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A national-scale assessment of climate change impacts on species: Assessing the balance of risks and opportunities for multiple taxa

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ABSTRACT

It is important for conservationists to be able to assess the risks that climate change poses to species, in order to inform decision making. Using standardised and repeatable methods, we present a national-scale assessment of the risks of range loss and opportunities for range expansion that climate change could pose for over 3000 plants and animals. Species were selected by their occurrence in England, the primary focus of the study, but climate change impacts were assessed across Great Britain, widening their geographical relevance. A basic risk assessment that compared projected future changes in potential range with recently observed changes classified 21% of species as being at high risk and 6% at medium risk of range loss under a B1 climate change scenario. A greater number of species were classified as having a medium (16%) or high (38%) opportunity to potentially expand their distribution. A more comprehensive assessment, incorporating additional ecological information, including potentially confounding and exacerbating factors (e.g. dispersal, habitat availability and other constraints), was applied to 402 species, of which 35% were at risk of range loss and 42% may expand their range extent. This study covers a temperate region with a significant proportion of species at their poleward range limit; the balance of risks and opportunities from climate change may be different elsewhere. The outcome of both risk assessments varied between taxonomic groups, with bryophytes and vascular plants containing the greatest proportion of species at risk from climate change. Upland habitats contained more species at risk than other habitats. Whilst the overall pattern was clear, confidence was generally low for individual assessments, with the exception of well-studied taxa such as birds. In response to climate change, nature conservation needs to plan for changing species distributions and an uncertain future.

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1. Introduction

To make the best use of conservation resources, it is necessary to prioritise species for action, for example according to their current status and the threats that they face. Globally, the most widely adopted framework for this is the IUCN Red List which quantifies extinction risk using information on the population size and range extent of a species, and the rate of change in those parameters (Mace et al., 2008; IUCN, 2016). Anthropogenic climate change is likely to exacerbate the extinction risk of many species over the course of this century (Thomas et al., 2004; Bellard et al., 2012; Warren et al., 2013; Foden et al., 2013). A number of approaches have been developed to assess the potential impact of climate change on species' future status (Akçakaya et al., 2015). One common approach uses species distribution models (widely termed bioclimatic-envelope or climate-envelope models) to link distribution to climate variables and project the likely future impact of climate change on species' distributions (e.g. Thomas et al., 2004; Huntley et al., 2007; Walmsley et al., 2007; Warren et al., 2013). An alternative approach is to undertake vulnerability assessments which may combine a measure of future projected climate change (exposure) with ecological traits to identify the sorts of species most likely to be both sensitive to and lack the capacity to adapt to climate change (e.g. Gardali et al., 2012; Foden et al., 2013).

Vulnerability assessments have often been applied to single taxonomic groups within particular regions or countries (e.g. Heikkinen et al., 2010; Barbet-Massin et al., 2012) or, less commonly across a global scale (Jetz et al., 2007; Foden et al., 2013). Relatively few vulnerability assessments have covered the full range of biodiversity present within a particular geographical area, despite the fact that a comprehensive assessment of as many taxa as possible would assist governments and conservation organisations plan and adapt to climate change. Achieving such wide coverage is challenging because many assessments require taxon-specific information or use approaches that have limited applicability to other taxa (e.g. Heikkinen et al., 2010; Gardali et al., 2012; Moyle et al., 2013). To date, it has been difficult to develop an approach which works across a range of taxa due to the different nature of ecological traits across contrasting taxonomic groups, and the variable availability of data (e.g. of species distributions, trends and traits). The strong tradition of biological recording in Britain across a wide range of taxa provides a rare opportunity to tackle this challenge.

