

Quantifying the importance of multi-scale management and environmental variables on moorland bird abundance

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UK moorlands are semi-natural habitats managed for a mix of livestock, game shooting and forestry, among other activities. An assessment of the importance of characteristics that correlate with moorland bird populations of high conservation importance can inform appropriate management at appropriate locations. We use hierarchical partitioning to assess the absolute and relative importance of climate, topography, soil, landscape management (wider scale habitat configuration of forestry and agriculture) and site-based management (indices of predator control, and vegetation characteristics) in determining the abundance of a suite of upland birds in four regions of the UK. Unmeasured region-specific effects often made the largest contribution to models. Physical characteristics (climate, topography, soil) were important and on average explained a similar amount of variation to site-based management. However, there was considerable interspecific variation in the importance of both. Landscape-scale variables were generally of low importance. An index of predator control was positively correlated with the abundance of Red Grouse *Lagopus lagopus scotica* and two waders. Vegetation characteristics (composition and structure) were, together, strong correlates of the abundance of passerine species. Vegetation characteristics were as important as indices of predator control for waders and grouse. The importance of regional effects, physical characteristics and variables relating to management suggest targeting site-based management (such as predator control or vegetation management) to the areas where physical characteristics are most favourable. The most beneficial management will vary between species, necessitating a mosaic of management options across upland areas to benefit all species.

Keywords: burning, habitat associations, heather, hierarchical partitioning, predation, uplands.

Globally, many long-term trends in biodiversity are negative, with environmental threats generally increasing, populations of many species declining and increasing numbers of species at risk of extinction (Butchart *et al.* 2010). Conservation action

can reduce the magnitude of these negative trends (Hoffmann *et al.* 2010), whether through the implementation of protective measures (e.g. Donald *et al.* 2007) or through active management (Wilson *et al.* 2009). However, it is clear that many factors can influence species population trends. Often, population trends at individual sites or in specific habitats are a function of large-scale ecological processes, rather than responses to site- or habitat-based environmental change (Sullivan *et al.* 2015), reducing the effectiveness of site- or habitat-specific management. Equally, the effectiveness of conservation management in reversing

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particular ecological pressures may be constrained by other factors that also change, such as interactions between habitat and predation pressure (e.g. Newton 1998). It is therefore important to understand fully the relative importance of factors that influence species populations, and the extent to which those populations may be amenable to site-based management or landscape-scale management or influenced by environmental factors. The last of these include physical characteristics such as soil-type, topography and climate that are likely to constrain the responses of species to management.

To compare the absolute and relative importance of site-scale management, landscape-scale management and the effects of the physical environment on species, we use a suite of birds breeding on UK moorland as a focal system of conservation concern. The UK uplands cover around 25% of the country (Haines-Young *et al.* 2000). UK moorlands (including blanket bog, rough grassland and dwarf shrub heath vegetation) are an extensive subset of this area, comprising unenclosed semi-natural open habitat of high international conservation importance (Anon 1995, Thompson *et al.* 1995). This includes 10–15% of the globe's blanket bogs (Lindsay *et al.* 1988, Milne & Brown 1997, Dunn & Freeman 2011), which are a major store of carbon (Grayson *et al.* 2012). Moorland breeding bird communities comprise a unique assemblage of species including waders, raptors and game birds, several with internationally important populations (Thompson *et al.* 1995, Pearce-Higgins *et al.* 2009a) and numerous species of high conservation concern with declining trends (Balmer *et al.* 2013, BirdLife International 2015). These species make a major contribution to the conservation value of these habitats and potentially their economic and social value through tourism and sport shooting (DEFRA 2004).

Moorlands have been subject to long-term agricultural (largely sheep grazing) and game (deer stalking and grouse shooting) management following historical deforestation, resulting in significant changes in upland vegetation (Anderson & Yalden 1981, Hudson 1992, Fuller & Gough 1999). Extensive afforestation of moorlands with exotic conifers has also occurred during the post-war period (Mackey *et al.* 1998). After increases in livestock densities in the UK uplands since the 1950s (Fuller & Gough 1999), densities have declined

since around 2000 (Pearce-Higgins *et al.* 2009a) with removal of livestock from some areas. Further major changes in moorland management and thus habitats are likely to occur. In a changing political climate, particularly in relation to the UK's future standing with respect to EU legislation, there remains uncertainty regarding future agricultural policy and management. Major EU policy instruments currently affecting UK moorlands include the Common Agricultural Policy, the Water Framework Directive (water catchment management) and the Birds and Habitats Directives (nature conservation including site designation). The importance of moorlands for carbon storage and the potential implications of management for climate change mitigation may also become an increasingly important consideration for management (Committee on Climate Change 2015). Additionally, moorlands might be altered directly by climate change (Trivedi *et al.* 2008) or by activities aimed at the mitigation of climate change, such as re-wetting, woodland expansion policies and the use of uplands for renewable energy generation (Pearce-Higgins *et al.* 2009b).

