Biological Conservation 142 (2009) 1515–1522

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Relationship between distributions of threatened plants and protected areas in Britain

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ARTICLE INFO

Article history:
Received 24 October 2008
Received in revised form 13 February 2009
Accepted 15 February 2009
Available online 24 March 2009

Keywords:
Britain
Biodiversity conservation
National priority species

ABSTRACT

The establishment and maintenance of a system of protected areas is central to regional and global strategies for the conservation of biodiversity. The current global trend towards human population growth and widespread environmental degradation means that such areas are becoming increasingly isolated in fragmented habitat islands. In regions in which this process is well advanced a high proportion of species are thus predicted to have become restricted to protected areas. Here using uniquely detailed datasets for Britain, a region with close to the global level of percentage coverage by statutory protected areas, we determine the extent of restriction of Red List vascular plant species of conservation concern to these areas. On the basis of currently known distributions, overall our results strongly support the importance of a dual conservation strategy in Britain, in which protected areas are maintained with particular reference to those biodiversity features (such as many threatened plant species) that are highly dependent on them, and in which components of the wider landscape are also managed in such a way as to promote the abundance and distribution of such features with particular reference to those which are unlikely to persist in protected areas alone.

1. Introduction

Globally, more than 100,000 protected areas have been designated, covering over 12% of the land area (Chape et al., 2005). This represents both a substantial investment in this mechanism for conserving biodiversity and a heavy reliance on the approach. To be effective, above all else protected areas must achieve two primary objectives (Margules and Pressey, 2000). First, they must capture a sample of biodiversity, and preferably a large one, with a particular emphasis on those features that are rare, threatened or otherwise of significant conservation concern. Second, protected areas must protect or buffer that sample from threatening processes, both now and into the future.

There has been much study of how well the first of these two objectives is met. In the main, however, this has focussed on determining the frequency with which protected areas fail to capture key biodiversity features (gap analysis; Fearnside and Ferraz, 1995; Oldfield et al., 2004; Powell et al., 2000; Rodrigues et al., 2004a), how representative is that capture relative to the extent of the occurrence of the features in the region of interest (e.g. Jackson et al., 2004b; Martinez et al., 2006; Pressey and Taffs, 2001; Pressey et al., 2002; Rouget et al., 2003; Sætersdal et al., 1993), and how efficient is that capture relative to random or optimised theoretical distributions of protected areas (e.g. Araújo, 1999; Castro Parga et al., 1996; Jackson et al., 2004a; Nantel et al., 1998; Pawar et al., 2007; Rodrigues et al., 1999). In general, it has been found that key biodiversity features are regularly entirely missing from protected area systems, and that the representation of those features that are captured is highly unrepresentative of their wider occurrence, and that real protected area systems are in consequence highly inefficient.

Rather surprisingly, discussion of how well protected areas capture biodiversity features has paid only limited attention to the level of dependence of species of conservation concern on those areas (Gaston et al., 2006). In principle, protected area systems could be performing rather poorly in other regards, including the level of representation of many important biodiversity features and the extent to which alternative systems could do better, and yet the occurrence of a significant number of native species could be entirely or largely restricted to them. This seems likely to occur particularly in regions which have experienced extensive land transformation and intensive land use, and thus where the opportunities for persistence in the wider landscape are much reduced. Much of the developed world, and increasing areas of the developing world, can of course be so characterised.

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doi:10.1016/j.biocon.2009.02.020

In a related vein, there has been rather little consideration of the potential importance of patterns of protected area coverage in shaping patterns of spatial variation in species richness (but see Deguise and Kerr, 2006; Evans et al., 2006; Sinclair et al., 2002). Nonetheless, it seems reasonable to predict that if existing protected areas are serving to maintain biodiversity in landscapes, then having controlled for environmental factors that influence broad geographic trends in species richness, those areas with higher coverage of protected areas should on average have higher levels of richness. This seems particularly likely to be the case for rare and threatened species assuming that protected areas have not been sufficiently effective as to result in formerly threatened species no longer being at significant risk (whilst protected areas may commonly serve to reduce the level of threat faced by a species, they are seldom adequate to entirely remove it).

Arguably, the paucity of studies both of the level of restriction of species to protected areas and of the influence of protected areas on patterns of species richness is in large part because the detailed and spatially explicit datasets needed for such analyses either have not been systematically compiled or simply do not exist. However, the fine resolution mapping of species distributions for some taxonomic groups across Britain, a region in which the proportional coverage by protected areas is close to that found globally, allows this issue directly to be addressed. In this paper, we use such data for those higher vascular plants on the 2005 UK. Red List (Cheffings and Farrell, 2005) to assess (i) the coverage of these higher vascular plants by protected areas; (ii) the degree to which these plants are restricted to protected areas; and (iii) the extent to which their richness is associated with the current distribution of protected areas.

2. Methods

2.1. Data

For present purposes, protected areas were defined as those receiving legal backing (i.e. statutory sites) for which biodiversity conservation (or some element(s) thereof) was the primary objective. Geo-referenced boundary data for each individual protected area across Britain were therefore obtained for Local Nature Reserves (LNRs), National Nature Reserves (NNRs), Ramsar Sites, Special Areas of Conservation (SACs), Special Protection Areas (SPAs) and Sites of Special Scientific Interest (SSSI) from English Nature (now part of Natural England), Scottish Natural Heritage, and the Joint Nature Conservation Committee in October 2005. Unfortunately, given constraints on the availability of strictly comparable data, it was not possible also to include Northern Ireland.

