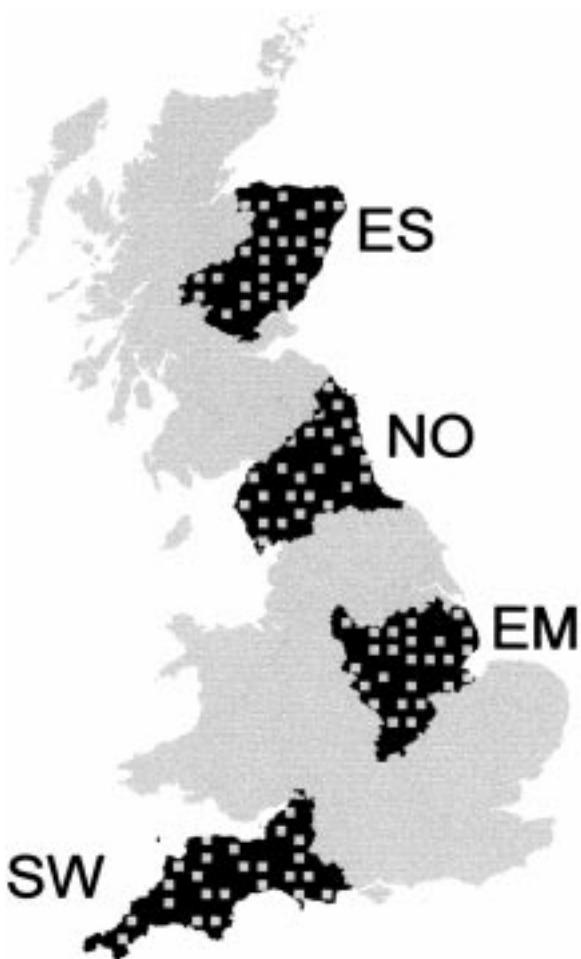


Figure 1. Map of Great Britain, showing the four regions, and the 25 10 × 10 km quadrats in each region, in which mammal occurrences and land cover variables were measured. The regions are defined by counties as follows: SW (Southwest): Cornwall, Devon, Somerset, Dorset, Avon; EM (East Midlands): Derbyshire, Leicestershire, Lincolnshire, Northamptonshire, Nottinghamshire; NO (North England): Cleveland, Cumbria, Durham, Northumberland, Borders, Tyne and Wear; ES (East Scotland): Grampian, Tayside.

variables, is desirable. Mapped habitat or land cover data, especially in the form of spatially referenced digital databases, are ideally suited for this purpose (Miller 1994; Veitch et al. 1995). Maps based on associative models can also circumvent some problems of traditional survey-based range maps, such as biased recording or overestimation of species distributions within range limits (Butterfield et al. 1994).

In this paper, we assess the extent to which land cover can be used to predict the species richness and geographic distributions of terrestrial mammals in Great Britain. Specifically, we examine the effective-

ness for this purpose of the Land Cover Map (LCM) of Great Britain, constructed by the U.K. Institute of Terrestrial Ecology using satellite imagery from the Landsat Thematic Mapper (Fuller et al. 1994). The LCM has been advocated as a useful system for quantifying the likely impacts of land use planning decisions (Fuller et al. 1994; Veitch et al. 1995). It is a potentially powerful and efficient tool for mapping and monitoring, because (a) it provides universal digital coverage of Great Britain at a relatively fine resolution (1 km); (b) it is constructed from Landsat imagery so it has the potential to be updated frequently; and (c) it is widely available within the platform of the Countryside Information System (CIS), a raster-based environmental database manipulation and presentation system for Great Britain. The CIS is currently used by over 40 institutions in the U.K., and is becoming increasingly widely used for monitoring and as the basis for conservation planning decisions (DETR 1998). However, the effectiveness of both the CIS and LCM, for the purpose of mapping the richness and distributions of species, remains largely untested. Therefore, although there are many mappable environmental features which could potentially be used for predictive purposes, in this study we confine our scope to the LCM within the CIS platform, as an evaluation of a widely available existing data source. This study also provides a test case for similar environmental information systems in other countries, upon which conservation and land use planning decisions are based.

Even with an efficient mapping system, the construction of associative models of species richness and distributions relies on the existence of close associations between species and surrogate variables, which can be reliably extrapolated across the region of interest. The strength and nature of these associations can be influenced by a range of methodological, as well as ecological, factors. In this study, therefore, we address the following issues:

(1) The basic question we ask is whether associations between land cover, as expressed in the LCM, and the distributions and species richness of mammals, are strong enough to be useful for predictive purposes.

(2) Associations between species and environmental features can be scale-dependent (Wright et al. 1993; Bohning-Gaese 1996), so we compare predictive models generated at two different geographic scales, national and regional.

(3) For extrapolation over large areas, it is important that associations are spatially consistent. To

Table 1. List of the five orders and 29 species of British terrestrial mammals for which distributions were predicted in this study, with the current status of the geographic distribution in Britain compiled from Harris et al. (1995). Note that a static distribution may hide a possible positive or negative trend in population size.