Thomas et al. (2011) developed a framework to assess the threats and potential benefits of climate change that is applicable to a wide range of taxa. It uses bioclimatic-envelope models, combined with information on recent trends and additional ecological information, to identify the likelihood of species' range expansion and contraction, and has so far been applied to UK butterflies and some exemplar species from other taxa (Thomas et al., 2011). Here, we use a modification of this approach to undertake a climate change vulnerability assessment of > 3000 terrestrial and wetland species, (and in a minority of cases, species aggregates and distinctive subspecies or varieties, hereafter all termed 'species' for brevity; see methods) across 17 taxonomic groups in Britain (Table 1). This provides the first opportunity to examine how an important aspect of vulnerability to climate change varies between taxonomic groups, and between species associated with specific habitat types, for as complete a biological assemblage as currently feasible.

This study was developed as part of a wider initiative of Natural England, the government conservation agency in England, to support decision making on adaptation (Natural England, 2014) and inform an adaptation plan (Natural England, 2015). It therefore focuses on species in England, the largest of the component countries within the United Kingdom (UK), but assesses the vulnerability of those species across Great Britain (GB), the single land mass within which England is located. This ensures that the outputs are also highly relevant for Wales and Scotland, for UK organisations, and more widely.

2. Materials and methods

The vulnerability assessment involved a number of steps (Fig. 1) outlined below:

1. Distribution data for over 5000 species were collated for a wide range of taxa that occur in England (Table 1).
2. Statistical models linking species' distributions to climate were used to assess the likely impacts of future climate change upon species' potential distributions.
3. Information from these projections was compared with observed changes in species distribution. By assessing recently observed changes in the context of projected future trends, a *simplified risk assessment* could be undertaken rapidly across all species.
4. For a representative subset of 402 species, additional ecological information enabled the application of the full Thomas et al. (2011) framework. By considering the potential for non-climatic factors and ecological constraints to affect species' responses to climate change, this framework produces a more comprehensive assessment (the *full risk assessment*).

Whilst the term 'risk assessment' can have specific meanings in different contexts, we follow Thomas et al. (2011) and use it to describe our methodology for assessing the potential risks of species decline and extirpation in parts of its current range, and opportunities that the same species may expand its distribution into other regions, both as a result of climate change. By using a combination of observed and modelled responses to climate change, the methodology deals with the long timescales over which species' responses to climate change are likely to occur.

2.1. Species distribution data

Species distribution data for GB were available from a range of biological recording schemes for a total of seventeen taxonomic groups (Table 1) at a hectad (10 km square) resolution. For inclusion, species had to be present in England and recorded from > 5 hectads (the minimum required for modelling; Hickling et al., 2006). Even with this threshold the climate envelope models (described below) failed to converge for 10% of the most sparsely distributed species, giving a total of 4540 species for which modelling was possible.

We used data from 1970 to 89 to represent baseline distributions prior to recent climate change, in order to minimise the risk of species' distributions being unsynchronised with the climate due to recent range shifts (Mason et al., 2015). For plants we used the period 1970–86; the time period (Braithwaite and Walker, 2012) that most closely matched the data for other taxa. For birds the period 1988–91 was used, which coincided with a national atlas (Gibbons et al., 1993). Cells for which climate data were not available were excluded from analyses. To aid model convergence, small islands, with little data, were also excluded for all taxa apart from birds, leaving 2561 hectads, or 2670 for birds.

Recording effort varied between taxa, with the highest coverage for groups with well-developed and popular volunteer recording schemes such as vascular plants and birds. To avoid species' distribution models being biased as a result of limited recording effort, we used the program FRESCALO (Hill, 2012) to estimate taxon-specific recorder effort in each 10 km square (see below).

2.2. Species distribution modelling

We used the climate envelope modelling approach of Beale et al. (2014) across all taxa (Appendix 1). The approach was devised to address the problem of spatial autocorrelation in large-scale species' distribution data, and applies a Bayesian, spatially explicit (Conditional Autoregressive) Generalised Additive Model (GAM) to species'

Table 1
Summary of the coverage of different species groups by this risk assessment.