All individual protected area boundaries were combined to create a single protected area layer with no overlapping sites (using ArcMap GIS), referred to as 'all statutory' (Fig. 1a). In addition, these data were clipped to a 10 km × 10 km vector grid covering Britain (thereby excluding non-terrestrial portions of some coastal sites). This spatial resolution was considered suitable for analyses of the relationship between protected area coverage and the richness of threatened species for various reasons. Namely, given the trade-offs between having sufficient variability in coverage by protected areas (the smaller the resolution the closer this comes to a binary state) and in the occurrence of threatened species, and constraints on the computer processor time and resources required for running spatially explicit multiple regression models (see below).

To control for the effects of potential confounding factors on the possible influence of protected area coverage on species richness in each 10 km × 10 km grid square, five variables were selected a priori as potentially important in shaping the distribution of threatened plant species (e.g. Thompson and Jones, 1999): (i) land area – calculated by clipping the 10 km × 10 km vector grid with a polygon for Britain; (ii) elevation – extracted from a UK Digital Elevation Model (DEM) at 50 m resolution (Edina Digimap©) and the mean calculated; (iii) proportional coverage by urban areas - calculated using 25 m resolution Land Cover 2000 data (Fuller et al., 2002); and (iv) human population density – taken from the 1991 population census (Martin and Tate, 1997) with data from enumeration districts allocated to 200 m squares using a weighted distance–decay redistribution function (which fits a smoothed surface), and corrected to average densities. Environmental temperature would be an obvious additional variable to include, but this covaries strongly with elevation, and a number of other candidate variables similarly covary markedly with some of those included.

Fig. 1. Map showing the geographic locations of statutory (legally backed) protected areas across Britain. Included are Local Nature Reserves, National Nature Reserves, Ramsar Sites, Sites of Special Scientific Interest, Special Areas of Conservation and Special Protection Areas.

Finally, currently known occurrence records for all species included within the 2005 UK vascular plants Red List were obtained directly from the Botanical Society of the British Isles. Only contemporary records from 1987 onwards (the most recent data collection period for the New Atlas of British and Irish Flora; (Preston et al., 2002a) were considered for analysis. Species categorised as either critically endangered (CE), endangered (EN), vulnerable (VU), or near threatened (NT) were retained, and those categorised as extinct (EX), extinct in the wild (EW), data deficient

(DD) or as least concern (LC) were excluded ($N = 1313$). In this instance, 'species' refers to a range of higher plant taxa (ferns, conifers, flowering plants), subspecies, critical species, and microspecies (e.g. *Heiracia, Sorbus, Euphrasia, Taraxacum*), hybrids, and some long established alien species (archaeophytes) with a long history of introduction to the UK (e.g. *Adonis annua, Bupleurum rotundifolium*). All individual species records ($N = 29,349$) were matched with protected areas using their geographic coordinates (if available at a fine [100 m] resolution) and any site names reported in the dataset. For those species for which such information were lacking, geographically less precise records were assigned to a particular locality by matching their specific habitat (landcover, geology and elevation) requirements to parcels of the same habitat type using the Land Cover 2000 data, and data extracted from the UK DEM. Records for which there was no detailed location information were discarded ($N = 72$). In total, 371 species were included in the analysis. These occurrence data were also assigned to each 10 km × 10 km grid square across Britain (Fig. 2), and the total richness (all species together and for each of the four threat categories individually: CE, EN, VU and NT) calculated for each square. It should be noted that these analyses use currently available distribution data for each of the higher vascular plant species, thus there may be instances where a species is known to occur at a site but for which there are no records.

Fig. 2. Contemporary (records from 1987 onwards) distribution of Red List vascular plant species richness across Britain ($N = 371$) at a 10 km^2 resolution. Species richness was square root transformed and subdivided into quartiles for display.

2.2. Analyses

To determine whether or not statutory protected area coverage is a significant positive correlate of Red List plant species richness across Britain, linear regression models of the relationships between richness and the five independent predictor variables (proportion of a grid square protected, land area, elevation, urban coverage and human population density) were constructed in SAS v. 9.1 (proc mixed). Red List species richness, mean elevation, urban coverage and mean human population density were each logarithmically transformed to base ten (after adding 1 to all Red List species richness, urban coverage and mean human population density records to take account of zero values). Land area (converted to the proportion of a grid square) was arc sine square root transformed. Finally, the proportion of a grid square protected was normalised through square root transformation. Colinearity between predictors was explored using tolerance levels (Quinn and Keough, 2002). These levels were sufficiently high in all cases (i.e. greater than 0.1; following Quinn and Keough, 2002), to enable separation of the independent effects of each of the predictors. The fit of quadratic terms was also tested to detect any simple, non-linear relationships. Models were constructed both including and excluding all cases where the proportion of a grid square protected was equal to zero. The results from these models were largely identical, and thus only those including zero values are reported here.

We first constructed a full set of independent errors linear regression models that contained all possible combinations of the five independent variables and their squared terms. We then used Akaike's Information Criteria (AIC) to determine which model(s) best approximates reality given the data considered. Following Johnson and Omland (2004), we calculated the difference between each model's AIC value and that of the best fitting model (the one with the smallest AIC) and used these data to calculate the weight of each model (AIC_w), i.e. the probability that it provides the best fit to the data. In this case, only those models for which all parameters were significant were assessed. The difference in model weights relates to the strength of evidence for one model versus another. Individual weights $\geqslant 0.95$ suggest that strong inferences can be made using just that one model. Where the AIC_w of the best fitting model was <0.95, we established a 95% confidence set of models by summing the AIC_w from largest to smallest until the sum was $\geqslant 0.95$; the corresponding subset of models is a type of confidence set on the best model (Burnham and Anderson, 2002).