Order	Common name	Scientific name	Status of British distribution
Insectivores	hedgehog	<i>Erinaceus europaeus</i>	static
	common shrew	<i>Sorex araneus</i>	static
	pygmy shrew	<i>Sorex minutus</i>	static
	mole	<i>Talpa europaea</i>	static
Carnivores	fox	<i>Vulpes vulpes</i>	static, but expanding into urban areas
	stoat	<i>Mustela erminea</i>	contracting
	weasel	<i>Mustela nivalis</i>	contracting
	pine marten	<i>Martes martes</i>	expanding
	badger	<i>Meles meles</i>	expanding
	wildcat	<i>Felis silvestris</i>	static
	muntjac	<i>Muntiacus reevesi</i>	expanding
Artiodactyls	red deer	<i>Cervus elaphus</i>	static/ slight expansion
	sika deer	<i>Cervus nippon</i>	expanding
	fallow deer	<i>Dama dama</i>	static/ slight expansion
	roe deer	<i>Capreolus capreolus</i>	expanding
	red squirrel	<i>Sciurus vulgaris</i>	contracting
Rodents	grey squirrel	<i>Sciurus carolinensis</i>	expanding
	bank vole	<i>Clethrionomys glareolus</i>	static/ contracting with intensive farming
	field vole	<i>Microtus agrestis</i>	static/ contracting with intensive farming
	harvest mouse	<i>Micromys minutus</i>	contracting
Lagomorphs	wood mouse	<i>Apodemus sylvaticus</i>	static
	yellow necked mouse	<i>Apodemus flavicollus</i>	contracting
	brown rat	<i>Rattus norvegicus</i>	static
	black rat	<i>Rattus rattus</i>	static
	house mouse	<i>Mus domesticus</i>	static/ contracting
	dormouse	<i>Muscardinus avellanarius</i>	contracting
	brown hare	<i>Lepus europaeus</i>	contracting
	mountain hare	<i>Lepus timidus</i>	static/ contracting
	rabbit	<i>Oryctolagus cuniculus</i>	static

test this for mammals and land cover, we compare predictive models generated in different regional subdivisions of Great Britain.

(4) Different taxa vary in their degree of habitat specificity, so predictive power of land cover may be taxon-dependent. We compare results for species richness of five mammal orders, and for the distributions of 29 mammal species.

(5) Ordination of predictor variables into orthogonal, composite axes can minimize problems of intercorrelation, but can also alter the predictive power

(Danell et al. 1996; Macdonald et al. 1996). We compare the power of original and ordinated land cover variables to predict mammal species richness and distributions.

We do not proceed to the stage of producing and verifying maps; our study is a preliminary assessment of the predictive value of the LCM, based on the strength of associations between mammals and land cover.

Methods

Selection of quadrats

All mammal and land cover data were measured from one hundred 10×10 km cells of the British national grid, which we refer to throughout this paper as ‘quadrats’. The size of the quadrats was determined by the source of mammal data used, as the most readily accessible source of distribution records for all British species was the Atlas of British Mammals (Arnold 1993), in which the presence or absence of each species is recorded in every 10×10 km cell of the national mapping grid. We chose quadrats from within four discrete regions of Britain (Fig. 1), firstly to allow a blocked statistical design to account for any purely geographical influence on species richness and distributions, and secondly to enable comparison of mammal-landscape associations between regions. A sample of 25 10×10 km quadrats was chosen randomly in each region, with the restriction that a quadrat was only accepted if it was at least 10 km from a previously selected quadrat, in order to minimize the effects of spatial autocorrelation.

Mammal data

In each quadrat the presence or absence of every terrestrial mammal species (all species excluding bats and marine mammals) was recorded, from the Atlas of British Mammals (Arnold 1993). The number of species present in each quadrat was counted to give a value for total species richness. Mammals were then subdivided into Orders, and species richness calculated for each Order. For the analyses of species distributions, a subset of 29 mammal species was used (Table 1). This subset was chosen to coincide with that currently being used as a focus for developing a national monitoring strategy for British mammals (Macdonald et al. 1998). We omitted riparian and aquatic species from our analyses as the LCM does not describe linear features.

Land cover data

The LCM was originally constructed by classifying 25×25 m Landsat pixels into 25 land cover types derived from a combination of summer and winter Landsat TM imagery (Fuller et al. 1994). The CIS has a resolution of 1 km, so for use within the platform of the CIS, the LCM data are pooled at the 1 km scale, and the 25 land cover types are aggregated into

Table 2. Original land cover variables used as predictors of mammal species richness and distributions, from the CIS version of the Land Cover Map of Great Britain. Where similar land cover types were aggregated into single variables, the original land cover types are shown in brackets.