Taxon	Recording scheme	Link	Total species with distribution data	Species for which climate models converged	Species for which trends could be calculated	Conservation priority species with trends calculated
Ants	Bees, Wasps and Ants Recording Society (BWARS)	www.bwars.com	36	28	13	0
Bees	Bees, Wasps and Ants Recording Society (BWARS)	www.bwars.com	225	187	143	6
Birds	British Trust for Ornithology	www.bto.org	180	180[a]	180	41
Bryophytes	British Bryological Society	www.britishbryologicalsociety.org.uk	1049	850	520	1
Carabid beetles	Ground Beetle Recording Scheme	http://www.brc.ac.uk/scheme/ground-beetle-recording-scheme	317	266	175	3
Centipedes & millipedes	British Myriapod and Isopod Group, Centipede and Millipede Recording Schemes	www.bmig.org.uk	85	66	39	0
Cerambycid Beetles	Cerambycidae Recording Scheme	http://www.coleoptera.org.uk/cerambycidae/home	52	40	0	0
Coccinelid beetles	Ladybird Recording Scheme	www.ladybird-survey.org	44	38	17	0
Craneflies	Dipterists Forum, Cranefly Recording Scheme	www.dipteristsforum.org.uk	78	64	11	0
Crickets & grasshoppers	Orthoptera Recording Scheme	www.orthoptera.org.uk	43	31	23	0
Dragonflies & damselflies	British Dragonfly Society, Dragonfly Recording Network	www.british-dragonflies.org.uk	45	35	26	0
Hoverflies	Dipterists Forum, Hoverfly Recording Scheme	www.hoverfly.org.uk	249	213	175	0
Moths	Butterfly Conservation, National Moth Recording Scheme	www.mothscount.org/text/27/national_moth_recording_scheme.html	668	622	422	58
Soldier Beetles and allies	Soldier Beetles, Jewel Beetles and Glow-worms Recording Scheme	http://www.brc.ac.uk/scheme/soldier-beetles-jewel-beetles-and-glow-worms-recording-scheme	53	46	22	0
Spiders	Spider Recording Scheme, British Arachnological Society	www.srs.britishspiders.org.uk, www.BritishSpiders.org.uk	512	374	297	7
Vascular plants	Botanical Society of Britiain and Ireland (BSBI)	www.bsbi.org.uk	1365	1,339[b]	852	38
Wasps	Bees, Wasps and Ants Recording Society (BWARS)	www.bwars.com	219	161	133	1
Total			5220	4540	3048	155

[a] Models for two species failed to converge when built using only GB data.
[b] For 354 of these, European data were also available.