Spatial autocorrelation may invalidate the assumption of independent errors, distorting classical tests of association and rendering correlation coefficients, regression slopes and associated significance tests misleading (Cressie, 1991; Legendre et al., 2002; Lennon, 2000). To avoid this, where appropriate (where significant spatial autocorrelation was found within the residuals of the independent errors models using the Moran's I statistic) analyses were also conducted that implemented spatially explicit models that fit a spatial covariance matrix to the data and use this to adjust test statistics accordingly (Littell et al., 1996). The choice of the exponential, over other spatial covariance structures, was based on visual examination of semi-variograms of independent error model residuals. Given that estimates of variance explained (i.e. r^2 values) cannot be derived from such spatial models, we used r^2 values from the equivalent non-spatial models as an indication only.

In principle, it is possible to determine whether the level of restriction of species to protected areas is greater or less than expected by chance. However, in practice this is logistically enormously complicated by the practicalities of redistributing a large set of protected areas of highly variable areas randomly across a landscape without overlap, and by the logical concern that such redistribution makes little sense given that protected areas are literally shaped by local constraints (coastlines, topography, urban areas, etc.). In the past, such exercises have thus tended to simplify the process by assuming that protected areas occupy none or all of a grid cell. This is not appropriate in the present case.

3. Results

3.1. Effectiveness of protected areas

Of the 371 species analysed, 331 (88%) were represented at least once within protected areas. Additionally, more than 80% of the species in each of the four threat categories have been recorded in at least one statutory protected area (Table 1). Considering each protected area type separately, 327 (88%) species were recorded at least once on SSSI, 288 (77.6%) on SACs, 227 (61.2%) on SPAs, 213 (57.4%) on NNRs, 159 (42.9%) on Ramsar Sites, and 58 (15.6%) on LNRs.

For 41 species no known contemporary records were coincident with statutory protected areas. Of these, five are categorised as CE, five as EN, 27 as VU, and four as NT. Considering all 371 species, 9% are largely confined to protected areas (>75% records from protected areas). Further, of these, 3% ($N = 10$) are totally confined (100% records from protected areas). By contrast, for just less than half (46%) of the species, less than 25% of records were from protected areas.

Considering each of the threat categories individually, 17% (5) of species categorised as CE, 7% (5) as EN, 16% (27) as VU, and 4% (4) as NT were entirely absent from statutory protected areas across Britain. Conversely, in all cases, less than 5% of species were totally confined to these areas (4% [1] CR, 4% [3] EN, 3% [5] VU, 1% [1] NT).

3.2. Patterns of restriction to protected areas

Considering all contemporary records across the 371 species collectively, just over a quarter (26.5%) coincide with statutory protected areas. For each of the Red List categories individually, less than a third of records were from statutory protected areas (32% EN, 27% CE, 25% NT, and 19% CR). For most species the number of representations within these areas was low. More than a half of the species were represented by less than ten occurrence records, and over 80% by less than 30%. Spatially explicit ANOVA showed no significant differences in the level of restriction to statutory protected areas (proportion of range protected) between the four Red List categories ($F_{3,367} = 0.79$; $P > 0.05$).

Range size was a significant correlate of the proportion of a species' range covered by statutory protected areas, although the relationship was non-linear (Fig. 3). At low to intermediate range sizes, range size was positively related to the proportion of the range protected (indicated by a significant positive linear term; $F_{1,368} = 35.49$; $P < 0.0001$) and at intermediate to large species range sizes it was significantly negatively related (indicated by a significant negative squared term; $F_{1,368} = 33.81$; $P < 0.0001$). Nonetheless, when those species for which the proportion protected was zero were removed from the analysis, the relationship was significantly negative ($F_{1,329} = 81.08$; $P < 0.0001$). Thus, excluding all species for which the proportion protected was zero, the proportion of the range size protected significantly decreased as range size increased.

3.3. Protected area coverage as a correlate of Red List species richness

Residuals from all models of the richness of Red list species were found to be significantly spatially autocorrelated using

Table 1
Total number of current records (1987 onwards), % protected, total number of species and % protected for each of the IUCN Red List threat categories (CE – critically endangered, EN – endangered, VU – vulnerable) and species categorised as near threatened (NT) as applied to higher vascular plants across Britain.

Threat category	Total records	% Records protected	Total species	% Species protected
CE	1358	18.9	29	82.8
EN	3954	32.1	77	93.5
VU	12,675	26.6	173	85
NT	11,362	25.3	92	95.7
Total	29,349	26.5	371	87.8

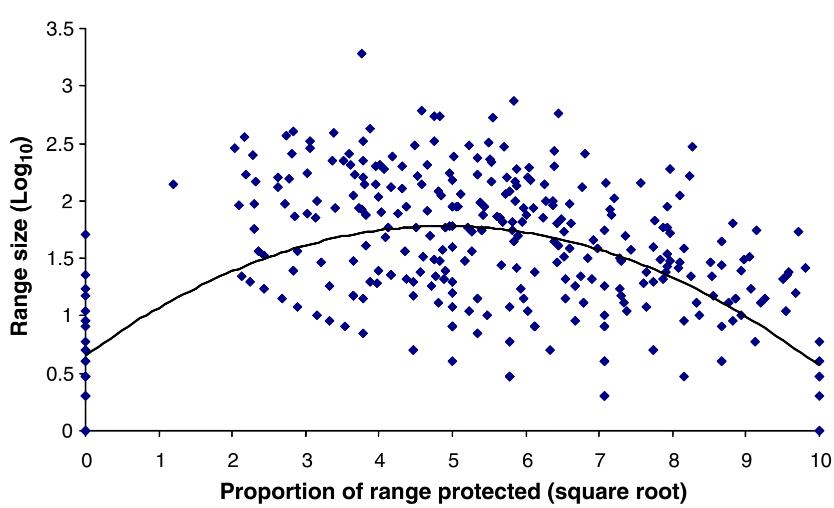

Fig. 3. Bivariate relationship between the proportion of a species' range protected and its range size. The proportion protected was square root transformed and range size was logarithmically transformed to base ten. The solid line represents predicted values from the best fitting independent errors linear regression model. The points represent the transformed raw data.