Environmental changes may operate at a number of different spatial scales. Changes in site-based management have been associated with changes in the abundance of moorland birds at those sites, whether through changing livestock practices (Calladine *et al.* 2002, Pearce-Higgins & Grant 2006, Sim *et al.* 2007, Amar *et al.* 2011) or aspects of sports shooting management (Tharme *et al.* 2001, Fletcher *et al.* 2010, Douglas *et al.* 2014). Landscape-scale management, such as commercial afforestation, may affect populations through a combination of direct habitat loss, fragmentation and predation-mediated edge effects (Buchanan *et al.* 2003, Douglas *et al.* 2014, Wilson *et al.* 2014). Larger-scale processes independent of management, such as climate change, may also drive change in bird populations (Pearce-Higgins *et al.* 2010).

Given the negative population trends of many moorland bird species, there is considerable interest in the potential for appropriate conservation action to reverse these declines. Action could be targeted through site-based management, such as vegetation management (Douglas & Pearce-Higgins 2014), predator control (particularly for waders and gamebirds; Tharme *et al.* 2001, Fletcher *et al.* 2010) and hydrological restoration (Carroll *et al.* 2011), across landscapes through agri-environment

schemes (e.g. Smart *et al.* 2013) or forestry removal (Wilson *et al.* 2014). So that limited resources can be targeted most effectively, it is important to understand the degree to which site-based or landscape-scale management may be important in driving moorland bird populations, and under what circumstances. Such information can be derived from the associations between species and habitat characteristics of relevance to management, and can be important to the effective conservation management of species and habitats, and the development of government policy (Ormerod *et al.* 2002).

In this study, we quantified the importance of site-based (plot scale) management, landscape-scale management and non-management-related physical effects in predicting moorland bird abundance across four regions of the UK. Specifically, we examined the components of species abundance that can be accounted for by groups of variables. These are characteristics amenable to site-based management of moorland habitats (vegetation manipulation through grazing, cutting or burning, or predator control), landscape-scale conversion and management of non-moorland habitats, and characteristics of the physical environment not amenable to management (climate, topography) or only over long timescales (soil). We also quantified the importance of regional effects that were not covered or explained by any of the above.

METHODS

Site selection

Data were collected from 159 plots of 2 km², but with variable shape, in four upland regions of Britain (Fig. 1). Twenty-nine plots were in the North Pennines (13 surveyed in 1999 and 16 in 2003), 37 in the South Pennines (surveyed in 2002), 72 in southern Scotland (surveyed in 1999 and 2000) and 21 in three of the main hill ranges in northern Wales (surveyed in 2002). Plot locations were identified using a random stratified sampling approach. Stratification was based on the cover of *Calluna*, *Empetrum*, *Erica* or *Vaccinium* species (henceforth dwarf shrub cover), such that they included a similar number of plots with a low (< 33%), medium (33–66%) and high (> 66%) cover of dwarf shrubs. Plots were generally rectangular (subject to constraints of access

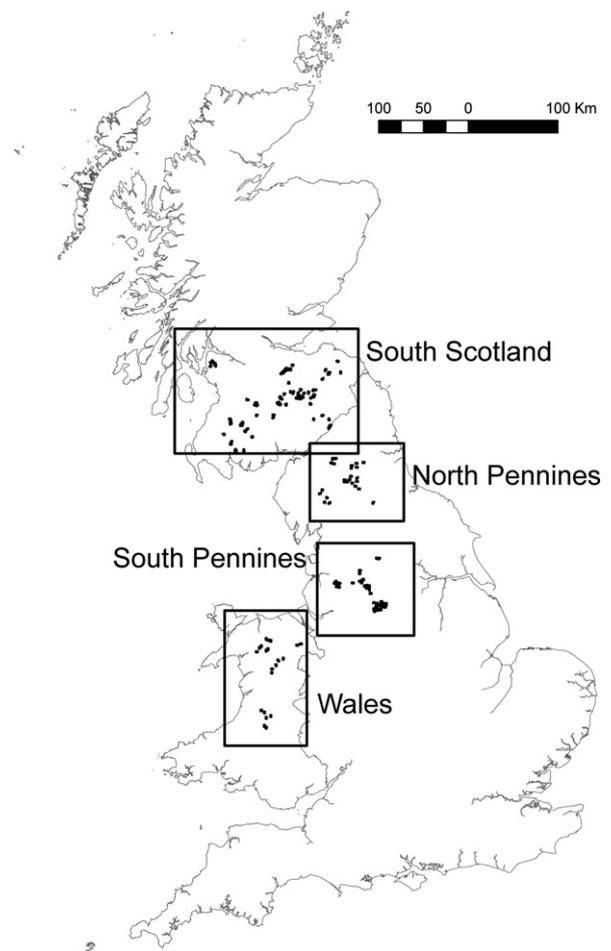


Figure 1. Distribution of 159 study plots across four regions of the UK.

boundaries and unsuitable topographical features), and sized so that multiple transects separated by 100 m (see below) could fit parallel to each other (i.e. plots were never long and elongated). Plots were at least 200 m from the nearest forest edge and excluded enclosed land. Sampling was informed by information extracted from a combination of National Countryside Monitoring Scheme plots (Mackey *et al.* 1998), a 1990 Landsat Thematic Mapper imagery map of Heather *Calluna vulgaris* distribution (RSPB unpubl. data) in south Scotland (Pearce-Higgins & Grant 2006), and from the Land Cover Map 2000 (Haines-Young *et al.* 2000) in the other three regions. However, due to access refusals, this selection was supplemented by 13 plots in the North Pennines and 22 plots in southern Scotland purely on the basis of access being assured. All plots were at least 1 km apart.