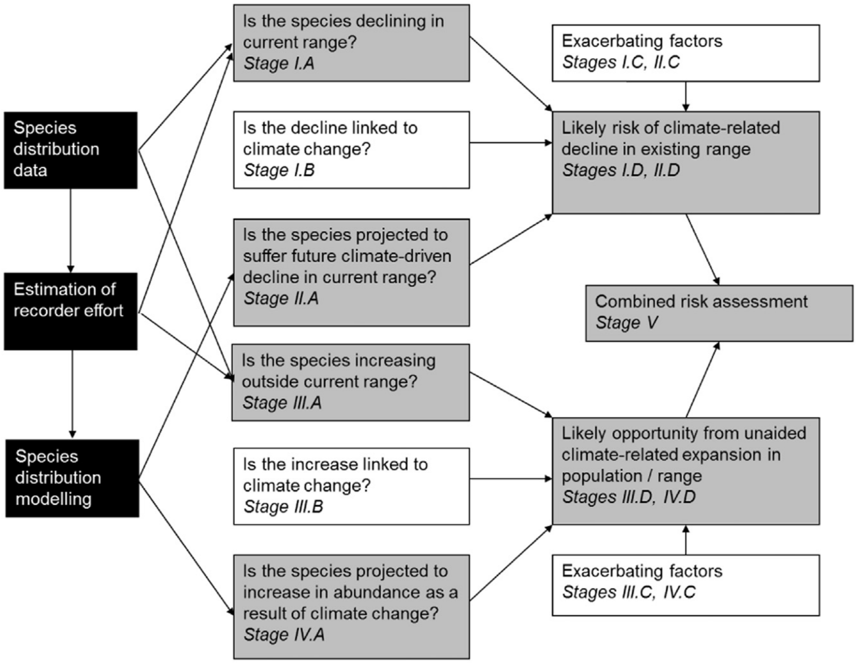

Fig. 1. Summary of the processes involved in the application of the *full risk assessment* (simplified from Thomas et al., 2011), and how those are represented by the various stages of the process. Black boxes indicate the information required prior to risk assessment. Boxes in grey represent the steps of the *simplified risk assessment*.

distribution data in order to separate climatic, spatial and random components in determining the distribution of each species. Four bioclimate variables were used to describe spatial variation in the climate, using 1961–1990 averages:

- mean temperature of the coldest month (MTCO): a measure of winter cold.
- growing degree days above 5 °C (GDD5): a measure of biologically useful warmth, calculated by applying a spline to mean monthly temperatures for each cell to convert monthly data to daily estimates.
- the coefficient of variation of temperature (cvTemp): a measure of seasonality
- soil moisture (soilWater): a measure of moisture availability calculated following the bucket model of Prentice et al. (1992), which takes inputs of temperature, rainfall, % sun/cloud and soil water capacities.

For birds and a quarter of vascular plants, we initially constructed 50 km resolution species distribution models across Europe to describe the relationship between occurrence and climate using uninformative priors (i.e. with no prior knowledge of what this relationship should be). Once converged, a second model was fitted to hectad data from GB using informative priors from the European-scale analysis. As a result, any strong climatic signal based on the European distribution would remain essentially unchanged when modelled using GB data only, unless there was strong evidence for a different climatic signal within GB. In cases where there was high uncertainty in the estimation of potential range shifts at a European level, the GB model would be more heavily informed by outputs from the British component of the model. We tested for differences between both models for birds and vascular plants under the A1B scenario. Predicted changes were strongly correlated, although models based on GB only data tended to result in fewer species showing potential increases in range (Appendix 1). For species for which data from GB only were available, only the second model was run using uninformative priors (e.g. Fig. 2).

Future climate projections for the UK were derived from UKCP09, which use outputs from an ensemble of variants of the HADSM3 climate model to produce a series of probabilistic outputs for individual climate variables for three IPCC SRES scenarios (A1F1, A1B and B1). These are regarded as the most suitable climate change projections for the UK, downscaled to a 25 km grid (Murphy et al., 2009). We considered two contrasting scenarios, the B1 scenario which is a low emissions scenario projected to lead to a *c*. 2 °C global temperature increase by the end of this century (equivalent to RCP4.5) and the A1B scenario, that represents vulnerabilities under a medium emissions scenario of c. 4 °C global warming by the end of this century (intermediate between RCP6 and RCP8.5) (Rogelj et al., 2012). As there was a strong correlation between the results of the two scenarios, we focus on the B1 results in this paper, and present the results from the A1B scenario in Appendix 1.

2.3. *Simplified risk assessment*

Distribution data from national schemes were used to identify post-1989 range changes within the baseline historical distribution (1970–89; or 1970–86 for plants and 1988–91 for birds, as described above), and outside this historic range (newly colonised areas). With the exception of birds, distributional changes required correction to account for variation in observer effort (Appendix 2).