Land cover variable	Code
Urban (urban + suburban land)	URB
Tilled land	TIL
Managed grass	MGR
Rough grass	RGR
Heath grass	HGR
Heath (open shrub heath + dense shrub heath)	HTH
Deciduous woodland	DEC
Coniferous woodland	CON

17 (CIS Users Guide, Dept. of Environment 1995). Thus, each 1×1 km grid cell in Great Britain contains a value for the number of Landsat pixels assigned to each of the 17 land cover types, which corresponds to an estimate of the percentage of the cell covered by each land cover type. To minimize potential analytical complications resulting from the large number of predictor variables, we further condensed the list of land cover types by excluding coastal and wetland habitats, which we presumed to have a relatively minor influence on mammals, and by aggregating urban with suburban land, and open shrub heath with dense shrub heath. A list of all land cover variables included in the analyses is given in Table 2; these were measured as the estimated percentage cover of each 10×10 km quadrat.

Measuring the predictor variables in this way meant they were intercorrelated to a large degree, introducing possible complications for statistical analyses. For this reason we carried out a parallel analysis using orthogonal, composite land cover axes produced by ordination of the original LCM variables. The ordination was done by Principal Components Analysis (PCA) using the SAS statistical package (PRINCOMP procedure). We retained the first five PCA axes, which explained 28%, 23%, 13%, 11% and 9% of variation in land cover, respectively. Loadings of original variables onto the five axes are shown in Table 3. The CIS can be used to determine scores for the five PCA axes in each 1 km grid cell, based on values of the original LCM variables; the axes are thus mappable and have potential predictive value. We compared the predictive power of the PCA axes with the original land cover variables.

Table 3. Loadings of original land cover variables onto the first five PCA ordination axes. Percent variance explained by each axis is shown at the bottom of each column.

Variable	PC1	PC2	PC3	PC4	PC5
URB	-0.44	-0.19	-0.02	0.01	0.55
TIL	-0.49	-0.37	-0.09	0.06	-0.12
MGR	-0.20	0.61	-0.04	-0.03	-0.14
RGR	0.11	-0.06	0.87	0.03	0.35
HGR	0.35	0.24	-0.36	-0.30	0.64
HTH	0.53	-0.27	0.09	-0.25	-0.31
DEC	-0.10	0.56	0.26	0.16	-0.12
CON	0.31	-0.05	-0.16	0.90	0.13
% variance explained	28	23	13	11	9

Table 4. Predictions of mammal species richness at the national scale. Summary of results of multiple linear regressions using (a) original land cover variables, and (b) PCA-ordinated land cover variables. Region was entered into each model as a categorical variable, so does not have a slope. The R^2 values for each predictor represent the partial contribution to the total variance explained for that model.

Taxon	Predictor	Direction of slope	P	R^2
(a)				
Total	region		0.002	0.15
Insectivores	region		0.123	0.05
	HTH	—	0.013	0.06
Carnivores	region		<0.0001	0.17
	HTH	—	0.024	0.05
Artiodactyls	region		<0.0001	0.20
	DEC	+	0.004	0.07
Rodents	region		0.014	0.29
	HTH	—	0.004	0.06
Lagomorphs	region		<0.0001	0.19
(b)				
Total	region		0.001	0.23
Insectivores	region		0.036	0.15
Carnivores	region		0.0003	0.17
Artiodactyls	PC4	+	0.012	0.05
	region		0.0009	0.17
Rodents	PC2	+	0.021	0.05
	PC1	—	0.002	0.21
	region		0.002	0.14

Table 5. Predictions of mammal species richness at the regional scale. Summary of results of multiple linear regressions using (a) original land cover variables, and (b) PCA-ordinated land cover variables. Simple R^2 values are shown for all land cover variables, and contributions to multiple R^2 values are shown only for those variables accepted into a best-fitting multiple regression model.

Region	Taxon	Predictor	Direction of slope	P	Simple R^2	Contribution to multiple R^2
(a)						
SW	artiodactyls	CON	+	0.005	0.30	
EM	total	TIL	-	0.016	0.23	0.23
		MGR	+	0.02	0.21	0.06
		DEC	+	0.019	0.22	0.04
		carnivores	TIL	-	0.019	0.22
		MGR	+	0.022	0.21	0.21
		DEC	+	0.024	0.20	0.10
NO	artiodactyls	CON	+	0.001	0.37	0.37
		RGR	+	0.002	0.36	0.14
		DEC	+	0.003	0.33	
		rodents	MGR	+	0.022	0.21
ES	total	TIL	+	0.0002	0.45	
		carnivores	TIL	+	0.001	0.37
		artiodactyls	DEC	+	0.0002	0.46
		rodents	TIL	+	0.0001	0.55
		HGR	-	0.021	0.21	
NO	insectivores	CON	+	0.012	0.25	0.25
		DEC	+	0.013	0.24	0.12
		carnivores	DEC	+	0.002	0.36
		artiodactyls	TIL	-	0.012	0.25
		HGR	+	0.011	0.25	0.25
ES	rodents	TIL	+	0.015	0.23	0.08
		HGR	+	0.003	0.44	
		URB	+	0.015	0.23	
		HTH	-			
(b)						
EM	total	PC2	+	0.004	0.31	
		PC3	+	0.016	0.23	
		carnivores	PC2	+	0.005	0.30
		artiodactyls	PC3	+	0.0001	0.65
NO	rodents	PC4	+	0.0004	0.43	0.04
		PC2	+	0.009	0.26	
		lagomorphs	PC2	+	0.016	0.23
		total	PC1	-	0.006	0.29
ES	carnivores	PC1	-	0.0003	0.43	
		PC4	+	0.006	0.29	
		PC5	+	0.004	0.31	
		artiodactyls	PC4	+	0.018	0.22
NO	insectivores	PC5	+	0.016	0.23	
		PC5	+	0.008	0.27	
		rodents	PC5	+	0.004	0.32
		PC4	+	0.003	0.32	
ES	PC5	PC4	+	0.023	0.21	
		PC5	+			