Moran's I. Thus, given that the results from the independent errors and the spatially explicit regression models were largely identical, only results from the latter set are reported.

Considering the 371 species collectively, after controlling for significant spatial autocorrelation, a single model provided the best fitting descriptor of the data ($AIC_w > 0.99$). Protected area coverage was the most important predictor of species richness across Britain, followed by land area, protected area coverage^2, mean human population density^2, urban coverage and, finally, urban coverage^2 (Table 2). Protected area coverage, land area, mean human population density^2 and urban coverage were significant positive predictors of species richness, whereas protected area coverage^2 and urban coverage^2 were significant negative predictors. The significance of both the linear and quadratic protected area coverage terms suggests that, at low to intermediate levels of coverage, species richness increased linearly with increasing coverage. Conversely, at intermediate to high levels of protected area coverage, the rate of increase in species richness declined with increasing coverage. All other models in the full set of candidate models were very unlikely ($\Delta AIC > 10$; difference between the AIC value of model i and the lowest AIC value).

Although no single best fitting model was found, protected area coverage was always retained as the most important predictor of species richness considering species categorised as CE, EN, VU and NT separately. Five models comprised the 95% confidence set for CE species, with the best fitting model explaining only 48% of the total variation across all models (Table 2). Similarly, three best fitting models explained >95% of the total variation across all models considering EN and NT species richness and two for VU species richness (Table 2).

Following a model averaging approach across all models, protected area coverage, mean human population density and urban coverage alone had a significant effect on species richness (i.e. 95% confidence intervals around the model averaged estimates did not overlap zero). Conversely, neither land area nor mean elevation were significant predictors. For each of the four response variables (CE, EN, VU and NT), the same decelerating curve observed between total species richness and protected area coverage prevailed, although for NT species richness the linear term was not significant. For CE, EN and VU species richness, the linear term was only significant when the squared term was also in the model.

4. Discussion and conclusions

The current portfolio of protected areas in Britain covers occurrences of the vast majority of species on the plant Red List for the region (Table 1). Assuming that these areas serve to reduce some of the pressures faced by these species, this is particularly encouraging for at least two main reasons. First, a high proportion of Red List plant species are found to occur within protected areas despite the fact that many of these areas were not originally designated for the purposes of conserving the Red List species that occur within their boundaries. Indeed, many were designated simply as being good representatives of particular habitat types, and have become progressively more significant as other areas have been lost, and at the time of designation some of these species were not recognised as being at particular risk. Second, as observed earlier, much has been made in the conservation biology literature of the uneven representation of many important biodiversity features within protected area systems and of the extent to which alternative systems could do better (Deguise and Kerr, 2006; Hopkinson et al., 2000; Jackson et al., 2004a; Pressey and Taffs, 2001; Rodrigues et al., 2004b; Scott et al., 2001). One could in consequence be led to believe that existing protected areas are providing little benefit. However, plainly in terms of harbouring species of conservation concern that is not so in the present case.

Table 2

Sets of best fitting spatially explicit mixed effect linear regression models (95% confidence set) for the relationship between threatened plant species richness (total Red List species richness (ALL), critically endangered (CE), endangered (EN), vulnerable (VU) and near threatened (NT)) and environmental variables. Shown for each model are: the r^2, ΔAIC (difference between the AIC value of model i and the minimum AIC), AIC weight (AIC_w), independent predictors (p refers to proportion and m to mean), parameter estimate (slope), standard error (SE), and F-value with associated significance values. See Section 2 for full details.