Bird surveys

Breeding grouse, waders and passerines (excluding Meadow Pipits *Anthus pratensis* and Skylarks *Alauda arvensis* – see below) were surveyed using a three-visit census method following Pearce-Higgins and Grant (2006). Each plot was visited once in each 3-week period from 17 April to 20 June, with successive visits to a plot made at least 7 days apart. Surveys were not undertaken in rain or strong winds. At least one visit was made within 3 h of dawn or dusk to increase the probability of detecting Common Snipe *Gallinago gallinago* (Green 1985, Hoodless *et al.* 2006). On each visit the surveyors walked parallel transects such that the entire plot was walked to within 100 m, during which bird locations were mapped and the numbers of breeding pairs derived by counting apparently paired individuals, singing, displaying or alarm-calling birds, nests or broods, or other single birds (excluding those overflying). The maximum count of breeding pairs over the three visits was used as a measure of abundance for all species, except for Eurasian Curlew *Numenius arquata*, for which the mean count was used, as recommended by Grant *et al.* (2000). At least two of the visits to each plot were undertaken by different observers to minimize potential bias resulting from observer variability.

The high density of Skylarks and Meadow Pipits made a bespoke survey method necessary. These species were surveyed (on only 145 plots), using two parallel, 1-km transects located at least 600 m apart. Transects were walked between 06:00 and 09:00 h on the latter two survey visits, with the two visits usually completed by different observers. The count of Meadow Pipits estimated to be within 25 m of transects (distance estimations were calibrated before each survey) and the total count of Skylarks were used as indices of abundance, as these are least prone to observer effects (Buchanan *et al.* 2006). Counts for each species were then averaged across the two transects on a plot for each visit and averaged across the two visits to produce the estimated abundance on each plot.

Covariates

We divided the covariates into pairs consisting of variable types (Table 1). These types were further classified as physical variables (climate, soil and

topography), landscape-scale management variables, and site-based management-related variables (predator control, vegetation structure and vegetation composition). Climate was represented by mean spring rainfall and temperature (Pearce-Higgins & Grant 2006) averaged from 1961 and 1990, at a 10-km square resolution, from the Climate Research Unit, University of East Anglia. Soil was assessed from the proportion of the plot covered by shallow peat (0–50 cm) or deep peat (> 50 cm), as measured in the field from sample points located along a 100 × 200 m grid across the plot. These field-collected data have better explanatory power for moorland birds than map-derived soil data do (Pearce-Higgins & Grant 2006). Topography was described by mean altitude and the proportion of the plot that had a slope < 5° (shallow slope), extracted from 50-m digital elevation models (Panorama, Ordnance Survey, UK). Both variables have been shown previously to have an important influence on moorland bird abundance (e.g. Pearce-Higgins & Grant 2006).

Populations of moorland birds can be affected by the management and extent of woodland (Douglas *et al.* 2014, Wilson *et al.* 2014) and extent of enclosed fields (Pearce-Higgins & Yalden 2003a, Dallimer *et al.* 2010) surrounding areas of open moorland. Therefore, potential landscape-scale effects were represented by the extent of adjacent woodland cover and enclosed farmland within a 1-km buffer of each plot. These data were extracted from Land Cover Map 2000 (Haines-Young *et al.* 2000) in a GIS.

Measures of site-based management variables were related to both predator control and vegetation management. Predator control was measured as the number of separate Carrion Crow *Corvus corone* and Hooded Crow *Corvus cornix* groups sighted during the bird surveys (an inverse measure of control, and a more representative measure than the total number of crows recorded; Pearce-Higgins & Grant 2006), and an index of gamekeeper activity, measured as number of full-time keepers per acre (c. 0.4 ha) following Tharme *et al.* (2001). The latter was based upon information provided by estates and landowners, and provided a direct measure of expected management intensity.

Vegetation composition was expected to reflect grazing and burning management. It was measured by the extent of dwarf shrubs compared with

Table 1. Summary of variable types used in model building. Region was also included in all models as a four-level fixed effect (South Scotland, North Pennines, South Pennines and Wales).

Variable	Definition
Climate	
Rainfall	30-year mean annual rainfall from 1961 to 1990 (mm)
Temperature	30-year mean spring temperature (April–June) from 1961 to 1990 (°C)
Soil	
Shallow peat	Percentage of sample points located on peat 0–50 cm deep
Deep peat	Percentage of sample points located on peat > 50 cm
Topography	
Shallow slope	Percentage of shallow ground (< 5° slope)
Altitude	Mean altitude (m)
Landscape	
Enclosed land	Percentage of plot within 400 m of enclosed farmland
Forestry	Percentage of plot within 400 m of woodland (largely commercial forestry)
Predator pressure	
Keeper activity	Density of gamekeepers/1000 acres
Crows	Mean number of individual groups of Carrion and Hooded Crows recorded during bird surveys
Vegetation structure	
Tall vegetation	Percentage of tall vegetation (> 30 cm)
Height heterogeneity	Mean variation in vegetation height between adjacent sample points (cm)
Vegetation composition	
Dwarf shrubs	Mean ratio of dwarf shrub/graminoid cover
Compositional heterogeneity	Mean change in ratio of dwarf shrubs to graminoids between adjacent vegetation sample points

graminoids (grasses, sedges and rushes), and the compositional heterogeneity of this measure across the plot, previously shown to provide a useful measure of habitat patchiness for moorland birds (Pearce-Higgins & Grant 2006). Vegetation structure, expected to be more closely related to rapid changes in response to grazing and burning, was assessed from the amount of tall vegetation and the spatial variation in tall and short vegetation across the plot (height heterogeneity).