Due to limited data availability across adequately sampled squares, it was not possible to use this method to produce effort-corrected observed trends for 1492 species, leaving a total of 3048 to which the risk assessment could be applied. Of these, 50 were species aggregates reflecting taxonomic changes over previous decades (1 bird, 3 carabid beetles, 28 bryophyte and 18 vascular plants), 123 were specific subspecies or varieties (38 bryophytes, 2 spiders and 83 vascular plants), and 80 were infraspecies, whose distribution may have been based on partial information, due to the separate recording of taxonomically distinct subspecies or related species aggregates (31 bryophytes, 1 carabid beetle and 48 vascular plants). The inclusion of this mix of taxonomic resolutions did not bias the risk assessment towards species of particular risk or opportunity categories; in a sensitivity analysis there was no significant difference in the allocation to different risk categories between ‘true’ species and these other taxonomic concepts combined, under either the B1 ($\chi_4{}^2 = 7.93$, $P = 0.094$) or A1B ($\chi_4{}^2 = 7.44$, $P = 0.11$) scenarios. We have therefore assessed all taxonomic concepts together, but for completeness also present the results for bryophytes and vascular plant species separately, excluding aggregates, subspecies and infraspecies.

Current contractions within the historical range were compared

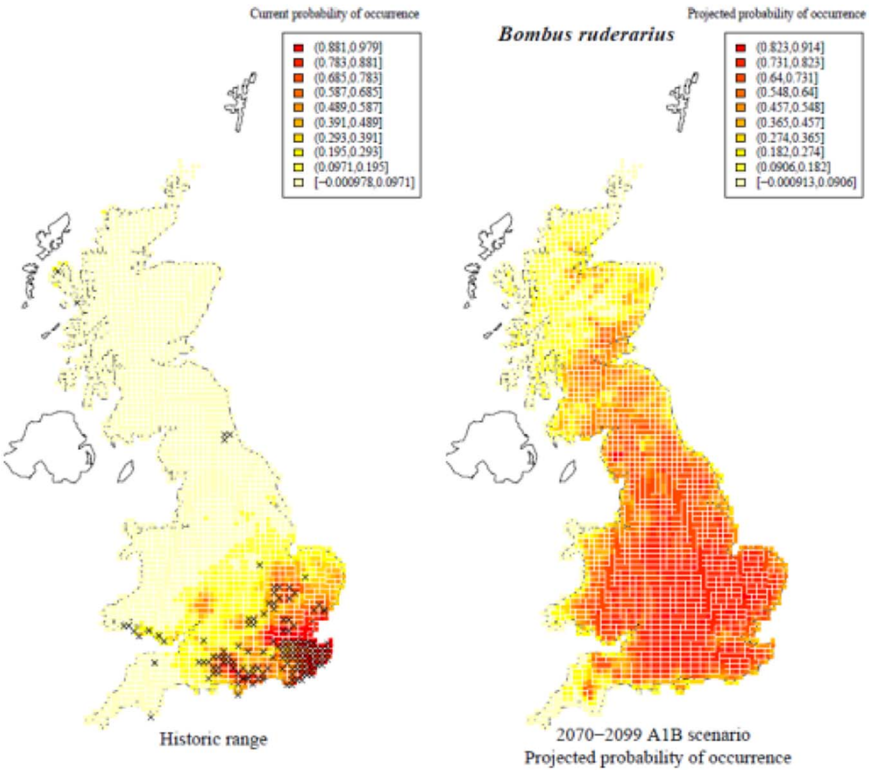

Fig. 2. The historic (1970–1990) probability of occurrence of an example species, *Bombus ruderarius*, (left) and the projected probability of occurrence under a medium emissions A1B scenario (right). Black crosses show actual records and coloured squares show modelled probability of occurrence.

against the magnitude of projected future contractions to assess risk from climate change, whilst observed range expansion was cross-tabulated with the magnitude of projected future range expansion to assess potential risks and opportunities from climate change (Appendix 3). The highest risk or opportunity categories were reserved for those species where projected future changes were consistent with observed changes. As the simplified risk assessment may have inflated the potential risk of climate change for species which have suffered recent declines and range contractions for non-climatic reasons, for a subset of 402 species, we also undertook a full risk assessment following the Thomas et al. (2011) framework to account for non-climatic factors and constraints.

