

RESEARCH ARTICLE

Predicting the combined impacts of future management and climate change on moorland bird species

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Abstract

1. Understanding the combined effects of wildlife management and climate change on species is important for planning appropriate interventions. However, predictions of the effectiveness of management interventions alongside climate change impacts remain rare.
2. We investigated the importance of combined management-climate change predictions for upland moorland bird populations in Great Britain (GB). Current management over many moorland areas comprises rotational burning of heather and predator control, which benefit some species but negatively impacts others. We used land cover data, heather moor burning data and bird survey data across 8095 2-km grid cells to model how upland bird populations may respond to land management and climate change scenarios.
3. More spatial variation in abundance of each species was explained by underlying environmental predictors, including key climate and land cover variables, than by moorland management intensity. We predicted red grouse (*Lagopus lagopus*), the primary target of current management, to decline by 33% [30%–38%] across GB if management promoting their numbers (for hunting) ceased, even if land continued to be dominated by suitable habitat. Under the same scenario, we predicted smaller declines in populations of curlew (*Numenius arquata*; 11% [7%–14%]) and golden plover (*Pluvialis apricaria*; 6% [3%–9%]), two species of high conservation value considered beneficiaries of current management.
4. When a cessation of grouse moor management was considered in conjunction with future climate change, predicted declines were much stronger. This difference was particularly noticeable for golden plover (30%–37% declines by the 2040s; 27%–34% by the 2080s), though stronger declines were also predicted in red grouse (2040s, 52%–62%; 2080s, 49%–80%) and curlew (2040s, 25%–32%; 2080s, 15%–26%). Such differences in population trajectories were particularly pronounced at a regional scale, with stronger population declines predicted in the combined scenario in most regions.

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5. *Synthesis and applications.* Our study illustrates the value of combining predictions of the impacts of management and climate change on animal populations. Management decisions guided by models fitted only under contemporary scenarios may lead to unexpected, and potentially undesirable, population trajectories as climatic conditions change over the short and medium term.

KEYWORDS

climate change, conservation conflict, grouse moor management, population dynamics, predictive models, upland birds, waders, wildlife management

1 | INTRODUCTION

Understanding the combined effects of environmental processes and wildlife management is important for planning appropriate interventions (Clark et al., 2001), such as harvesting strategies that maximize yield but minimize the risk of depletion (e.g. Brodie et al., 2013). Environmental processes, such as climate change, and management interventions can influence wildlife populations additively, for example, if vital rates are similarly influenced by both management and climate change (Regehr et al., 2017), or interactively, for example, if management alters the impacts of climate change on wildlife (Pearce-Higgins et al., 2019). The importance of predicting the future states of ecological systems to inform conservation and wider decision-making is increasingly recognized (Mouquet et al., 2015). Large-scale analyses of the combined ecological impacts of different types of environmental change, such as land-use and climate change, are becoming more common (e.g. Hof et al., 2018; Marshall et al., 2018). However, model predictions of the likely effectiveness of management interventions under different scenarios of environmental change remain rare (Marolla et al., 2021; Merino et al., 2019). Combined management–climate change predictions could be particularly useful for systems that are sensitive to climate change and where contrasting stakeholder objectives regarding wildlife species must be balanced.

In this study, we use such a model system—grouse moors in Great Britain (GB)—to investigate the importance of considering the impacts of climate change on animal populations when planning wildlife management. Driven grouse shooting, where red grouse (*Lagopus lagopus*) are flushed towards lines of shooters, is a major land use across 15% of upland moorland in the United Kingdom (Redpath et al., 2010). It is the source of a long-running conservation conflict (sensu Redpath et al., 2015) over shooting versus wider interests (Thompson et al., 2016). Grouse moors are managed to maximize grouse populations, principally through the rotational burning of heather (*Calluna vulgaris*)—which ensures that heather of different ages is available for grouse—and legal control of predators (e.g. mustelids, red fox *Vulpes vulpes*, carrion crow *Corvus corone*) that might affect the breeding success of grouse. Other more variably applied managements include: controlled grazing, drainage, and the treatment of grouse diseases (Tharme et al., 2001; Thompson

et al., 2016). The habitat conditions and low predator environment created by burning and predator control also benefit some non-target species (Tharme et al., 2001). Other activities associated with some grouse moors negatively impact wildlife populations, particularly the illegal killing of birds of prey (Newton, 2021) and culling of mountain hares (*Lepus timidus*) (Watson & Wilson, 2018).

Conservation, animal welfare and environmental groups have argued for rethinking how GB uplands are managed, including changes to agricultural grazing, forestry practices, and game shooting. Moorland burning is restricted in some protected areas in England (UK Government, 2021), and there is a consultation ongoing to extend these regulations (DEFRA, 2025). An Act of the Scottish Parliament has been passed that regulates certain forms of predator control and requires licences for moorland burning and grouse shooting (Scottish Parliament, 2024). With the potential for changes in future upland land use and management, potential impacts on target and non-target wildlife populations need to be explored to guide future conservation decision making. As upland species are especially susceptible to climate change (Pearce-Higgins, 2010), it is vital that future predictions consider the likely impacts of climate change.

Here, we investigate the combined impacts of changes in grouse moor management and climate on three species: red grouse, the target bird species of management, and two non-target bird species of conservation concern, Eurasian curlew (*Numenius arquata*) and Eurasian golden plover (*Pluvialis apricaria*). Specifically, we test the hypothesis that predicted population trajectories driven by changes in climate and management in combination will diverge from predicted trajectories driven by changes in management alone. The combined impacts of changes in grouse moor management and climate on these species are uncertain. Various studies have demonstrated that grouse moor management benefits populations of curlew and golden plover (Tharme et al., 2001), including moorland burning (Douglas et al., 2017) and predator control specifically (Buchanan et al., 2017), although some studies point to relatively weak effects of each activity (Littlewood et al., 2019) or, for burning, even negative effects (Franks et al., 2017). Montane and upland birds appear particularly vulnerable to climate change, in part due to their limited capacity to shift their ranges upslope in response to warming temperatures and the compounding effects of habitat degradation (Chamberlain & Pearce Higgins, 2013; Scridel et al., 2018).