Vegetation data were collected from point samples distributed evenly across each plot (Pearce-Higgins & Grant 2006). Both composition and structure were measured at 100 points (located every 100 m along transects separated by 200 m) between 21 June and late July. At each point, vegetation cover was assessed to the nearest 5% along a 1-m length of cane, marked at 5-cm intervals, placed horizontally on the ground. Most dwarf shrubs and common grasses and sedges were identified to species. The ratio of dwarf shrubs to graminoids on plots was calculated to measure dwarf shrub cover. Compositional heterogeneity was an index of variation in dwarf shrub cover and was derived from the change in the log-ratio of dwarf shrub to graminoid cover between adjacent sampling points (Pearce-Higgins & Grant 2006). Vegetation height was measured at each point using a

marked cane held at arm's length to the front and either side of the observer, recording the heights of all vegetation. Height measurements were averaged for each sampling point and the proportion in each plot over 30 cm was calculated as a measure of height. Variation in vegetation height (termed height variation) was calculated as the mean absolute change in maximum vegetation height between successive sampling points from the late visit. Correlations between these covariates are shown in Supporting Information Table S1.

Data analysis

To reduce the number of variables considered in the models, the single strongest correlate of bird abundance from the paired variables (i.e. one each from climate, soil, topography, landscape, predator control, vegetation composition and vegetation structure) was identified for each species in turn. The variables that explained the greatest amount of deviance (irrespective of significance) were entered into a generalized linear model (GLM) of abundance with a Poisson error distribution and log link function. This method of variable reduction is commonly used to remove correlated variables (e.g. Pearce-Higgins & Grant 2006). Linear and quadratic relationships were examined, with

degrees of freedom adjusted appropriately (Crawley 1993). In cases where the quadratic form of the relationship explained the greatest deviance, we generated fitted values (i.e. the predicted values from the regression line) from the relationship. These were used in the subsequent analysis, as they summarized the curvilinear relationship in one variable (rather than two variables), without altering the pattern of variation in the covariate. The strengths of the correlation between the dependent variable and the transformed variable or the quadratic relationship were identical.

Hierarchical partitioning was used to determine the independent contribution that each of the strongest predictors from each pair of variables made to abundance. Hierarchical partitioning separates the independent contribution from the joint contribution of other, potentially correlated, variables. This separation allows users to rank each variable in terms of the contribution that it alone made to models. We used hierarchical partitioning in the R package Hierpart (<https://cran.r-project.org/web/packages/hier.part/hier.part.pdf>) to assess the absolute and relative contribution each variable made to the overall amount of variation explained. Each species was modelled against each of the best predictor variables from the seven pairs of variables and region, which was entered as a four-level fixed effect (south Scotland, North Pennines, South Pennines and Wales). We used R^2 as a measure of the variance explained by the covariates. We noted both the absolute variance that was explained, which was the amount of variance explained by a covariate as a percentage of total variance, and the relative variance that was explained, which was the amount of variance explained by a covariate as a percentage of total explained variance. In addition, we also assessed the independent contribution of each variable to the model across 1000 randomizations using the `hp.rand` command. If 95% confidence intervals from the variance explained by the randomized reassignment of the variable values did not overlap zero (indicating the variable consistently contributed to the model), the variable was deemed to have explained a significant amount of deviance.

RESULTS

Species were unevenly distributed between the regions. Passerines, in particular the three

Muscicapidae species, were prevalent in Wales, where waders were scarce. The opposite was true of the North Pennines, where waders were recorded on almost all plots (Table 2). The abundance models generally explained between a third and a half of the absolute variance in bird abundance (Figs 2 & 3). This varied between species, ranging from the Red Grouse *Lagopus lagopus scotica* model, which explained almost 70% of the absolute variance in the abundance for that species, to models for Northern Lapwing *Vanellus vanellus* and Common Snipe, which explained less than 30% of the absolute variance (Fig. 2). Region explained between 3.5% and 35.8% ($\bar{x} = 14.4\%$) of the absolute variance in all species. For the two widespread passerines (Skylark and Meadow Pipit), and Red Grouse, region alone explained more of the absolute variance than the other variables combined (Fig. 2). For these species, and Eurasian Golden Plover *Pluvialis apricaria*, Stonechat *Saxicola rubicola* and Whinchat *Saxicola ruberta*, regional effects explained more variance than physical characteristics (Fig. 2).