2.4. Full risk assessment

The 402 species (including 4 subspecies/varieties and 1 infra-species) for full assessment comprised 155 conservation priority species listed under the Section 41 of the Natural Environment and Rural Communities (NERC) Act 2006 (http://www.legislation.gov.uk/ukpga/2006/16/pdfs/ukpga_20060016_en.pdf), termed NERC species, as well as at least 13 randomly selected species from each taxonomic group. This provided a broad appraisal across taxa, whilst ensuring as many species of highest conservation concern as possible were included. The full risk assessment used additional ecological information on population size and range extent, the link between population and range changes to climate, and on potential exacerbating factors (e.g. range extent and population size, ecological constraints associated with habitat-availability, dispersal and species interactions) to moderate the likely risk and opportunity scores, and the overall assessment of confidence (Thomas et al., 2011). Small and range-restricted populations, or species associated with other constraints, received a higher risk score, whilst the likelihood of range expansion was reduced if habitat availability, dispersal ability and other limiting species were judged as likely to result in species achieving a lower level of range expansion than predicted by the models. This information was gathered from a literature search for each species using Google Scholar and Web of Science, supplemented by additional information from UK species experts (see Acknowledgements). The confidence associated with ecological information was regarded as good if based upon peer-reviewed literature. If it was based on expert knowledge then the expert was asked to assign the confidence level.

The full risk assessment consisted of four stages (Figure 1, Appendix 4), requiring information on observed changes in occurrence within the current range (Stage I), projected changes within the current range (Stage II), observed changes in occurrence outside the current range (Stage III) and projected changes outside the current range (Stage IV). The results of the four stages were synthesised into a single table (Table A4). The overall confidence for species 'at risk' was the confidence associated with the assessment of threat, whilst for species with an opportunity for expansion, we used the confidence associated with that. For species classed as having 'risks and opportunities' or 'limited impact', we averaged the two confidence scores.

2.5. Statistical analysis

Significant differences in the proportion of species allotted to different risk categories were tested by Chi-square, as were contrasts between taxonomic groups and between NERC and other species. Information on the broad habitat associations of the 155 NERC priority species, summarised into wetland, urban, farmland, upland woodland and coastal categories, was used to test the extent to which species' vulnerability to climate change, from the full risk assessment, varied between habitats.

Formal differences between the results from the simplified and full risk assessments for each of the 402 species assessed using both risk assessment methods were tested by Chi-square test and by regression. For the latter, we converted the categorical risk assessment into rank scores from high risk (-2) to high opportunity (2), with both 'risks & opportunities' and 'limited impact' categories scored as 0. Scores were regressed within a generalised linear mixed model, with taxonomic identity as a random effect, using PROC MIXED in SAS v9.2. We used the same scores to test for differences in full risk assessment outcomes between different taxa, and between NERC and other species.

Table 2
Cross-tabulation of the risks and opportunities associated with climate change for all 3048 species run through the *simplified risk assessment*, based upon a low emission B1 projection for 2070–2099 (see Tables A3 and A4 for the derivation and interpretation of each category). Values are the numbers of species in each category.

		Risk				
		Very high	High	Medium	Low	Totals
Opportunity	Low	25	1	7	6	39
	Medium	614	157	481	84	1,336
	High	24	27	358	142	551
	Very high	56	44	662	360	1,122
	Totals	719	229	1,508	592	3,048

3. Results

3.1. Simplified risk assessment

Of the 3048 species assessed, 640 were classified as being at high risk of a decline in the area of projected suitable climate under the B1 climate change scenario and 188 at medium risk (a total of 27.2% species at risk). A greater number of species were identified as likely to have a medium (486) or high (1164) potential opportunity as a result of projected increases in the area of potentially suitable climate (totalling 54.1%; Table 2). For only 6 was limited impact predicted. These estimates of risk were similar under the A1B warming scenario ($\chi_5{}^2 = 2.96$, $P = 0.71$), although with slightly more species (28.1%) classified as being at risk (Appendix 1 Table A1).