Model	r^2	ΔAIC	AIC_w	Independent predictor	Estimate	±SE	F
ALL	15.7	0	0.99	*p*Protected	1.38^{***}	0.096	204.47
				Land area	0.32^{***}	0.032	101.79
				*p*Protected^2	-1.05^{***}	0.117	79.85
				*m*Density^2	0.03^{***}	0.004	44.46
				*p*Urban	3.67^{***}	0.713	26.45
				*p*Urban^2	-40.75^{***}	9.018	20.42
CE	11.4	0	0.48	*p*Protected	1.14^{***}	0.192	35.75
				*m*Density^2	0.02^{***}	0.005	16.46
				*p*Protected^2	-0.76^{**}	0.238	10.16
				pUrban^2	-48.47^{ns}	33.063	2.15
				*p*Urban	2.21^{ns}	1.923	1.32
	12.1	0.6	0.36	*p*Protected	1.13^{***}	0.191	35.21
				*m*Density^2	0.02^{**}	0.005	13.56
				*p*Protected^2	-0.73^{**}	0.238	9.37
				*p*Urban^2	-62.35^{ns}	33.879	3.39
				Land area	0.11^{ns}	0.059	3.27
				*p*Urban	3.19^{ns}	1.993	2.56
	13.5	4.5	0.05	*p*Protected	1.15^{***}	0.191	36.77
				*m*Density^2	0.02^{***}	0.005	16.93
				*p*Protected^2	-0.76^{**}	0.238	10.26
				*p*Urban^2	-11.96^{ns}	9.312	1.65
	13.7	5.1	0.04	*p*Protected	1.13^{***}	0.193	34.38
				*p*Protected^2	-0.79^{ns}	0.240	10.76
				Land area	0.15^{*}	0.059	6.11
				*p*Urban^2	-74.20^{*}	34.083	4.74
				*p*Urban	3.87^{*}	2.005	3.73
	13.6	6.4	0.02	*p*Protected	1.15^{***}	0.190	36.62
				*m*Density^2	0.02^{***}	0.005	14.76
				*p*Protected^2	-0.74^{**}	0.238	9.67
				Land area	0.08^{ns}	0.057	2.03
				*p*Urban^2	-10.22^{ns}	9.384	1.19
EN	14	0	0.72	*p*Protected	1.50^{***}	0.154	95.15
				*p*Protected^2	-1.20^{***}	0.180	44.45
				*p*Urban^2	-39.18^{ns}	28.470	1.89
				*p*Urban	1.31^{ns}	1.254	1.10
	13.8	3.4	0.13	*p*Protected	1.51^{***}	0.153	96.70
				*p*Protected^2	-1.20^{***}	0.180	44.50
				*p*Urban^2	-11.58^{ns}	10.772	1.16
	13.9	4.2	0.1	*p*Protected	1.50^{***}	0.154	94.81
				*p*Protected^2	-1.19^{***}	0.181	43.57
				*p*Urban^2	-41.23^{ns}	29.136	2.00
				*p*Urban	1.45^{ns}	1.317	1.21
				Land area	0.02^{ns}	0.045	0.11
VU	10.6	0	0.76	*p*Protected	1.21^{***}	0.111	119.90
				*p*Protected^2	-0.94^{***}	0.137	47.53
				*m*Density^2	0.01^{***}	0.003	21.06
				Land area	0.08^{**}	0.029	7.59
				*p*Urban	2.61^{*}	1.034	6.35
				*p*Urban^2	-47.71^{*}	20.292	5.53
	9.9	2.3	0.23	*p*Protected	1.23^{***}	0.111	123.20
				*p*Protected^2	-0.96^{***}	0.137	49.62
				*m*Density^2	0.02^{***}	0.003	29.92
				*p*Urban	1.84^{ns}	0.998	3.41
				*p*Urban^2	-36.22^{ns}	19.891	3.32
NT	8.5	0	0.88	*p*Protected	1.07^{***}	0.111	93.07
				*p*Protected^2	-0.86^{***}	0.135	40.72
				Land area	0.10^{**}	0.027	14.23
				*p*Urban	1.82^{*}	0.786	5.39
				*p*Urban^2	-22.26^{*}	9.767	5.19
	8.4	5.4	0.06	*p*Protected	1.08^{***}	0.111	94.68
				*p*Protected^2	-0.85^{***}	0.135	39.58
				Land area	0.09^{**}	0.028	9.64
				*m*Density^2	0.01^{*}	0.003	4.51
				*p*Urban	1.64^{*}	0.790	4.33
				*p*Urban^2	-20.07^{ns}	9.812	4.19

(*continued on next page*)

Table 2 (*continued*)

Model	r^2	ΔAIC	AIC_w	Independent predictor	Estimate	±SE	F
8.3	6.7	0.03		*p*Protected	1.09^{***}	0.111	95.77
				*p*Protected^2	-0.87^{***}	0.135	41.51
				Land area	0.09^{**}	0.027	11.14
				*p*Urban^2	-0.83^{ns}	3.202	0.07

* $P < 0.01$.
** $P < 0.001$.
*** $P < 0.0001$.

An effective portfolio of protected sites should, all else being equal, give rise to positive relationships between the number of species present in a region and the amount of protected land in that region. Two mechanisms may contribute to such correlations. First, protected areas may tend to be located in areas of high species richness. Second, protected area status may prevent habitat degradation and overexploitation, or at least reduce their rates of occurrence, and thus reduce extinction rates and promote species richness. Both mechanisms reflect high protected area effectiveness. Nonetheless, tests for such predicted positive relationships between species richness and protected area coverage are astonishingly scarce. Indeed, six previous studies have considered the relationship between species richness and the amount of protected land. In South Africa both total avian species richness and that of threatened species exhibit weak positive relationships with the amount of protected land (Evans et al., 2006). Conversely, across tropical forested countries, ecozones of Canada, administrative regions of Chile, and elevational gradients in China and Nepal, the species richness of various taxonomic groups were either negatively or not correlated with the coverage of protected areas (Armesto et al., 1998; Deguise and Kerr, 2006; Hunter and Yonzon, 1993; Kerr and Burkey, 2002; Lan and Dunbar, 2000). The results of most of these studies must, however, be interpreted cautiously as they failed to take explicit account of environmental factors that influence broad geographic trends in biodiversity (but see Evans et al., 2006). Clearly, additional studies from other regions are required before generalisations can be made regarding the form of such relationships.

Despite such good overall species coverage, statutory protected areas across Britain cover less than one third of the total number of occurrence records for Red List plant species, and the level of multiple representation is rather low (>50% species represented <10 times). This limits the extent to which there is effective risk-spreading amongst protected areas, and increases the importance of ensuring the continued persistence of these species within those protected areas in which they do occur. Perhaps of most immediate concern, however, is that at least 40 species are apparently entirely absent from protected areas, five of which are considered to be critically endangered (*Armeria maritima* subsp. *elongata, Chenopodium urbicum, Clinopodium jethifolium*, *Galium tricornutum, Ranunculus arvensis*). Considering this list of 40 missing species, several are unsurprising given their confinement to single/few sites (e.g. *Armeria maritime* subsp. *elongate*, *Clinopodium menthifolium*, *Crepis praemorsa*, *Diapensia lapponica*, *Hydrilla verticillata*, *Phyteuma spicatum*, *Tepbroseris integrifolia* subsp. *maritime*, *Stachys germanica*). A second group of species are the arable weeds, largely absent from statutory protected areas given the historical avoidance of their associated habitats for conservation efforts (e.g. *Bromus secalinus*, *Clinopodium acinos*, *Euporbia exigua*, *G. tricornutum*, *Misopates oronium*, *R. arvensis*, *Silene noctiflora*, *Spergula arvensis*). It should be pointed out that, although currently available distribution records for these species indicate absence from statutory protected areas, local records will likely exist in some instances but these are not widely available. This coverage, however, includes only those statutory protected areas specifically designated for the purpose of biodiversity conservation, thereby disregarding a range of other conservation designations (e.g. Areas of Outstanding Natural Beauty, Biosphere Reserves, Biogenic Reserves, Heritage Coasts). The total extent of protected areas within Britain is inevitably much greater when all of these protected land categories are considered. In addition, non-governmental organisation (NGO) reserves, including more than 2500 Wildlife Trust reserves, 1153 Woodland Trust reserves and more than 170 Royal Society for the Protection of Birds reserves (http://www.wildlifetrusts.org; http://www.woodland-trust.org.uk; http://www.rspb.org.uk), a proportion of which are also statutorily designated, inevitably contribute to biodiversity conservation nationally and internationally, particularly given that management activities are specifically targeted towards key taxonomic groups and habitats.