Table 6. Predictions of mammal species occurrence at the national scale. Summary of results of multiple logistic regressions using (a) original land cover variables, and (b) PCA-ordinated land cover variables. Region was entered into each model as a categorical variable, so does not have a slope. Where more than one variable is entered into a model, the R^2 value for each variable represents the partial contribution of that variable to the total variance explained by the model.

Species	Predictor	Direction of slope	P	R^2
(a)				
Fox	TIL	+	0.006	0.04
Stoat	HTH	-	0.005	0.04
	region		0.009	0.04
Weasel	TIL	+	0.021	0.03
	URB	+	0.019	0.03
Badger	DEC	+	0.002	0.07
Wildcat	TIL	-	0.008	0.06
Red deer	HTH	+	0.0001	0.14
	DEC	+	0.0003	0.09
Roe deer	region		0.0001	0.11
	CON	+	0.009	0.04
Grey squirrel	region		<0.0001	0.14
	DEC	+	0.003	0.05
Red squirrel	DEC	+	0.007	0.06
	region		0.039	0.03
Harvest mouse	TIL	+	0.0002	0.10
	MGR	+	0.025	0.03
Dormouse	DEC	+	0.017	0.04
	region		0.07	0.01
Mountain hare	TIL	-	0.009	0.05
(b)				
Hedgehog	PC1	-	0.001	0.16
Fox	PC4	+	0.001	0.14
	PC3	-	0.024	0.09
Weasel	PC1	-	0.0001	0.26
Badger	PC2	+	0.0004	0.26
Muntjac	region		0.0005	0.16
Red deer	PC1	+	0.0001	0.24
	PC5	-	0.009	0.06
Fallow deer	region		0.013	0.12
Roe deer	PC1	+	0.0001	0.29
	region		0.009	0.07
	PC2	+	0.002	0.10
Red squirrel	region		0.003	0.18
Grey squirrel	region		0.0001	0.51
Field vole	PC1	-	0.006	0.11
Harvestmouse	region		0.0001	0.41
	PC2	-	0.001	0.13
Woodmouse	PC1	-	0.001	0.15
Brown rat	PC1	-	0.0006	0.19
Housemouse	PC1	-	0.004	0.17
Dormouse	PC2	+	0.002	0.52
	region		0.007	0.08
Mountain hare	PC1	+	0.0001	0.52
	PC5	-	0.003	0.23

Table 7. Predictions of mammal species occurrence at the regional scale. Summary of results of multiple logistic regressions using (a) original land cover variables, and (b) PCA-ordinated land cover variables. Only simple R^2 values are shown for each land cover variable, as no best-fitting model consisted of more than one variable.

Region	Species	Predictor	Direction of slope	P	R^2
(a)					
EM	fallow deer	RGR	+	0.015	0.35
NO	weasel	TIL	+	0.022	0.40
	bank vole	HGR	+	0.023	0.42
	wood mouse	TIL	+	0.014	0.44
ES	common shrew	DEC	+	0.025	0.24
	stoat	HTH	-	0.011	0.40
		MGR	+	0.021	0.33
		DEC	+	0.019	0.27
	wildcat	TIL	-	0.012	0.30
		MGR	-	0.024	0.24
	red deer	TIL	-	0.006	0.43
		HTH	+	0.013	0.42
		MGR	-	0.014	0.41
		URB	-	0.02	0.31
	bank vole	URB	+	0.011	0.38
		HTH	-	0.014	0.29
		DEC	+	0.019	0.28
	mountain hare	TIL	-	0.014	0.58
		HTH	+	0.008	0.43
		URB	-	0.02	0.31
(b)					
SW	dormouse	PC2	+	0.014	0.50
EM	grey squirrel	PC2	+	0.025	0.62
NO	fox	PC4	+	0.02	0.49
	weasel	PC1	-	0.022	0.34
ES	fox	PC3	-	0.018	0.37
		PC2	+	0.013	0.48
		PC4	+	0.016	0.43
	wildcat	PC1	+	0.011	0.45
	red deer	PC1	+	0.005	0.64
	bank vole	PC4	+	0.025	0.41
	brown hare	PC3	-	0.024	0.33
	mountain hare	PC1	+	0.006	0.75