Physical characteristics (climate, topography, soil) explained from 5.6% to 20.7% ($\bar{x} = 11.2\%$) of the absolute variance across all species. The contribution of physical characteristics to the models for Eurasian Curlew, Northern Lapwing, Meadow Pipit and Common Snipe was approximately double that of the contribution of site-based management (Figs 2 & 3). Landscape-scale variables explained from 1.8% to 4.0% ($\bar{x} = 2.6\%$) of the absolute variance. These were not the strongest predictors for any species, but were important in some species. Negative correlations with surrounding forest and enclosed land were the most important management variables for Northern Lapwing and Meadow Pipit, respectively. Site-based management variables explained from 3.8% to 29.1% ($\bar{x} = 12.3\%$) of the absolute variance. The contribution of site-based management variables to the models for Skylark and Whinchat was roughly double that of physical characteristics. Site-based management variables explained about a third more of the variance of Red Grouse, Eurasian Golden Plover and Stonechat compared with physical characteristics (Figs 2 & 3). There was little difference between the contribution of physical and management effects for Northern Wheatear *Oenanthe oenanthe*.

An examination of the contribution of the individual effects within the management variables

Table 2. Mean count of each species (± 1 se), and number of plots that each species was recorded in each region and the number of plots surveyed in each (in parentheses). Skylark and Meadow Pipit counts were not undertaken on eight plots in south Scotland and five plots in North Pennines, and one plot in South Pennines for Meadow Pipit only.

	North Pennines	South Pennines	South Scotland	Wales	Total
Red Grouse	12.4 \pm 1.82 (26)	25.2 \pm 4.26 (34)	7.2 \pm 0.9 (58)	1.8 \pm 0.58 (13)	11.6 \pm 1.37 (131)
Curlew	5.5 \pm 0.73 (27)	3 \pm 0.48 (32)	4.6 \pm 0.61 (57)	0.3 \pm 0.31 (4)	3.8 \pm 0.37 (120)
Golden Plover	11.1 \pm 2.77 (23)	5.1 \pm 0.83 (31)	1.4 \pm 0.4 (31)	0.5 \pm 0.47 (5)	3.9 \pm 0.77 (90)
Snipe	2.2 \pm 0.31 (25)	0.6 \pm 0.24 (14)	2.4 \pm 0.31 (55)	0.7 \pm 0.26 (10)	1.7 \pm 0.19 (104)
Lapwing	1 \pm 0.53 (10)	0.5 \pm 0.49 (6)	1.5 \pm 1.21 (15)	0	1 \pm 0.6 (31)
Wheatear	1 \pm 0.36 (13)	0.9 \pm 0.36 (17)	1.6 \pm 0.24 (50)	2.2 \pm 0.35 (19)	1.4 \pm 0.16 (99)
Whinchat	0.1 \pm 0.18 (3)	0.2 \pm 0.47 (3)	0.8 \pm 0.27 (28)	2.1 \pm 0.7 (16)	0.7 \pm 0.22 (50)
Stonechat	0.2 \pm 0.23 (4)	0.1 \pm 0.16 (3)	0.8 \pm 0.22 (30)	1.6 \pm 0.48 (14)	0.6 \pm 0.16 (51)
Meadow Pipit	10 \pm 0.79 (24)	12.1 \pm 1.29 (35)	11 \pm 0.58 (64)	25.4 \pm 1.89 (21)	13.2 \pm 0.66 (144)
Skylark	35 \pm 9.86 (15)	40.6 \pm 10.32 (29)	39.4 \pm 4.36 (58)	190.1 \pm 26.74 (21)	61.5 \pm 7.35 (123)
No. of plots	29	37	72	21	159

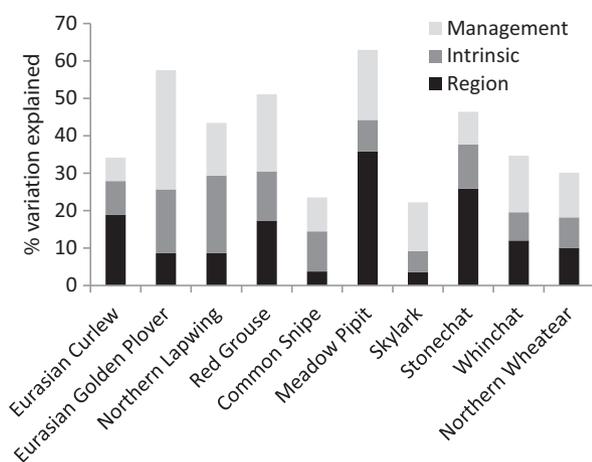


Figure 2. Cumulative proportion (summarized by R^2) of variation in species count across plots explained by variable types. Physical variables includes climate, soil and topography. Management includes landscape, predator control and vegetation composition and structure.

indicated that landscape-scale management explained 2% of the absolute variance (9% relative variance) in the waders and grouse, and 3% absolute variance (15% relative variance) in the passerines. This indicated that the passerines might be marginally more affected by landscape-scale effects as a whole, but these levels were lower than the variance explained by the site-based management variables. Predator control variables explained 7% absolute, or 20% relative, variance among the waders and grouse (Table 2). Predator control (gamekeeper index) correlated positively with the abundance of three of the five species (Red Grouse, Eurasian Curlew, Eurasian Golden Plover;