Of course, it can also be regarded as encouraging that many threatened plant species in Britain currently persist in the wider countryside outside protected areas, whether they also occur in protected areas or not. However, their long-term future is far from uncertain. On the one hand, the history of extensive land transformation is long (Rackham, 1986), the region has already experienced high levels of local and regional species extinction (Biesmeijer et al., 2006; Thomas et al., 2004; Yalden, 1999), and many of the remaining species have benefited from the new resource patterns created (at least prior to the recent intensification of land use; Shrubb, 2003; Yalden, 1999). Arguably, this might have reduced the likelihood that species of conservation concern would be restricted to protected areas, compared with regions in which major land transformation has been more recent and more rapid, and larger protected areas have often been maintained. In such regions, levels of restriction of species of conservation concern to protected areas could plausibly be even higher. On the other hand, many of the reasons for declining numbers and local extinctions of many threatened vascular plant species are ongoing (e.g. habitat fragmentation, intensive land use, encroaching human population, infrastructure development, eutrophication, pollution). Many presently threatened plant species previously were much more widespread and have declined particularly as a result of an increase in the intensity of landuse since the 1940s, reducing the availability of semi-natural habitat (Preston, 2000; Preston et al., 2002b; Rich and Woodruff, 1996). For example, orchid species across Britain have declined by an average of more than 50% since 1969 (Kull and Hutchings, 2006). Thus, although many protected areas may not originally have been designated for the conservation of Red List species, they are increasing in importance as fragmentation and intense land use continued to restrict ranges.

This may be unfortunate, because at present it seems unlikely that a refugium role for protected areas is sustainable in the long-term, for two main reasons. First, the majority of patches of statutory protected area across Britain are extremely small ($N = 10{,}351$; mean (±SE) = 3.33 (±0.52) km^2; S.F. Jackson unpubl. analysis). Such a system has resulted in large edge effects, increased interference from outside activities, and a reduced potential for maintaining local populations, not least because small populations are particularly vulnerable to the effects of demographic, environmental and genetic stochasticity (Goodman, 1987; Menges, 1991). Furthermore, dispersal between local populations is becoming more difficult for many species as matrix habitats become progressively more inhospitable and protected areas increasingly resemble isolated habitat islands. Thus, if a species is lost from a habitat fragment it is unlikely that it will naturally be able to recolonise.

In large part as a direct or indirect consequence of area effects, intensive management measures are being undertaken on many protected areas in Britain to maintain small populations of particular species. For plants these measures include caging individuals, hand pollination, sowing seeds, watering, and fencing and wardening of sites (Marren, 2005). One example of where such extreme measures have been adopted is for the critically endangered *Cypripedium calceolusis* (lady's slipper orchid). Thought at one time to be extinct due to over-collection for herbaria and gardens, it is now found at a single natural site where natural pollination has yet to be observed (Ramsay and Stewart, 1998). In addition to wardens and public access controls, a variety of measures have been employed in an attempt to maintain this fragile population, including hand pollination, in vitro germination, and micropropagation techniques (Ramsay and Stewart, 1998). It seems likely that many protected areas in Britain are carrying significant extinction debts, as is the case elsewhere (Báldi and Vörös, 2006; Carroll et al., 2004; Newmark, 1987), but that at present these are not being fully realised because of such actions.

Second, protected areas in Britain continue to be damaged and destroyed. An assessment of the condition of Sites of Special Scientific Interest (SSSI; the majority of statutory protected areas), carried out over a 6-year period between 1997 and 2003, revealed that 44% of sites assessed are considered to be in an unfavourable state as a consequence of a range of damaging factors (Williams, 2006). In terms of Red List vascular plant conservation, under- or over-grazing is one of the most important destructive forces on these protected areas, particularly threatening the persistence of mid-successional (e.g. grassland, woodland) species. In lowland areas, problems of persistence are occurring due to cessation of grazing, particularly sheep but also cattle, as small grassland sites become increasingly inaccessible within predominantly arable landscapes. The reverse is true in the uplands, where an increase in subsidies has resulted in higher grazing intensities.

Overall our results strongly support the importance of a dual conservation strategy in Britain, in which protected areas are maintained with particular reference to those biodiversity features (such as many threatened plant species) that are highly dependent on them, and in which components of the wider landscape are also managed in such a way as to promote the abundance and distribution of such features with particular reference to those which are unlikely to persist in protected areas alone.

Acknowledgements

This work was conducted during a U.K. Population Biology Network (UKPopNet) Project ('The ecological effectiveness of protected areas') which was funded by the Natural Environment Research Council (Agreement R8-H12-01) and English Nature. Particular thanks go to the many dedicated volunteers who collected the plant atlas information, to Alex Lockton and Kevin Walker at BSBI for species-level information and invaluable discussion, David Roy at CEH for providing spatially referenced species-level information, and to M. Parnell and I. Fishburn for their valuable comments on draft versions of this manuscript. K.J.G. holds a Royal Society-Wolfson Research Merit Award.