As a result, widespread population declines have been observed among cold-adapted bird species across Europe (Scridel et al., 2018). Overall, research points to negative impacts of increasing temperatures on all three species (Fletcher et al., 2013; Franks et al., 2017; Pearce-Higgins et al., 2010). However, higher air temperatures have been positively linked to some population parameters, for example, chick growth rate in golden plover (Douglas & Pearce-Higgins, 2019). Here, we model the spatial relationship between the abundance of each species and management intensity, land cover, and climate. We make model predictions of how each species would be affected by an end to grouse moor management, under both present climatic conditions and future climate change.

2 | MATERIALS AND METHODS

2.1 | Study system

The study area is the upland moorlands of GB (Figure 1c; Figure S1a). We delineated areas dominated by upland moorland using the 25-m scale UK Land Cover Map 2007 (Morton et al., 2011)—the land cover dataset that most closely matched the timing of the bird survey data—as described in the Supporting Information. The study area represents 15,253 2-km grid cells (61,012 km²). We divided the study area into nine regions, based on biogeographical and national boundaries, to explore regional variation in projected changes to upland bird populations (Figure S1c).

We focused on three upland moorland specialist bird species which are associated with grouse moor management (Littlewood et al., 2019) and thus which we hypothesise will exhibit population responses to changes in grouse moor management: red grouse, curlew and golden plover. We did not include non-upland moorland specialists that are likely to be less affected by changes in grouse moor management. Such species include those that are more associated with grassland than moorland habitats, such as Eurasian skylark (*Alauda arvensis*), meadow pipit (*Anthus pratensis*) and snipe (*Gallinago gallinago*). Neither did we include rarer upland bird species for which data are too sparse to fit robust models relating spatial abundance patterns to climate and land use; for example, persecuted raptor species such as hen harrier (*Circus cyaneus*). The study species are sufficiently common and widespread to have sufficient data to fit robust models of spatial abundance.

2.2 | Data

2.2.1 | Relative bird abundance

We used GB-wide data on the number of adult individuals of each species recorded during standardised 1-h surveys of 2-km grid cells, carried out during 2007–2011 as part of a British Trust for Ornithology Bird Atlas project for Britain and Ireland (Balmer et al., 2013; Gillings et al., 2019; data available from <https://zenodo.org/records/10599935>).

Given the short duration of surveys, these data can be considered measures of relative (but not absolute) abundance. See Supporting Information for more details of the surveying protocol. Surveys were undertaken in 39,055 2-km cells across GB. Within our study area, 8095 grid cells were surveyed, covering 53.1% of the area (Figure 1a). As this study was based on previously collected field survey data, no new licences or permits were required.

2.2.2 | Management intensity

We used data on the extent of moorland burning within each 2-km cell to represent grouse moor management intensity, hereafter GMMI (Figure 1b). Although legal predator control is an important component of moorland management for red grouse, such data are only available across limited areas. Consequently, we had no suitable metric of this management. However, as predator control has been found to be highly correlated (Pearson's r , 0.70) with moorland burning across northern England and southern Scotland (Littlewood et al., 2019), we considered moorland burning extent a suitable index of GMMI. Similarly, there were no national datasets on other forms of management, such as controlled grazing, drainage and the treatment of grouse diseases.

Data on moorland burning extent came from Douglas et al. (2015) for the period 2001–2010, produced by visually examining high-resolution aerial photographs and satellite images, following a protocol developed by Anderson et al. (2009) to map burning across all GB upland moorland (<https://opendata-rspb.opendata.arcgis.com/datasets/RSPB::muirburn-extent/about>; data available on request from the RSPB [dataunit@rspb.org.uk]). We calculated our index of GMMI—the proportion of burned area per 2-km cell—from these estimates. We assumed that any 1-km cells not assessed by Douglas et al. (2015) contained no burning. See the Supporting Information for more information on calculating GMMI.

2.2.3 | Environmental variables

We quantified land cover, topography and climate predictor variables for each 2-km cell (Figure 1b). Land cover and topography predictors were included to explain any spatial variation in relative abundance related to habitat suitability. We calculated the proportional cover of four key upland land cover types from the UK Land Cover Map 2007 data (satellite imagery collected 2005–2008; Morton et al., 2011); these being dwarf shrub heath (29.4% of upland GB), acid grassland (23.7%), bog (15.9%), and forest (10.9%). We produced a topographical variable representing the proportion of flat areas (<10° slope) suitable for ground-nesting birds covering each cell (Littlewood et al., 2019), using 30-m resolution elevation data (USGS, 2017). We calculated four climate variables from the UK Met Office's 'HadUK' 1-km gridded climate data for a baseline period of 1981–2010 (Hollis et al., 2019), a period