Fig. 3). The average amount of absolute variance explained by predator control was greater than the absolute variance explained by any of the other variable groups. The relative contribution of predator control was lower among the passerines, with the only significant effects being positive associations with crow groups, which were therefore unlikely to be causal. Vegetation composition and structure variables contributed approximately equally to the models of abundance for both waders and grouse, and passerines (Table 3). Combined, the amount of absolute variance explained was similar at about 7%, although the relative variance was about 50% larger for passerines. Eurasian Curlew, Red Grouse and Common Snipe benefited from increased compositional heterogeneity (Fig. 3). Eurasian Curlew and Northern Lapwing abundance increased with structural complexity, and Common Snipe numbers increased with increasing vegetation height. The opposite was true for Eurasian Golden Plover, which was more abundant in areas of shorter vegetation (Fig. 3). Stonechat and Whinchat benefited from vegetation that was more complex in terms of species composition and height, respectively, whereas Skylark appeared to benefit from vegetation that was less complex in terms of species composition. Northern Wheatear was only weakly associated with vegetation that was more variable in height (Fig. 3).

DISCUSSION

We quantified the contribution of a suite of variables operating at different spatial scales to explain

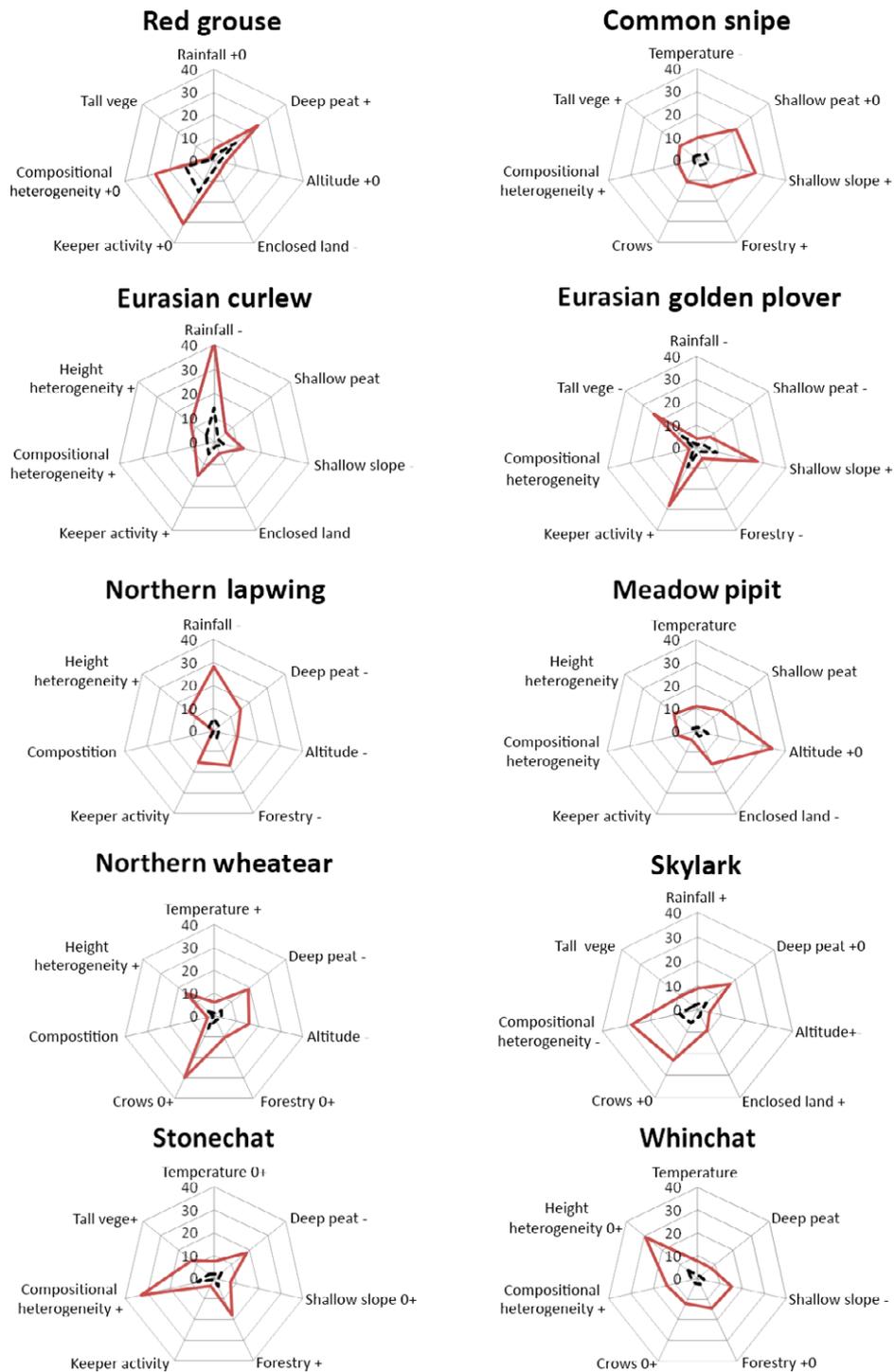


Figure 3. Relative (solid line) and absolute (broken line) percentage contribution of variables representing variable groups to abundance of upland bird species, determined from hierarchical partitioning. Relative contribution is based on rescaled values to exclude the effect of region. The form of significant relationships is shown after the variable name (+ positive, - negative, +0 positive then asymptotic quadratic, 0+ asymptotic then positive quadratic, +- mid point inflection quadratic). Non-significant relationships have no annotation.