Data analysis

Associations between species richness and land cover were tested using multiple linear regression (GLM in SAS), and associations between the occurrence of each mammal species and land cover were tested using multiple logistic regression (LOGISTIC in SAS). All associations were first tested for the four regions

combined ('national scale'), with region included as a categorical factor in each regression model. Associations were then tested in each region separately ('regional scale'). As a preliminary sifting of land cover variables to aid in model selection, separate univariate regressions were first carried out for each land cover variable, with region included in each model

for the national scale analyses. Bivariate scatterplots were examined, and outliers were removed if they were clearly causing a spurious significant relationship (where the remaining datapoints did not appear to show an association, and removal of the outlier meant the association was no longer significant). Variables which were significant at the arbitrary level of $P \leq 0.025$ were included in the final models; the lower than usual P value was used to reduce problems of multiplicity associated with significance tests using several predictor variables. A more generous P value of 0.1 was set as the criterion for including region in the final model at the national scale, to ensure that any geographical influence was properly accounted for. The small magnitudes and ranges of species richness involved meant that uneven variances were not a problem, and log-transformation did not improve the results, so all analyses were carried out using untransformed data. Possibly for the same reason, no non-linear associations were apparent from visual inspection, so we restricted our analyses to linear models.

Results

Predictions of species richness at the national scale

When the four regions were combined in a single analysis, the original land cover variables were poor predictors of the species richness of mammals (Table 4a). The strongest associations were with region ($R^2 = 0.05–0.29$). Only two land cover variables, HTH and DEC, were significantly associated with species richness, and they contributed little additional information to the regression models ($R^2 = 0.05–0.07$).

When PCA axes were used as predictors (Table 4b), the models, with the exception of that for rodent richness, were still dominated by region ($R^2 = 0.14 – 0.23$), although the strength of the effect varied from the models using original variables. As with the original variables, the PCA axes generally contributed little information to the regression models (none for total richness, insectivores and lagomorphs, $R^2 = 0.05$ for carnivores and artiodactyls). The exception was the model for rodents, for which PC1 accounted for the largest component of variance in species richness ($R^2 = 0.21$).

Predictions of species richness at the regional scale

When regions were analyzed separately, the predictive power of the original land cover variables improved dramatically over the national scale results ($R^2=0.21–0.55$, Table 5a). It also became apparent that there was considerable geographic heterogeneity in associations between species richness and land cover, with different land cover variables being selected as the best predictors of richness in different regions. Predictive power was poorest in SW; only one significant association was detected there. Furthermore, the models generated at the regional scale bore little resemblance to those generated at the national scale.

The results of analyses using PCA axes (Table 5b) present a similar picture. As with the original land cover variables, the predictive strength of the PCA axes at the regional scale ($R^2=0.21–0.69$) was much improved over the results at the national scale. Again, best fitting models varied between regions. The strength of predictive models using PCA axes differed from those using the original variables: in most cases best fitting models were stronger when original variables were used. In SW, no significant associations were detected at all. Only in the EM region, for artiodactyls, rodents and lagomorphs, did the PCA axes produce stronger models than the original variables. For total richness and carnivore richness, the original variables consistently produced stronger predictive models than the PCA axes.

Predictions of species occurrence at the national scale

Of the 29 mammal species included in the analysis, the occurrences of 12 were significantly associated with one or more of the original land cover variables (Table 6a). Region was selected in the regression models for only five species ($R^2 = 0.01–0.14$), and it was the dominant predictor only for roe deer and grey squirrel. The original land cover variables were poor predictors of species occurrences ($R^2 = 0.03 – 0.14$), although the associations generally appear to be accurate in that they are in agreement with known habitat preferences of species (see Corbet and Harris 1991). For example, deciduous woodland (DEC) was positively associated with occurrence of badger, red deer, grey squirrel, red squirrel and dormouse, all characteristic woodland species. Tilled land (TIL) was associated positively with occurrence of fox and harvestmouse,

both common in agricultural landscapes, and negatively with occurrence of wildcat and mountain hare, both of which occur predominantly in undeveloped, upland areas of Scotland.

Using PCA axes as predictors of species occurrence greatly improved the strength of the regression models at the national scale (Table 6b). The occurrences of 17 of the 28 species were now significantly associated with land cover ($R^2=0.11-0.75$), with seven species also associated significantly with region ($R^2=0.07-0.51$).

Predictions of species occurrence at the regional scale

At the regional scale, original land cover variables were far stronger predictors of mammal species occurrence ($R^2=0.24-0.58$, Table 7a) than at the national scale. As with species richness, associations between mammals and land cover varied from region to region. For all but one species (bank vole), significant associations with land cover occurred in one region only. By far the greatest number of associations were in the EM region, and as with species richness, predictive power was poorest in SW, where no significant associations occurred. The models generated at the regional scale did not, on the whole, correspond with those from the national scale.