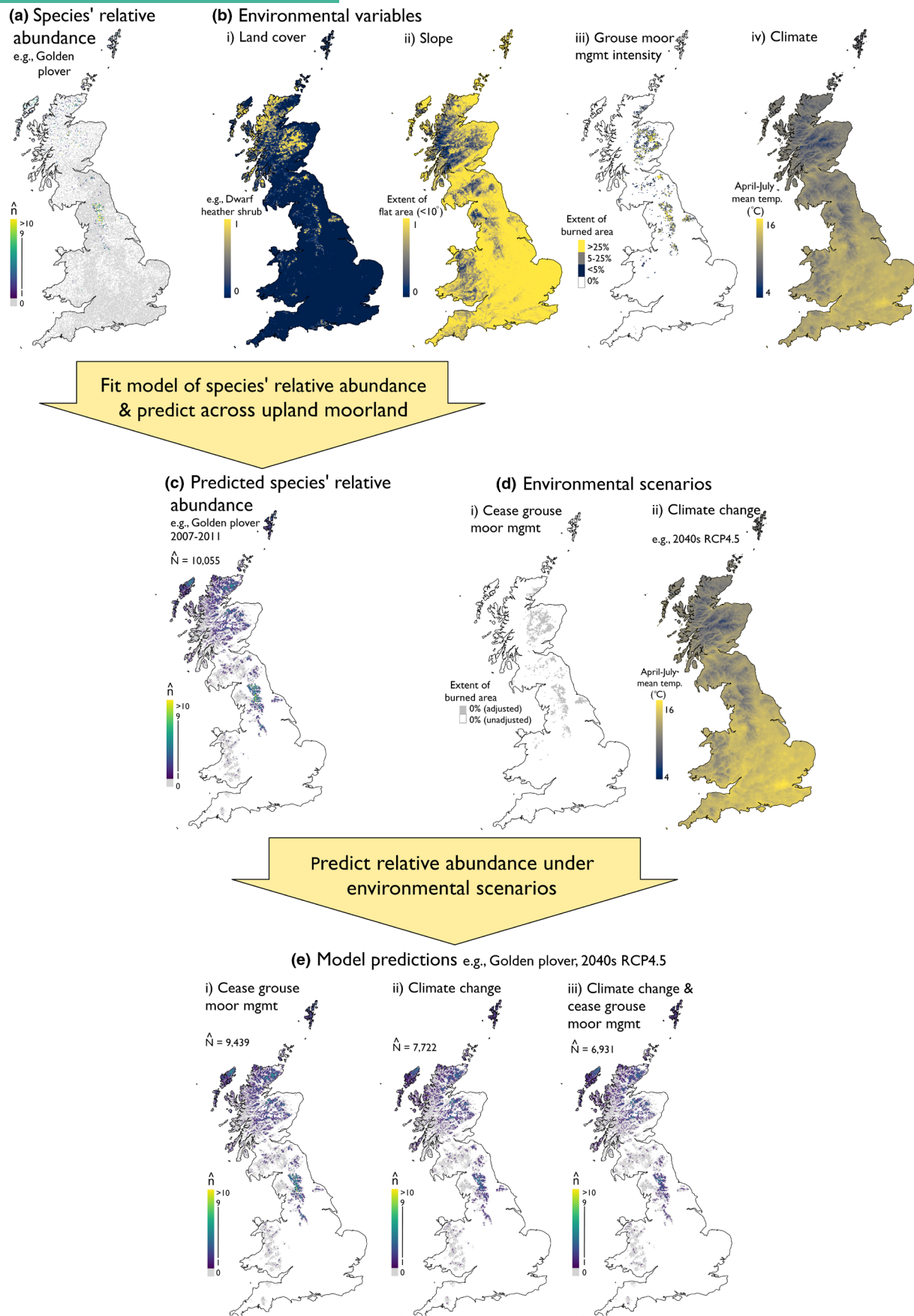


FIGURE 1 Our approach for predicting the relative abundance of GB upland birds under alternative scenarios of management and future climate, illustrated for Eurasian golden plover (*Pluvialis apricaria*).

running up to and culminating in the bird and burn census periods. We used two variables to represent the climatic conditions during the breeding season, April–July mean temperature and total precipitation; these months encompass the main period of nesting, hatching, chick rearing, and prey abundance for each species (Butterfield & Coulson, 1975; Wilson et al., 2021). We used two additional climate variables—mean temperature of the coldest month (i.e. an index of winter harshness) and August–March total precipitation—to represent the climatic conditions in the non-breeding season, which are likely to influence habitat conditions and prey availability during the breeding season.

2.3 | Statistical analyses

2.3.1 | Model fitting

We modelled spatial variation in the relative abundance of each species across GB as a function of the environmental predictors: GMMI, the four climate variables, the four land cover types and slope. We included surveyed lowland GB cells in model fitting to ensure that the full range of environments available to each species was considered (Figure 1a). We fitted random forest models for each species based on all candidate predictors, implemented using the 'randomForest' package in R (Liaw & Wiener, 2002). Random forests are a machine learning technique robust to overfitting and that can capture complex, nonlinear relationships (Breiman, 2001). They are recognised as producing high-performing predictive models (Breiman, 2001), including specifically for bird atlas data (Howard et al., 2014).

We fitted models using five-fold cross-validation to minimise spatial autocorrelation, thus fitting five models per species, adapting the procedure of Bagchi et al. (2013). See the [Supporting Information](#) for further details on the model fitting procedure. We evaluated model performance using the area under the receiver operating characteristic curve (AUC) (Manel et al., 2002) and weighted Cohen's kappa statistic (Landis & Koch, 1977). We used AUC to identify the ability of models to discriminate between grid cells unoccupied and occupied by each species. We used weighted Cohen's kappa to test the ability of models to predict the abundance of each species across five abundance classes, dividing the observed data into zeros and four equally spaced non-zero classes (each non-zero class containing 25% of the remaining data).

2.3.2 | Model predictions

Using our models, we predicted the potential effects of changes in grouse moor management and climate on the relative abundance of each species across the entirety of upland GB (i.e. not only surveyed areas; see Figure 1). First, we calculated mean relative abundance per cell under the observed environmental conditions, averaged across the five models fitted for each species and rounded to the

nearest integer. We summed these predictions to produce a value of relative population size for upland GB in 2007–2011, hereafter the GB population index. We quantified uncertainty using the minimum and maximum index values calculated across each species' models. We also summed predictions for each of the nine regions, producing regional population indices.

We evaluated how upland bird populations might be affected by future changes in GMMI and climate by making model predictions under different environmental scenarios. We developed a scenario in which all management of upland moorland for grouse shooting ceased, by converting GMMI in each cell to zero. Our predictions under this scenario assume that the uplands would continue to be dominated by upland moorland land cover, which would depend on the form of land management replacing grouse shooting (see Discussion for further details).