References

Araújo, M.B., 1999. Distribution patterns of biodiversity and the design of a representative reserve network in Portugal. Diversity and Distributions 5, 151–163.

Armesto, J.J., Rozzi, R., Smith-Ramirez, C., Arroyo, M.T.K., 1998. Conservation targets in South American temperate forests. Science 282, 1271–1272.

Báldi, A., Vörös, J., 2006. Extinction debt of Hungarian reserves: a historical perspective. Basic and Applied Ecology 7, 289–295.

Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J., Kunin, W.E., 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science 313, 351–354.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Inference: A Practical Information–Theoretical Approach. Springer-Verlag, New York.

Carroll, C., Noss, R.F., Paquet, P.C., Schumaker, N.H., 2004. Extinction debt of protected areas in developing landscapes. Conservation Biology 18, 1110–1120.

Castro Parga, I., Moreno Saiz, H.C., Humphries, C.J., Williams, P.H., 1996. Strengthening the Natural and National Park system of Iberia to conserve vascular plants. Botanical Journal of the Linnean Society 121, 189–205.

Chape, S., Harrison, J., Spalding, M., Lysenko, I., 2005. Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 360, 443–455.

Cheffings, C., Farrell, L., 2005. The vascular plant Red List for Great Britain. ISSN 1473–0154.

Cressie, N., 1991. Statistics for Spatial Data. John Wiley and Sons, New York.

Deguise, I.E., Kerr, J.T., 2006. Protected areas and prospects for endangered species conservation in Canada. Conservation Biology 20, 48–55.

Evans, K.L., Rodrigues, A.S.L., Chown, S.L., Gaston, K.J., 2006. Protected areas and regional avian species richness in South Africa. Biology Letters 2, 184–188.

Fearnside, P.M., Ferraz, J., 1995. A conservation gap analysis of Brazil's Amazonian vegetation. Conservation Biology 9, 1134–1147.

Fuller, R.M., Smith, G.M., Sanderson, J.M., Hill, R.A., Thompson, A.G., Cox, R., Brown, N.J., Clarke, R.T., Rothery, P., Gerard, F.F., 2002. Countryside Survey 2000 Module 7. Land Cover Map 2000. Final Report CSLCM/Final. Centre for Ecology and Hydrology, Monks Wood, Huntingdon, Cambs.

Gaston, K.J., Charman, K., Jackson, S.F., Armsworth, P.R., Bonn, A., Briers, R.A., Callaghan, C.S.Q., Catchpole, R., Hopkins, J., Kunin, W.E., Latham, J., Opdam, P., Stoneman, R., Stroud, D.A., Tratt, R., 2006. The ecological effectiveness of protected areas: the United Kingdom. Biological Conservation 132, 76–87.

Goodman, D., 1987. The demography of chance extinction. In: Soulé, M.E. (Ed.), Viable Populations for Conservation. Cambridge University Press, Cambridge.

Hopkinson, P., Travis, J.M.J., Prendergast, J.R., Evans, P.R., Gregory, R.D., Telfer, M.G., Williams, P.H., 2000. A preliminary assessment of the contribution of nature reserves to biodiversity conservation in Great Britain. Animal Conservation 3, 311–320.

Hunter, M.L.J., Yonzon, P., 1993. Altitudinal distributions of birds, mammals, people, forests, and parks in Nepal. Conservation Biology 7, 420–423.

Jackson, S.F., Gaston, K.J., Kershaw, M., 2004a. The performance of procedures for selecting conservation areas for waterbirds in Great Britain. Biological Conservation 118, 261–270.

Jackson, S.F., Gaston, K.J., Kershaw, M., 2004b. Size matters: the value of small populations for wintering waterbirds. Animal Conservation 7, 229–239.

Johnson, J.B., Omland, K.S., 2004. Model selection in ecology and evolution. Trends in Ecology and Evolution 19, 101–108.

Kerr, J.T., Burkey, T.V., 2002. Endemism, diversity, and the threat of tropical moist forest extinctions. Biodiversity and Conservation 11, 695–704.

Kull, T., Hutchings, M.J., 2006. A comparative analysis of decline in the distribution ranges of orchid species in Estonia and the United Kingdom. Biological Conservation 129, 31.

Lan, D., Dunbar, R., 2000. Bird and mammal conservation in Gaoligongshan Region and Jingdong County, Yunnan, China: patterns of species richness and nature reserves. Oryx 34, 275–286.

Legendre, P., Dale, M.R.T., Fortin, M.-J., Gurevitch, J., Hohn, M., Myers, D., 2002. The consequences of spatial structure for the design and analysis of ecological field surveys. Ecography 25, 601–615.

Lennon, J.J., 2000. Red-shifts and red herrings in geographical ecology. Ecography 23, 101–113.

Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D., 1996. SAS System for Mixed Models. SAS Institute Inc., Cary, NC, USA.

Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. Nature 405, 243–253.

Marren, P., 2005. Caged flowers. British Wildlife 17, 33–41.

Martin, D., Tate, N., 1997. Surpop V2.0: Introduction (online) Census Dissemination Unit, University of Manchester. <http://census.ac.uk/cdu/surpop>.

Martinez, I., Carreno, F., Escudero, A., Rubio, A., 2006. Are threatened lichen species well-protected in Spain? Effectiveness of a protected areas network. Biological Conservation 133, 500.

Menges, E.S., 1991. The application of minimum viable population theory to plants. In: Falk, D.A., Holsinger, K.E. (Eds.), Genetics and Conservation of Rare Plants. Oxford University Press, Oxford, pp. 47–61.