The outcome of the risk assessment varied significantly between taxonomic groups ($\chi_{64}{}^2 = 475.54$, $P < 0.0001$; excluding the limited impact category due to the small sample size). These differences remained ($\chi_{32}{}^2 = 339.73$, $P < 0.0001$) when simply splitting species into those at risk, likely to have an opportunity, or likely to be unaffected (i.e. risks & opportunities and limited impact categories combined). The proportion of species at risk varied from 6% for wasps to 39% for vascular plants, whilst the proportion of species with opportunity varied from 37% for bryophytes to 90% for wasps (Figure 3). Repeating this appraisal for bryophytes and vascular plants without subspecies and infraspecies produced equivalent assessments for both (bryophytes: high opportunity 107 spp. (25%), medium opportunity 48 spp. (11%), risks and opportunity 134 spp. (32%), medium risk 32 spp. (8%), high risk 102 spp. (24%); vascular plants: high opportunity 210 spp. (30%), medium opportunity 103 spp. (15%), risks and opportunity 131 spp. (19%), medium risk 59 spp. (8%), high risk 200 spp. (28%)). The groups with the greatest proportion of species at risk from climate change were bryophytes and vascular plants (> 30% in both cases), whilst a number of groups were largely (> 70%) comprised of species for which climate change may present an opportunity for range expansion in GB (ants, bees, centipedes, coccinellid beetles and wasps).

NERC species contained slightly more ‘high risk’ and ‘medium opportunity’ species and fewer ‘high opportunity’ species than expected from the pattern across the other species ($\chi_4{}^2 = 10.30$, $P = 0.036$), but there was no overall difference between these two species groups when the categories were simplified to risk, opportunity or unaffected ($\chi_2{}^2 = 1.07$, $P = 0.58$).

3.2. Full risk assessment

Across all 402 species run through the full framework for the B1 scenario, 141 (35.1%) were classified as being at high or medium risk of being negatively affected by climate change, compared to 168 (41.8%) which were listed as likely to have a medium or high opportunity (Table 3). Limited impact was predicted for 19% of species. There was no significant difference from this classification of species under the

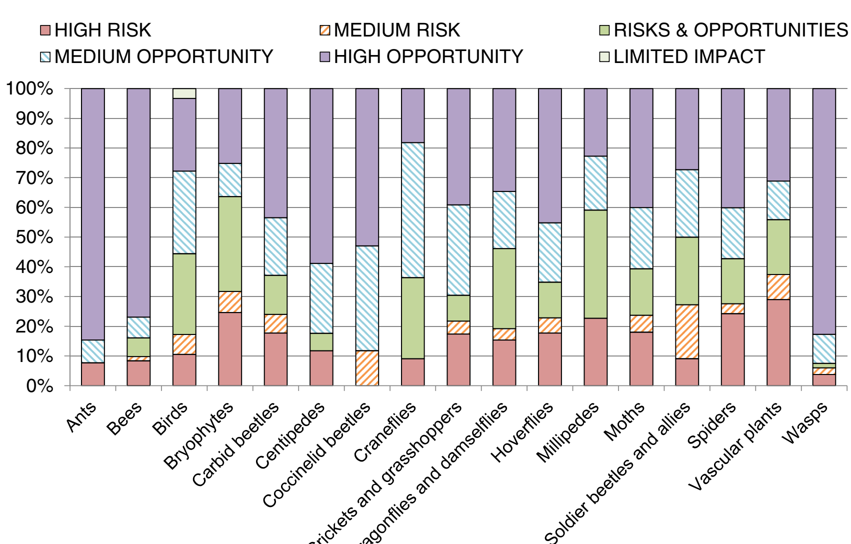

Fig. 3. Proportion of species categorised as likely to be at risk or to have an opportunity for expansion from climate change, based upon a low emission B1 projection for 2070–2099, in different taxonomic groups, as assessed by the *simplified risk assessment*. The sample size of species for each group is given in Table 1.