We developed future climate scenarios for GB using the Met Office's UKCP18 25km gridded probabilistic future climate projections, which are available as averaged 30-year time slices (Gohar et al., 2018). Here, we prepared future climate data centred on the 2040s (2030–2059) and 2080s (2070–2099), representing mid- and late-century future climate conditions, respectively. For each time period, we considered four Representative Concentration Pathways (2.6, 4.5, 6.0 and 8.5 W m⁻²), which correspond to increases in mean global surface temperatures of 1.6°C, 2.4°C, 2.8°C and 4.3°C, respectively, between a pre-industrial baseline and the late 21st century. Thus, we used a total of eight potential climate change scenarios. We used the 50th percentiles (i.e. most probable estimates) of the probabilistic future anomalies, linearly interpolated onto the 2-km grid, to adjust the baseline 1981–2010 climate variables (Gohar et al., 2018).

We predicted the relative abundance of each species in each upland cell under (i) observed grouse moor management, and (ii) cessation of grouse moor management, using climate projections for the 2040s and 2080s. We calculated relative abundances and population indices for each species, year and RCP, following the same procedure as used with the 2007–2011 predictions. We calculated proportional change in population indices relative to 2007–2011 in response to the independent and combined effects of management and climate change. We also calculated proportional changes in regional population indices.

2.3.3 | Variable importance and effects

We explored the relative importance of GMMI, climate and other environmental variables using marginal effects and variable importance measures. Firstly, we evaluated the relative importance of management and background environmental suitability (i.e. climate, land cover and topography) in driving the abundance of species' populations by exploring spatial variation in the marginal effects of GMMI relative to other environmental predictors across upland areas (i.e. model predictions with either the effects of management or environment held at zero).

Secondly, we quantified the relative importance of individual variables by calculating variable importance measures and marginal effects from models refitted to upland GB data only to ensure these metrics were specific to upland populations. We produced marginal effects by predicting relative abundance with other variables held at mean values. We calculated variable importance using a permutation accuracy measure (Strobl et al., 2007), standardized by dividing the importance of each variable by the summed importance across all variables per species to enable comparisons between species (Howard et al., 2015).

3 | RESULTS

3.1 | Evidence of grouse moor management

Grouse moor management (as indicated by burning) was evident across 13.1% of upland GB moorland. We estimated that 23.8% of these managed areas were under high-intensity management ($\geq 25\%$ burned area), while 37.8% were under low-intensity management ($\leq 5\%$ burned area). Across the upland area surveyed for birds, 63.1% of red grouse were recorded in areas with evidence of burning, while the same was true for 34.5% and 30.7% of curlew and golden plover, respectively.

3.2 | Model performance

Our models distinguished accurately between grid cells unoccupied and occupied by each species across upland GB according to AUC (red grouse, 0.856; curlew, 0.859; golden plover, 0.854). There was fair to moderate agreement between modelled and observed abundance classes for each species according to Cohen's kappa (Figure S2; red grouse, 0.417; curlew, 0.382; golden plover, 0.333) (Landis & Koch, 1977).

3.3 | Modelled effects of management and climate on upland bird populations

The four climate variables were the most important predictors of the relative abundance of each species in the upland-only model (Figure 2a). Higher numbers of red grouse were found in upland areas with colder winters and drier non-breeding seasons. Golden plover were more abundant in areas with cooler breeding seasons and winters, and curlew were more abundant in areas with colder winters and both drier breeding and non-breeding seasons (Figure S3).

GMMI was the fifth, sixth, and tenth most important predictor of the relative abundance of, respectively, red grouse, curlew and golden plover in upland areas (Figure 2a). The relative abundance of each species was positively associated with GMMI (Figure 2b). For red grouse and curlew numbers, this relationship plateaued at higher levels of GMMI. Predicted numbers of red grouse, curlew and golden plover were, on average, 2.3, 1.4 and 1.1 times higher, respectively, in areas of median management intensity (10% burned area) than in moorland not managed for grouse shooting (0% burned area). In the most intensively managed areas (50% burned area), predicted numbers were 3.0, 1.7 and 1.7 times higher than in unmanaged areas. The marginal effect of GMMI was much weaker than that of the non-management environmental variables, explaining only a small proportion of the variation in the abundance of each species (Figure S4).

3.4 | Independent predictions of management and climate change

We predicted that, if management for grouse shooting were to cease, upland populations of red grouse, curlew and golden plover would decline by 33.2% (30.2%–37.8%), 10.5% (6.6%–13.6%) and

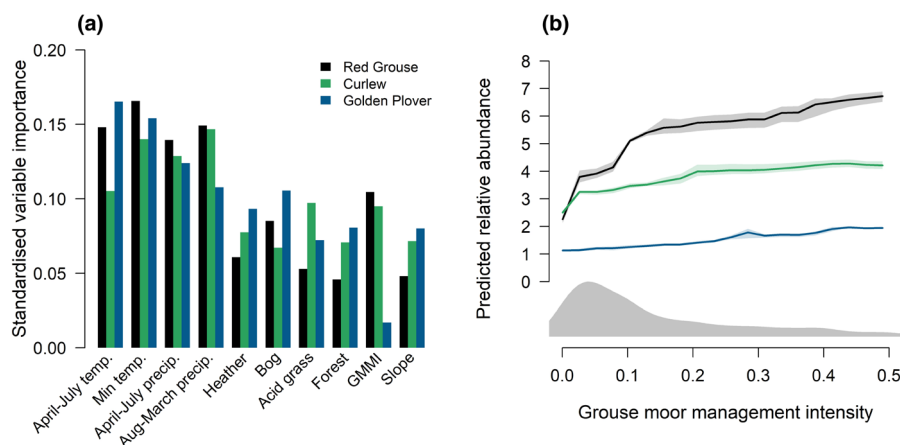


FIGURE 2 The relative importance and functional form of the effect of grouse moor management intensity (GMMI) from upland-only models: (a) standardised variable importance measures, and (b) the marginal effects of GMMI. In (b) the lines show mean predictions per species, with other variables held at mean values. Shaded areas around lines are the 95% percentiles of deviations around those means. Marginal effects are displayed up to the 95% percentile of GMMI recorded across the study area. The grey shaded area is the frequency distribution of GMMI across upland cells.