Predictive models of species occurrences using PCA axes were slightly stronger than those using original variables, for most species ($R^2=0.33-0.75$, Table 7b). In ES, where most of the significant associations occurred, the occurrences of wildcat, red deer, bank vole and mountain hare were predicted more strongly by the PCA axes than by the corresponding original land cover variables. In this region, those species characteristic of upland areas (wildcat, red deer, mountain hare) were positively associated with PC1 ($R^2 = 0.45, 0.64$ and 0.75 , respectively), which describes a gradient from lowland to upland land cover types. Several species (dormouse, grey squirrel, fox, brown hare) were significantly associated with land cover when PCA axes were used but not when original variables were used. Only one species (weasel in NO) was associated more strongly with original variables ($R^2 = 0.4$) than PCA axes ($R^2 = 0.34$).

Discussion

With reference to the five issues outlined in the Introduction, the results of this study may be summarized as follows:

- (1) Overall, the power of the LCM land cover variables to predict mammal distributions and species richness was low, although in some cases up to 75% of variance was explained, suggesting that the system may have predictive value in certain situations.
- (2) Predictive strength was strongly scale-dependent.
- (3) There was very little spatial consistency in the strength and types of associations between mammals and land cover.
- (4) Predictive strength varied between mammal taxa.
- (5) Predictive strength was both improved and diminished by ordination of land cover variables.

We discuss each of these results below, with some additional discussion of the implications for the use of the LCM, and similar systems, in conservation and land use planning.

With a few exceptions, land cover explained less than half of the variation in species richness and occurrence, which is probably too little for the LCM to be of value in its own right as a predictive tool. The first step towards refining and improving the procedure into a system for accurately mapping species richness and distributions is to examine the reasons why the LCM did not account for more of the variation in mammal species richness and occurrence. There are a number of potential contributing factors:

(1) *Dynamic species distributions.* The geographical distributions of a large proportion of Britain's mammal species are currently either contracting or expanding (Table 1), independently of changes in land cover, and usually as a direct or indirect result of human activity (see Corbet and Harris 1991; Harris et al. 1995, for details of individual cases). Thus many species, regardless of the degree of habitat-specificity, do not occupy the full extent of their preferred habitat type. A typical case is the red squirrel, which once occupied deciduous and coniferous woodlands throughout Britain, but through competition with the introduced grey squirrel is now largely restricted to coniferous woodlands in the north of the country, and still declining (Gurnell and Pepper 1993). Conversely, the grey squirrel is still expanding its range and has, presumably, yet to occupy the full extent of suitable habitat in

Britain. This effect obscures underlying associations between land cover and mammal occurrences (and hence species richness), particularly across large areas, reducing the accuracy of associative models based on land cover. One way of overcoming this is by using historical information to determine species' 'ideal broad distributions' before recent human influences, which would presumably be more closely associated with landscape features. In this way, Turpie and Crowe (1994) were able to use land cover variables alone to explain over 85% of the variance in species richness of large mammals across Africa. In effect, this approach represents the modeling of species' fundamental, rather than realized, niches. This method may be of value in identifying habitat types capable of supporting maximum diversity or unique species assemblages, but contributes little to conservation planning based on contemporary patterns.

(2) *Quality of the mammal data.* The Atlas of British Mammals was constructed by compiling *ad hoc* voluntary records of mammal occurrences from around Britain. It should therefore be expected that more remote areas with lower human populations would receive a smaller proportion of the total recording effort (Arnold 1993). In particular, the frequency of recording small, elusive species is likely to be lower in such areas. This may result in both geographic and taxonomic biases in the estimates of species richness. This could explain, for example, the negative associations between heath (HTH), which predominates in remote upland areas, and richness of three of the five mammal orders at the national scale. The only effective way of overcoming this bias would be through a sampling regime which disproportionately emphasizes more remote areas.

(3) *Quality of the land cover data.* Firstly, shortcomings in spectral and radiometric resolution, and the possibility of misclassification, mean that land cover classifications based on Landsat TM imagery do not always accurately represent true land cover (Miller 1994), and thus may not necessarily reflect meaningful habitat distinctions for many species (Short et al. 1996). The LCM classifications were verified against classifications from independent ground reference data and showed correspondences ranging from 67–85%, with Fuller et al. (1994) and Veitch et al. (1995) concluding that 'a realistic assessment of LCM accuracy was probably 80–85%'. This still leaves some room for classification error, although it seems

unlikely this would have had a major influence on our results.

Secondly, problems may have arisen with the scaling up process which preceded our use of the LCM. The LCM was originally constructed at a spatial resolution of 25 m, but for use in the CIS, values for each land cover type were pooled at the 1 km scale. In our study, we further pooled these at the 10 km scale for compatibility with the Atlas of British mammals. Aggregation of spatial data in this way may have a variety of effects, including a loss of information detail, increase in spatial autocorrelation, and possible decrease in model performance (Bian 1997; Turner et al. 1989). Unfortunately there was no opportunity to test the performance of our models at different resolutions, because there is only one scale (10 km) at which data for the occurrence of all British mammal is available. It is likely that the optimum resolution for distribution modeling will vary between species, depending on the scale at which each species utilizes the landscape.