Nantel, P., Bouchard, A., Brouillet, L., Hay, S., 1998. Selection of areas for protecting rare plants with integration of landuse conflicts; a case study for the west coast of Newfoundland, Canada. Biological Conservation 84, 223–234.

Newmark, W.D., 1987. A land-bridge island perspective on mammalian extinctions in western North American Parks. Science 325, 430–432.

Oldfield, T.E.E., Smith, R.J., Harrop, S.R., Leader-Williams, N., 2004. A gap analysis of terrestrial protected areas in England and its implications for conservation policy. Biological Conservation 120, 303–309.

Pawar, S., Koo, M.S., Kelley, C., Ahmed, M.F., Chaudhuri, S., Sarkar, S., 2007. Conservation assessment and prioritization of areas in Northeast India: priorities for amphibians and reptiles. Biological Conservation 136, 346.

Powell, G.V.N., Barborak, J., Rodriguez, S.M., 2000. Assessing representativeness of protected natural areas in Costa Rica for conserving biodiversity: a preliminary gap analysis. Biological Conservation 93, 35–41.

Pressey, R.L., Taffs, K.H., 2001. Scheduling conservation action in production landscapes: priority areas in western New South Wales defined by irreplaceability and vulnerability to vegetation loss. Biological Conservation 100, 255–376.

Pressey, R.L., Whish, G.L., Barrett, T.W., Watts, M.E., 2002. Effectiveness of protected areas in north-eastern New South Wales: recent trends in six measures. Biological Conservation 106, 57–69.

Preston, C.D., 2000. Engulfed by suburbia or destroyed by the plough: the ecology of extinction in Middlesex and Cambridgeshire. Watsonia 23, 13–26.
Preston, C.D., Pearman, P.A., Dines, T.D., 2002. New Atlas of British and Irish flora. Oxford University Press, Oxford.
Preston, C.D., Telfer, M.G., Arnold, H.R., Carey, P.D., Cooper, J.M., Dines, T.D., Hill, M.O., Pearman, D.A., Roy, D.B., Smart, S.M., 2002. The Changing Flora of the UK. DEFRA, London.
Quinn, G.P., Keough, M.J., 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge, UK.
Rackham, O., 1986. The History of the Countryside. Dent, London.
Ramsay, M.M., Stewart, J., 1998. Re-establishment of the lady's slipper orchid (*Cypripedium calceolus* L.) in Britain. Botanical Journal of the Linnean Society 126, 173–181.
Rich, T.C.G., Woodruff, E.R., 1996. Changes in the vascular plant floras of England and Scotland between 1930–1960 and 1987–1988: the BSBI monitoring scheme. Biological Conservation 75, 217.
Rodrigues, A.S.L., Tratt, R., Wheeler, B.D., Gaston, K.J., 1999. The performance of existing networks of conservation areas in representing biodiversity. Proceedings of the Royal Society of London B 266, 1453–1460.
Rodrigues, A.S.L., Akçakaya, H.R., Andelman, S.J., Bakarr, M.I., Boitani, L., Brooks, T.M., Chanson, J.S., Fishpool, L.D.C., Da Fonseca, G.A.B., Gaston, K.J., Hoffmann, M., Marquet, P.A., Pilgrim, J.D., Pressey, R.L., Schipper, J., Sechrest, W., Stuart, S.N., Underhill, L.G., Waller, R.W., Watts, M.E.J., Yan, X., 2004a. Global gap analysis: priority regions for expanding the global protected area network. BioScience 54, 1092–1100.
Rodrigues, A.S.L., Andelman, S.J., Bakarr, M.I., Boitani, L., Brooks, T.M., Cowling, R.M., Fishpool, L.D.C., da Fonseca, G.A.B., Gaston, K.J., Hoffmann, M., Long, J.S., Marquet, P.A., Pilgrim, J.D., Pressey, R.L., Schipper, J., Sechrest, W., Stuart, S.N., Underhill, Waller, R.W., Watts, M.E.J., Yan, X., 2004b. Effectiveness of the global protected area network in representing species diversity. Nature 428, 640–643.
Rouget, M., Richardson, D.M., Cowling, R.M., 2003. The current configuration of protected areas in the Cape Floristic region, South Africa-reservation bias and representation of biodiversity patterns and processes. Biological Conservation 112, 129–145.
Sætersdal, M., Line, J.M., Birks, H.J.B., 1993. How to maximise biological diversity in nature reserve selection: vascular plants and breeding birds in deciduous woodlands, western Norway. Biological Conservation 66, 131–138.
Scott, J.M., Davis, F.W., McGhie, R.G., Wright, R.G., Groves, C., Estes, J., 2001. Nature reserves: do they capture the full range of America's biological diversity? Ecological Applications 11, 999–1007.
Shrubb, M., 2003. Birds, Scythes and Combines. Cambridge University Press, Cambridge.
Sinclair, A.R.E., Mduma, S.A.R., Arcese, P., 2002. Protected areas as biodiversity benchmarks for human impact: agriculture and the Serengeti avifauna. Proceedings of the Royal Society of London Series B-Biological Sciences 269, 2401–2405.
Thomas, J.A., Telfer, M.G., Roy, D.B., Preston, C.D., Greenwood, J.J.D., Asher, J., Fox, R., Clark, R.T., Lawton, J.H., 2004. Comparative losses of British butterflies, birds and plants and the global extinction crisis. Science 303, 1879–1881.
Thompson, K., Jones, A., 1999. Human population density and prediction of local plant extinction in Britain. Conservation Biology 13, 185–189.
Williams, J.M., 2006. Common Standards Monitoring for Designated Sites: First Six Year Report. JNCC, Peterborough.
Yalden, D., 1999. The History of British Mammals. Poyser, London.