6.1% (3.1%–8.6%), respectively (Figure 3). These effects varied regionally (Figure 4a,d,g), with the largest changes predicted in intensively managed regions (Table 1). The strongest declines were predicted to occur in southern Scotland and northern England for red grouse (Southern Uplands, 40.6%; North Yorkshire Moors, 65.6%; Pennines, 38.7%), and in the North Yorkshire Moors for curlew (37.3%) and golden plover (48.7%).

The climate of upland GB is projected to become, on average across all RCPs, 0.8°C warmer in April–July and 0.6°C warmer in winter by the 2040s (relative to 1981–2010) and 1.6°C and 1.4°C warmer, in spring and winter respectively, by the 2080s. Upland GB is projected to experience average increases in April–July precipitation of 48mm (+12.1%) by the 2040s but only 3mm (+0.1%) by the 2080s. Precipitation between August–March is projected to increase by 280mm (+20.7%) by the 2040s and by 362mm (+26.8%) by the 2080s. Assuming the same level of moorland management in future as occurred in 2001–2010, we predicted declines in red grouse of 16.0%–25.8% [mean, all RCPs] due to climate change by the 2040s and potentially stronger declines by the 2080s (13.2%–47.1%) (Figure 3a). We predicted declines of 10.0%–15.7% and 21.9%–28.1% in numbers of upland curlew and golden plover, respectively, due to climate change by the 2040s. In both species—but most markedly for curlew—weaker declines were predicted in response to climate change by the 2080s [curlew, 0.4%–8.6%; golden plover, 19.3%–24.8%] (Figure 3b,c).

3.5 | Combined predictions of management and climate change

If management for grouse shooting were to cease in parallel with changes in climate, we predicted all species to decline more strongly (Figure 3). Declines would be strongest in red grouse, with mean predicted declines of 51.6%–62.0% (all RCPs) by the 2040s and 48.9%–80.0% by the 2080s. Strong declines were also predicted in golden plover (2040s, 29.8%–36.6%; 2080s, 27.4%–33.6%) and curlew (2040s, 24.6%–31.6%; 2080s, 15.2%–25.9%). In all species, predicted declines were larger than those caused by management cessation under 1981–2010 climatic conditions. Additionally, predicted declines in the combined scenario were slightly larger than the additive effects of management cessation and climate change in all species, suggesting an interactive effect between management and climate. The absolute increases in declines (relative to additive predictions, across all RCPs) were: by the 2040s, red grouse +2.6%, curlew +4.4% and golden plover +1.9%; and by the 2080s, red grouse +1.7%, curlew +6.6% and golden plover +2.3%.

Upland bird populations in some regions appear particularly vulnerable to both changes in management and climate (Figure 4). The Pennines and North Yorkshire Moors in particular are projected to become less climatically suitable yet hold significant populations of each species (Figure 4; Table S1). Under the combined cessation of management and climate change scenarios, these regions are

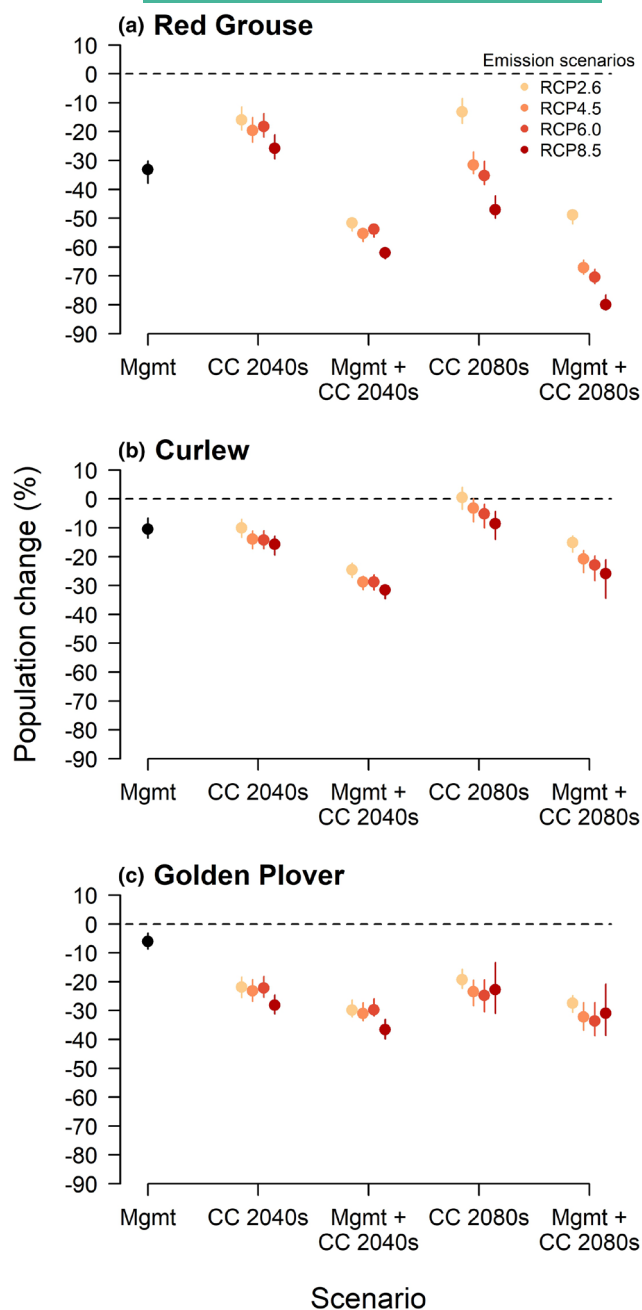


FIGURE 3 Predicted independent and combined effects of ceasing grouse moor management (Mgmt) and climate change (CC) on upland bird populations. Points indicate predicted changes in population index relative to the baseline scenario (2001–2010 management and 1981–2010 climate), averaged across each species' five models. Lines represent maximum and minimum estimates across models. We considered two climate change periods (the 2040s and 2080s) and four Representative Concentration Pathways (RCP; 2.6, 4.5, 6.0 and 8.5 W m⁻²).

predicted to lose high proportions of each species. In some regions, such as the Grampians and Cheviots, there were predicted improvements in climate suitability for curlew resulting in weaker population declines than would be anticipated from the cessation of management alone (Figure 4; Table S1).