(4) *Influence of factors other than land cover.* Aside from methodological considerations, it is possible that land cover alone simply accounts for only a small proportion of variation in mammal species richness and distributions. If this is the case, much of the residual variance in the regression models is probably attributable to other environmental features, operating on a variety of scales, such as landscape structure (e.g., dormice: Bright et al. 1994), soil types and topography (e.g., badgers: Thornton 1988; Macdonald 1996), or climatic variables (e.g., dormice: Bright et al. 1994). Thus, species richness and distributions of animals would be best predicted by sets of variables which included land cover in combination with other landscape features, such as habitat structure, vegetation species composition or soil attributes (Adams 1996; Short et al. 1996). Future generations of satellite sensors should provide enhanced resolution which may be able to classify additional landscape features useful for predicting and mapping species richness and distributions (Fuller et al. 1994).

Geographic scale, region, taxon, and ordination of land cover variables all affected the power of land cover to predict species richness and distributions. Models for both species richness and occurrences were, for the most part, considerably stronger at the regional than at the national scale. We can see two possible reasons for this. First, a reduction in geographic scale would also have reduced geographic bias in the mammal Atlas data due to under-recording in more re-

mote areas. Second, and probably more importantly, is the dynamic nature of many species' distributions, as previously discussed. Restricting the geographic extent of the models reduces the discrepancy between the distributions of species and habitats, making land cover a more prominent factor determining patterns of distributions and species richness. Furthermore, the relative importance of habitat over other environmental factors, as a predictor of species richness, may be stronger at more restricted scales (Bohning-Gaese 1996). Not only were models stronger at the regional scale, but associations were not consistent between scales, or between regions. These results further suggest that some level of regional stratification is essential for predicting and mapping current species richness and distributions from associative models.

The strength of associations between mammals and land cover was also largely taxon-dependent: Species richness models varied considerably in strength between orders, and species distribution models varied in strength between species. The effect of land cover on species richness is at least partly a result of influences on individual species; for example, the relatively strong association between land cover and species richness of artiodactyls in one region, EM, stems from strong associations with the occurrences of red and roe deer in the same region. We would suggest several logical explanations for differences between species in the predictive power of land cover, including (a) species which are more specialized in their habitat requirements should be more strongly associated with particular land cover types; (b) the scale of interaction of species with the landscape may differ depending on species' home range sizes; (c) species with more dynamic geographic ranges should be less closely associated with land cover. However, our results do not really support any of these explanations: the models were no stronger for habitat specialists or generalists, species with large or small home ranges, or species which saturate their habitat more than others. This seems to lend further weight to the earlier suggestion that land cover is not necessarily a more important determinant of species distributions and richness than other environmental features such as climate, soils or topography.

Ordination of variables had a less dramatic effect on the results than geographic scale, region or taxon. The PCA axes were generally slightly better predictors of species occurrences, but similar or poorer predictors of species richness, than the original variables. Previous studies have found that ordinating variables either

enhances (Danell et al. 1996) or diminishes (Macdonald et al. 1996) the predictive power of environmental variables. In our study, it seemed that for most species predictive power was enhanced when variables were ordinated, because of the additional land cover information incorporated into the PCA axes. For example, at the national scale, the occurrence of mountain hare was associated negatively with tilled land (TIL) ($R^2 = 0.05$). In the PCA ordination, TIL was absorbed into PC1, which describes a more general gradient of the degree of land development, ranging from strongly urban and agricultural lowland landscapes, through to less developed upland landscapes dominated by heath and heathgrass. PC5 accounts for additional aspects of the same gradient, and together these two axes formed a strong predictive model of mountain hare occurrence ($R^2 = 0.75$). On the other hand, predictive power for some species was diminished when PCA axes were used. For example, both squirrel species were positively associated with deciduous woodland (DEC), but DEC was absorbed into PC2 in which MGR was the most important variable. This meant that in the PCA models, occurrence of neither of the squirrel species was significantly associated with land cover. Clearly, then, while the use of ordinated variables for prediction can be an effective way of accounting for the influence of several land cover types without the need to include intercorrelated predictor variables in the same model, the advantage of using ordinated variables needs to be established separately for each taxon.

In summary, this study has provided an assessment of a new digital land cover classification for Great Britain, the Land Cover Map, within the platform of the Countryside Information System, for the purpose of predicting and mapping mammal species richness and distributions. The results underscore the importance of regional stratification in producing maps based on associative models, even within a relatively small, homogeneous area such as Great Britain. This is likely to be even more important in larger, more heterogeneous countries. Although there is probably some room for improvement in the accuracy with which mammal distributions and land cover are represented, the major obstacle in producing accurate maps is the dynamic nature of many species' distributions and the resulting non-saturation of habitats. Therefore, although the LCM and CIS do show some promise as predictive tools, we advise caution in basing landuse and conservation planning decisions too firmly on the results obtained from systems such this.