Table 3. Mean percentage of variance explained by covariates, and percentage variance explained by covariates relative to the total explained variance of each type of variable to determining species abundance. There was no significant difference between the contribution of variables types in an ANOVA with species group (wader/grouse or passerine) for either absolute ($\chi^2_6 = 3.88$, $P = 0.69$) or relative ($\chi^2_6 = 3.29$, $P = 0.77$) contribution.

Variables		No. of significant relationships	Mean \pm se absolute % variance explained	Mean \pm se relative % variance explained
All species	Climate	8	3.41 \pm 1.209	12.9 \pm 0.337
All species	Soil	7	4.06 \pm 0.921	15.18 \pm 0.237
All species	Topography	10	3.76 \pm 0.710	15.87 \pm 0.178
All species	Landscape	9	2.61 \pm 0.206	11.39 \pm 0.061
All species	Predator pressure	6	5.12 \pm 1.348	17.36 \pm 0.324
All species	Vegetation composition	6	3.8 \pm 1.238	13.2 \pm 0.341
All species	Vegetation structure	7	3.4 \pm 0.614	14.09 \pm 0.164
Wader/grouse	Climate	5	5.14 \pm 2.148	17.63 \pm 0.512
Wader/grouse	Soil	4	4.88 \pm 1.676	15.15 \pm 0.431
Wader/grouse	Topography	5	4.68 \pm 1.144	16.26 \pm 0.284
Wader/grouse	Landscape	4	2.47 \pm 0.266	9.2 \pm 0.088
Wader/grouse	Predator pressure	3	7.02 \pm 2.149	20.02 \pm 0.480
Wader/grouse	Vegetation composition	3	3.72 \pm 2.075	9.31 \pm 0.680
Wader/grouse	Vegetation structure	4	3.63 \pm 1.091	12.42 \pm 0.310
Passerines	Climate	3	1.68 \pm 0.187	8.17 \pm 0.065
Passerines	Soil	3	3.24 \pm 0.562	15.21 \pm 0.144
Passerines	Topography	5	2.85 \pm 0.608	15.47 \pm 0.155
Passerines	Landscape	5	2.76 \pm 0.301	13.59 \pm 0.082
Passerines	Predator pressure	3	3.22 \pm 1.098	14.71 \pm 0.286
Passerines	Vegetation composition	3	3.88 \pm 1.349	17.09 \pm 0.326
Passerines	Vegetation structure	3	3.16 \pm 0.543	15.76 \pm 0.137

the abundance of birds in a semi-natural habitat. We attempted to disentangle the variation in abundance that can be attributed to site-based management, as measured by vegetation condition and variables relating to predator management, landscape-scale management and physical characteristics which either cannot be manipulated (climate, topography) or which take time to manipulate (soil-type). A high proportion of the variance in abundance was explained by region. Regional effects, which we were not able to explore further with the current data, explained a higher proportion of variation in abundance than the summed effects of physical and management effects for three species. Exploration of what factors contribute to these regional effects may be of use for informing management for these species. For example, there could be regional variation in the level of forest cover or gamekeeper activity that affects abundance.

Our results suggest that both physical characteristics and site-based management variables account for similar levels of variation in moorland bird abundance (11% and 12%, respectively). This was more than landscape management, which

accounted for 3%, albeit based on a single variable in the final model rather than three physical and three site-based management variables. By decomposing the explained variation in moorland bird abundance, we found evidence that site-based management that was implemented without considering the physical and landscape management-related suitability of a particular site for species of interest may have only a relatively small impact on bird abundance. Across all species, management (including landscape-scale management) accounted for about 15% of the variation in abundance. This percentage is likely to represent a minimal figure, as we constrained the number and type of such management variables in the models in order to produce an equivalent comparison with other variables, but it represents the component of abundance that can rapidly be altered through management. This relatively small proportion may account for the relatively limited impact of site-based moorland management upon bird communities documented by Calladine *et al.* (2014), and is supported, for species such as Eurasian Golden Plover, by the role of climate in driving population fluctuations (Pearce-Higgins *et al.* 2010).

The small percentage of variation in abundance explained by site-based management variables does not mean that site-based management is unimportant in managing populations of upland birds. There are examples of relatively rapid responses in upland bird abundances to experimental manipulation of predator control (Fletcher *et al.* 2010) or afforestation of surrounding moorland (Parr 1992). Instead, our results support the results of some previous studies (e.g. Concepción *et al.* 2008) in showing that conservation management needs to be targeted at locations that are otherwise suitable for the species in terms of physical measures such as topography, climate and soil. Thus, management for Common Snipe, which may involve raising water levels (Smart *et al.* 2008), might be most appropriate on flat sites with shallow peat soils.