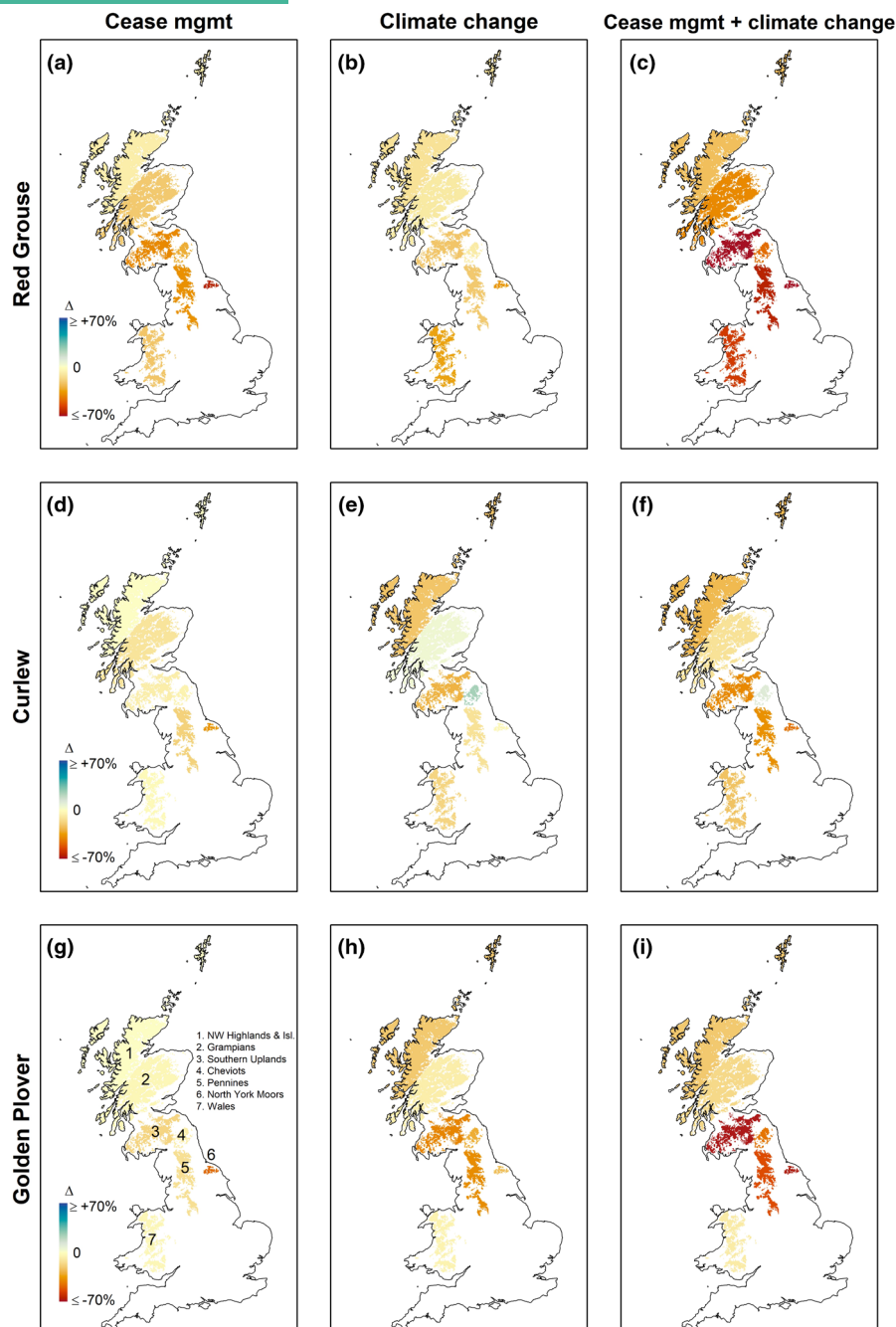


FIGURE 4 Predicted regional upland bird population changes due to ceasing management for grouse shooting (a–c), climate change (d–f) and ceasing management in conjunction with climate change (g–i). Predictions are proportional changes in regional population indices, which were summed for each region from GB model predictions. Climate change effects are illustrated for the 2040s and median values across the four RCPs. Regional predictions under both time periods and individual RCPs are provided in [Table S1](#). Two regions with very low relative abundances (<100), Lake District and South West, are not displayed.

4 | DISCUSSION

Our study illustrates the utility of predicting the combined impacts of management and climate change for informing wildlife management. By studying these impacts concurrently, we reveal how the

combined effects of management and climate change might lead to different changes in populations than would be anticipated by studying the effects of management alone. This has important implications for making decisions about the future management of ecosystems affected by ongoing climate change.

TABLE 1 Regional variation in grouse moor management and climate.

Region	Area (km ²)	GMMI (%)	April–July temp. (°C)	Min temp. (°C)	April–July precip. (mm)	August–March precip. (mm)
North West Highlands and Islands	22,640	0.2	9.6	2.8	402	1496
Grampians	17,868	3.3	9.1	1.6	407	1401
Southern Uplands	6660	1.7	9.9	2.2	365	1144
Cheviots	1408	2.5	9.8	2.1	307	811
Lake District	1484	0.2	10.0	2.4	502	1735
North Yorkshire Moors	544	14.4	10.6	2.6	284	710
Pennines	5252	7.7	9.9	2.0	354	1062
Wales	6376	0.1	10.6	2.9	429	1372
South West	952	0.1	11.1	3.7	431	1400

Note: GMMI (grouse moor management intensity) is the percentage of each region with evidence of moorland burning. Regional means of the four climate predictors are shown for the 1981–2010 baseline period: April–July mean temperature, mean temperature of the coldest month ('min. temp'), April–July total precipitation and August–March total precipitation.