Acknowledgements

Thanks to Lindell Bromham for help with designing the study, and to Richard Cormack, Paul Johnson, Mike Packer and Tim Robinson for helpful advice and comments. Thanks also to David Lambert in the Department of Ecology, Massey University, New Zealand, for providing facilities while the manuscript was being completed. The work was partly funded by the Department of Environment and the Joint Nature Conservation Committee.

References

- Adams, J. A. 1996. Towards a better vegetation scheme for global mapping and monitoring. *Global Ecol. Biogeogr. Lett.* 5: 3–6.
- Arnold, H. 1993. The Atlas of British mammals. Institute of Terrestrial Ecology and Joint Nature Conservation Committee, U.K.
- Bian, L. 1997. Multiscale nature of spatial data in scaling up environmental models. In *Scale in remote sensing and GIS*. pp. 13–26. Edited by D. A. Quattrochi and M. F. Goodchild. CRC Press, Boca Raton.
- Bohning-Gaese, K. 1996. Determinants of avian species richness at different spatial scales. *J. Biogeogr.* 24: 49–60.
- Bright, P. W., Mitchell, P. and Morris, P. A. 1994. Dormouse distribution: survey techniques, insular ecology and selection of sites for conservation. *J. Appl. Ecol.* 31: 329–339.
- Butterfield, B. R., Csuti, B. and Scott, J. M. 1994. Modeling vertebrate distributions for Gap Analysis. In *Mapping the diversity of nature*. pp. 53–68. Edited by R. I. Miller. Chapman and Hall, London.
- Clarke, R. (ed.) 1986. The handbook of ecological monitoring. Clarendon Press, Oxford.
- Corbet, G. B. and Harris, S. (eds.) 1991. The handbook of British mammals. Blackwell Scientific Publications, Oxford.
- Danell, K., Lundberg, P. and Niemela, P. 1996. Species richness in mammalian herbivores: patterns in the boreal zone. *Ecography* 19: 404–409.
- DETR 1998. CIS World Wide Web site: <http://www.nmw.ac.uk/ite/cisflier.html>.
- Fuller, R. M., Groom, G. B. and Jones, A. R. 1994. The Land Cover Map of Great Britain: An automated classification of Landsat Thematic Mapper data. *Photogram. Engng. Remote Sensing* 60: 553–562.
- Gurnell, J. and Pepper, H. 1993. A critical look at conserving the British red squirrel *Sciurus vulgaris*. *Mammal Rev.* 23: 127–137.
- Harris, S., Morris, P., Wray, S. and Yalden, D. 1995. A review of British mammals: population estimates and conservation status of British mammals other than cetaceans. Joint Nature Conservation Council, Peterborough.
- Macdonald, D. W., Mace, G. M. and Rushton, S. P. 1998. Proposals for future monitoring of British mammals. *Mammal monitoring: a plan for the 21st century*. Department of Environment, Transport and the Regions and Joint Nature Conservation Council, U.K.
- Macdonald, D. W., Mitchelmore, F. and Bacon, P. J. 1996. Predicting badger sett numbers: evaluating methods in East Sussex. *J. Biogeog.* 23: 649–655.
- Miller, R. I. (ed.) 1994. *Mapping the diversity of nature*. Chapman and Hall, London.
- Short, H. Z., Hestbeck, J. B. and Tiner, R. W. 1996. Ecosearch: a new paradigm for evaluating the utility of wildlife habitat. In *Conservation of faunal diversity in forested landscapes*. pp. 569–594. Edited by R. M. DeGraaf and R. I. Miller. Chapman & Hall, London.
- Spellerberg, I. F. 1991. Monitoring ecological change. Cambridge Univ. Press, Cambridge.
- Thornton, P. S. 1988. Density and distribution of badgers in southwest England – a predictive model. *Mammal Rev.* 18: 11–23.
- Turner, M. G., O'Neill, R. V., Gardner, R. H. and Milner, B. T. 1989. Effects of changing spatial scale on the analysis of landscape pattern. *Landscape Ecol.* 3: 153–162.
- Turpie, J. K. and Crowe, T. M. 1994. Patterns of distribution, diversity and endemism of larger African mammals. *S. Afr. J. Zool.* 29: 19–31.
- Veitch, N., Treweek, J. R. and Fuller, R. M. 1995. The Land Cover Map of Great Britain – A new data source for environmental planning and management. In *Advances in environmental remote sensing*. pp. 157–170. Edited by F. M. Danson and S. E. Plummer. John Wiley and Sons, Chichester.
- Wright, D. H., Currie, D. J. and Maurer, B. A. 1993. Energy supply and patterns of species richness on local and regional scales. In *Species diversity in ecological communities: historical and geographical perspectives*. pp. 66–74. Edited by R. E. Ricklefs and D. Schlüter. University of Chicago Press, Chicago.