Our analysis suggested that the importance of landscape-scale management was generally smaller than that of site-based management, in contrast to some previous work (e.g. Dallimer *et al.* 2010), but landscape-scale management effects were nonetheless the most important variables amenable to management for Northern Lapwing and Meadow Pipit. Management of landscape-scale characteristics has previously been shown to have an impact on species abundance, either because these species use the habitats considered in our analysis during the breeding season (e.g. enclosed land for foraging; Pearce-Higgins & Yalden 2003a) or as a result of their fragmentation of otherwise suitable breeding habitat, and their potential to harbour predators (Valkama *et al.* 1999, Douglas *et al.* 2014). Our results for some species were consistent with some of these previous studies with, for example, our Northern Lapwing result being a parallel of Eurasian Golden Plover abundance declining with increased proximity to conifer plantations (e.g. Finney *et al.* 2005), and possibly a result of the Northern Lapwing vulnerability to nest predation (e.g. Bolton *et al.* 2007). The positive association between greater neighbouring forest cover and the abundance of Stonechat and Whinchat also follows previous studies; this may not be causal, but instead might be a surrogate for moorland edge habitats (e.g. Pearce-Higgins & Grant 2006). It is important to note that all plots in our study were sited at least 200 m from forest edges, so effects operating at a distance less than this might not have been detected, and we might therefore have underestimated the contribution of

edge effects associated with landscape-scale management in our analysis.

Perhaps of greater short-term management interest for the remaining species is our assessment of the relative importance of variables relating to predator control, vegetation composition and vegetation structure (site-based management variables). As noted above, site-based management variables explained a small proportion of the variation in bird abundance in our study. This will in part be due to the constrained number and type of such management variables in the models. However, based on the results of this study and others, we can provide some guidance to inform moorland management. Our findings that Red Grouse, Eurasian Golden Plover and Eurasian Curlew showed strong positive associations with gamekeeper density reflects previous correlative (Tharme *et al.* 2001) and experimental (Fletcher *et al.* 2010) studies, both in the general pattern and with respect to the individual species involved, and may also apply to Northern Lapwing (Bolton *et al.* 2007). Although the effect may be partly confounded by vegetation management that is also associated with game management, such as strip burning (Tharme *et al.* 2001, Douglas *et al.* 2015), this should have been at least partially controlled for by the inclusion of vegetation composition in our models. Thus our results support species-level evidence about the influence of predation, and the role that predator control can play in increasing productivity or maintaining populations of ground-nesting moorland birds (Grant *et al.* 1999, Pearce-Higgins & Yalden 2003b, Fletcher *et al.* 2010, Douglas *et al.* 2014), and studies that indicate that legal predator control could benefit the populations of some upland birds (Bolton *et al.* 2007). These benefits must, however, be set against the potential wider environmental impact of game management in the UK uplands, including illegal persecution of some species of upland bird and consequences of burning for carbon storage and water quality (Thompson *et al.* 2016). The cost of many aspects of moorland management, including the deployment of gamekeepers for game management, can be expensive and labour-intensive (Sotherton *et al.* 2009). Therefore, in some cases, especially where the threat to species is coming from surrounding forestry, longer-term approaches to reducing predation pressure could also consider tree removal (Douglas *et al.* 2014).

Variables relating to vegetation composition and structure were of similar importance in explaining variation in abundance, although there was considerable interspecific variation. These relationships, together with information derived from previous studies (e.g. Smith *et al.* 2001, Pearce-Higgins & Grant 2006), could be used to guide vegetation management, for example through grazing, cutting or burning. Responses to variation in vegetation structure may be more indicative of likely rapid responses to grazing and burning management. For example, the negative association between Eurasian Golden Plover abundance and tall vegetation matches previous associations of the species with short vegetation (Pearce-Higgins & Grant 2006, Douglas & Pearce-Higgins 2014) and suggests the species may respond rapidly to management such as increases in grazing pressure, cutting and burning. In common with previous work (Pearce-Higgins & Grant 2006), our results emphasize the value of heterogeneity in vegetation structure. This requires appropriately set grazing and burning/cutting regimes to deliver the required mix of tall, short and intermediate structures to maintain the greatest diversity and abundance of moorland birds.

Our results, especially when supported by previous studies, indicate that a mix of stocking densities across landscapes might be the most appropriate way to produce the mix of vegetation composition and structure that would be required to benefit multiple species. However, given the importance of physical characteristics, exactly which species respond to such variation in management will depend upon soil-type, topography and climate. No single management will suit all species, but instead conservationists and land managers should aim to maintain a mix of vegetation composition and structures across both sites and landscapes, to benefit the greatest range of species. This could be achieved by a mixture of grazing by cattle and sheep at different densities. More specific managements for individual species should be targeted at areas within appropriate regions that are of suitable topography, soil and climate.

As with many previous studies of this type, it is important to note that the analysis here is correlative. Additionally, we have only sampled a small number of the range of variables that could be important in determining the abundance of moorland birds, which is likely to mean that our model

performance is less than might be achieved using more bespoke variables for individual species (e.g. Pearce-Higgins & Grant 2006). However, this restriction was appropriate for this study, as we are focused on comparing the importance of broad types of variables.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Correlation matrix of Pearson correlations and significance between variables. Correlations between variable pairs (see Table 1) are highlighted in bold.