4.1 | Impacts of grouse moor management on non-target species

Management for grouse shooting, as assessed using area of burned moorland, had a surprisingly weak effect on the relative abundance of curlew (management cessation predicted to lead to 11% decline) and golden plover (6% decline). A key factor is that only 35% of curlew and 31% of golden plover recorded in upland moorland were found in areas with evidence of burning. Evidence of positive effects of management (for driven grouse shooting) on upland wader populations (e.g. Tharme et al., 2001) has been used to support grouse shooting in the 'shooting versus environment versus conservation' debate (Sotherton et al., 2017). Our analysis builds on a previous study of moorland sites in northern England and southern Scotland that found similar saturating positive effects of management intensity on wader numbers (Littlewood et al., 2019). Our GB-wide analysis may be better able to disentangle the effects of management and environmental drivers than previous studies. A series of underlying environmental predictors, including key climate and land cover variables, explained most of the variation in the abundance of these species across the uplands (Figure S4). These key variables included temperature and precipitation during the breeding and non-breeding seasons, dwarf shrub heath, bog and acid grassland habitats.

We used moorland burning as an index of grouse moor management intensity, which has two potential limitations. First, the method used to quantify areas of burned vegetation (visual assessment of satellite images) could underestimate burning extent in some cases. This method could miss older burns in environments with faster post-burning regeneration rates (Yallop et al., 2006). However, it is likely to be effective at identifying patches that have been burned recently, and yet to form a dense canopy of heather (which takes approx. 15 years). Thus, it is likely to produce a reliable index of contemporary management intensity. Second, we were not able to consider directly the intensity of predator control, which can boost local wader abundance (Buchanan et al., 2017; Fletcher et al., 2010).

While predator control tends to be carried out in the same areas as moorland burning is practiced (Littlewood et al., 2019), considering burning alone could mask some local variations linked to varying predator suppression. This seems unlikely to strongly impact our findings for the non-grouse species given that large proportions of upland populations of curlew (65%) and of golden plover (69%) were recorded in areas without any evidence of burning, where levels of predator control are likely to be low. Regardless, the lack of data on predator control effort (with sufficient geographic coverage to include in our models) means that our estimates may under- or over-estimate the true effect of grouse moor management intensity on the abundance of the study species. Further research to disaggregate the effects of predator control and burning across wider areas is needed to resolve some of this uncertainty.

4.2 | Importance of combined management–climate change predictions

Our results indicate that combined effects of management and climate change would lead to stronger population declines across much of GB in all three species than anticipated from predictions of management effects alone. This difference was particularly striking for golden plover with, for example, declines of 30%–37% predicted by the 2040s compared to 6% declines due to the cessation of management alone. Reduced climate suitability is likely to lead to substantial declines in golden plover populations across GB this century, regardless of ongoing management for grouse shooting. Declines in golden plover populations under climate change have been projected previously in the Pennines (Pearce-Higgins, 2011). Potential mechanisms driving such declines include reductions in prey (e.g. *Tipulidae* crane fly larvae) and increased tick loads due to warming temperatures (Douglas & Pearce-Higgins, 2019; Pearce-Higgins et al., 2010). Stronger declines were also predicted in upland curlew when cessation of management was considered in conjunction

with climate change (e.g. 25%–32% decline by 2040s vs. 11% due to management alone). This difference was less pronounced due to weaker effects of climate change on curlew than on golden plover. The weaker predicted effects of climate change on upland curlew populations may reflect, in part, the species' ability to breed in warmer, lowland wet-grassland habitats in parts of GB. Particularly weak impacts of 2080s climate change were predicted on curlew, likely due to the limited projected changes in April–July precipitation under this scenario.

Additionally, there was evidence for interactive effects of management and climate change, with slightly stronger declines predicted in the combined scenario than the additive effects of the individual scenarios (Figure 3). This further underlines the importance of integrating the potential impacts of climate change into predictions of the effects of management. Interactions between the ecological impacts of climate change and other anthropogenic processes are thought to be common, representing a major challenge to quantifying and understanding the relative contribution of different drivers of ecological change (Parmesan et al., 2013). Various potential mechanisms could underlie the management–climate interactions observed here, such as spatial biases in the implementation of management activities other than burning. However, quite how the observed interactions are operating is difficult to tease apart and would merit further investigation.

The relevance of combined management–climate change predictions to conservation decision-making was particularly evident at regional scales. In many cases—particularly in red grouse and golden plover—much stronger population declines were predicted when the impacts of climate change were considered (Figure 4). Without testing the effects of management under climate change, predictions of population trajectories would have been misleading for all species in the medium and long term. There were also examples of predicted improvements in regional climate suitability, for example, curlew in the Cheviots (all 2040s RCPs) and Grampians (all 2040s and 2080s RCPs), resulting in weaker population declines than would be anticipated from the cessation of management alone (Table S1). The mechanisms for these effects are unclear but could reflect improvements in climatic conditions and thus increases in the extent of high-quality habitat in some northern upland areas.

The potential impacts of ceasing grouse moor management also varied regionally, with intensively managed regions predicted to experience the strongest declines. Some intensively managed regions in England, such as the Pennines and North Yorkshire Moors, were projected to become both less climatically suitable and to be hardest hit by the loss of management activities. This resulted in some very strong predicted declines, for example, 88%–92% and 68%–72% declines in red grouse and golden plover, respectively, in the North Yorkshire Moors by the 2040s (Table S1). It may be necessary either to refocus efforts to other regions in the future, or to invest heavily in adaptation management to mitigate against the impacts of climate change. Peatland restoration could be an effective tool benefitting golden plover, given the modelled importance of bog for this species. Manipulating the hydrology of peatland ecosystems,

such as by blocking drainage ditches, could benefit *Tipulidae* crane fly larvae populations; a major prey item of golden plover (Carroll et al., 2011, 2015). Predator control is another potential conservation tool (Brown et al., 2015); however, our findings suggest that this would have only modest mitigatory effects on curlew and golden plover populations. Further research seeking to understand what drives the (as yet unexplained) majority of variation in curlew and golden plover abundance is required to identify the most appropriate conservation actions. Our predictions for the Pennines and North Yorkshire Moors indicate that, without mitigation, the most intensively managed grouse moors could become less suitable for supporting red grouse over the course of this century (see Table 1). This calls into question the long-term future of driven grouse shooting on English moorland.

Anticipatory predictions of the potential effectiveness of wildlife management interventions do not normally consider the potential impacts of climate change on wildlife populations (but see Marolla et al., 2021). However, such predictive approaches are regularly applied in other fields, such as fisheries science. Predictive models of optimal harvest sizes in fisheries are routinely performed under alternative climate change scenarios (e.g. Merino et al., 2019). More conceptually, the potential effectiveness of protected areas to retain key species is often explored under future climate (e.g. Bagchi et al., 2013). Our study illustrates the value of predictive approaches for understanding the potential impacts of management and climate change on wildlife population dynamics. Such approaches could be applied more widely to inform conservation decision-making in systems sensitive to climate change. When applied to conservation conflicts, these predictive approaches would provide managers with a more accurate assessment of future system states with which to balance the competing objectives of different stakeholders.

4.3 | Future impacts on upland moorland species

The results of our study need to be placed in the context of potential changes to a wider group of species. An end to driven grouse shooting would very likely benefit a variety of animal species that are negatively affected by this activity, including generalist predator species that are legally controlled, such as foxes, crows and mustelids; raptor species that are illegally persecuted on grouse moors; and a range of other species (Crowle et al., 2022; Newton, 2021; Tharme et al., 2001). Our study suggests that the loss of management for grouse shooting would result in substantial national declines in red grouse populations but more modest declines in non-target wader species. Thus, even for the non-target bird species that are most likely to be sensitive to changes in grouse moor management, the loss of grouse moor management may only lead to modest abundance declines at the scale of Great Britain. Our predictions assume that the uplands would continue to be dominated by dwarf shrub heath and acid grassland, which would depend on the form of land management that would replace grouse shooting. Heather moorland is a semi-natural habitat, much of which is currently maintained

largely by burning and grazing to promote high heather cover, preventing woodland succession (Gimingham, 1989). The study species would be likely to decline strongly if woodland cover increased significantly (Littlewood et al., 2019). In contrast, currently rare species such as black grouse (*Lyrurus tetrix*) and Eurasian woodcock (*Scolopax rusticola*) could benefit from increased cover of woodland and scrub. However, due to a range of biophysical and regulatory constraints (e.g. site designations, incentive payments), grouse moors are more likely to be replaced by a range of less intensive land uses rather than large-scale forestry or intensification of sheep grazing (Crowle et al., 2022). The retention of elements of grouse moor management at lower intensities could mean that the declines in the study species would be weaker than predicted here. Further observational and experimental studies are needed to assess the potential effects of alternative forms of management, such as peat restoration, less intensive forms of shooting, grazing, burning and afforestation. This will enable the development of more realistic, intermediate scenarios of upland land management to be incorporated into predictive models.

AUTHOR CONTRIBUTIONS

Mark J. Whittingham, Stephen G. Willis, Tom H. E. Mason and Nick Littlewood conceived the ideas and designed the methodology; Tom H. E. Mason analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors of this study have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The bird abundance data used in this study are openly available via <https://doi.org/10.5281/zenodo.10599935> (Gillings et al., 2025). The moorland burning data used in this study are available on request from the RSPB (<https://opendata-rspb.opendata.arcgis.com/datasets/RSPB::muirburn-extent/about>; contact dataunit@rspb.org.uk to enquire about accessing the data).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Regional variation in predicted change in relative abundance (%) due to ceasing management for grouse shooting (a), climate change (a) and ceasing management in conjunction with climate change (b). Predictions are proportional changes in regional population indices, which were summed for each region from GB model predictions. Climate change effects are shown for two future climate periods (2040s and 2080s) and four emission scenarios (RCP), representing different levels of radiative forcing (2.6, 4.5, 6.0 and 8.5 W m⁻²). Predictions from two regions with relative abundance of each species <100 are not displayed (Lake District and South West).

Figure S1. The study area and associated regions. Panel (a) shows the study area (i.e. upland moorland habitat), encompassing 61,012 km² (15,253 2-km grid cells), delineated from land cover data. Bird relative abundance data were available from the British Trust for Ornithology for 32,380 km² of this area (dark blue areas; 8095 grid cells). Panel (b) shows the area delineated by the upland moorland line for England, for comparison only (Rural Payments Agency 2023; <https://www.data.gov.uk/dataset/0817bc9e-341f-4d8c-be66-38b1fab69b21/less-favoured-areas-lfa-and-moorland-lines-layer>). Panel (c) shows

nine upland regions, separated based on biogeography and national boundaries, used to explore spatial variation in model predictions.

Figure S2. The relationship between model predictions and observed relative abundance data. Observed data were divided into zeros and four equally spaced non-zero abundance classes, each containing 25% of the remaining data. Shaded areas, vertical bars and horizontal bars represent the smoothed distributions, interquartile ranges, and median values of model predictions, respectively. Weighted Cohen's kappa statistics are shown for each species.

Figure S3. The marginal effects of climate predictors on the relative abundance of each species, from upland-only models: (a) April–July mean temperature, (b) mean temperature of the coldest month, (c) April–July total precipitation and (d) August–March total precipitation. Lines show mean predictions, with other variables held at mean values. Shaded areas around lines are the 95% percentiles of deviations around those means. Marginal effects are displayed for the central 95% percentiles of each temperature variable across upland areas. The grey curve shows the frequency distributions of each temperature variable across the uplands.

Figure S4. Spatial variation in predicted relative abundance ($\hat{n}$) of each species across upland GB (left column), and in the marginal effects of environmental variables (central column) and management intensity (right column), where the effects of management and environment respectively were held at zero. Population indices ($\hat{N}$)—summed relative abundance—are shown.

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