Table 3
Cross-tabulation of the risks and opportunities associated with climate change for 402 species from all taxonomic groups run through the *full risk assessment*, based upon a low emission B1 projection for 2070–2099. Values in parentheses are the values for the species of conservation concern only.

		Risk				
		Very high	High	Medium	Low	Totals
Opportunity	Low	67 (34)	37 (11)	21 (7)	75 (27)	200 (79)
	Medium	5 (3)	2 (0)	1 (0)	22 (11)	30 (14)
	High	9 (4)	9 (4)	7 (3)	64 (26)	89 (37)
	Very high	8 (5)	4 (2)	5 (1)	66 (17)	83 (25)
	Totals	89 (46)	51 (17)	34 (11)	227 (81)	402 (155)

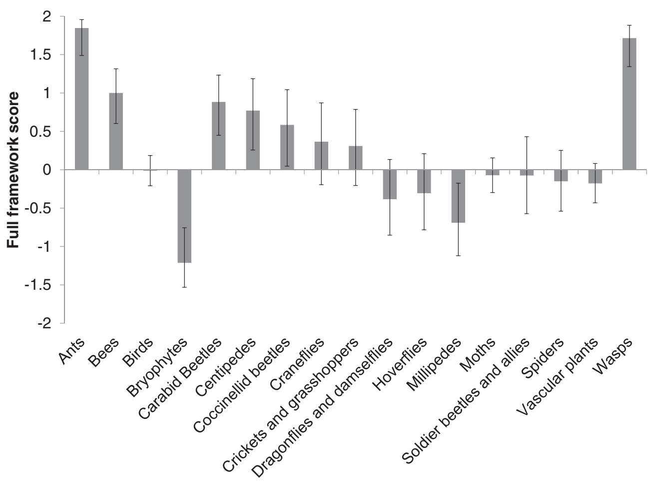

Fig. 4. Modelled *full risk assessment* score for each taxonomic group, from a GLM containing taxonomic group and conservation status. Presented are least-square means from the model with standard errors. A score of 2 is equivalent to high opportunity, 1, medium opportunity, 0 risk and opportunity or no impact, − 1 medium risk and − 2 high risk.

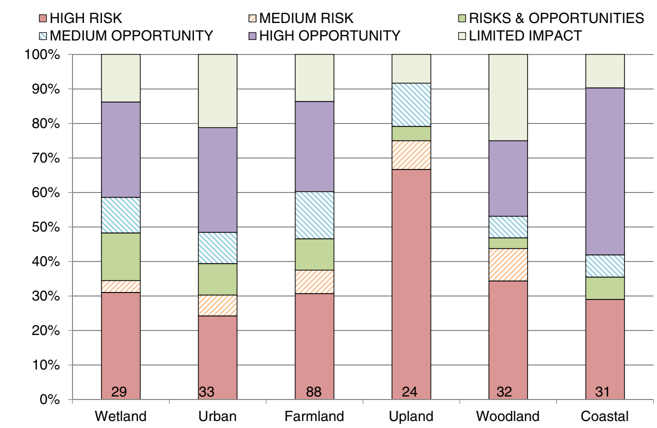

Fig. 5. Proportion of species categorised as likely to be at risk from climate change, or to have an opportunity, using the *full risk assessment*, according to the habitat each species is associated with. The sample size for each habitat is shown by the number on each column. About half of species contributed information to more than one habitat. Habitat association information was available for the NERC species of conservation concern only. The results are based upon a low emission B1 projection for 2070–2099.

A1B scenario ($\chi_5{}^2 = 0.94$, $P = 0.92$; Appendix 1 Table A2). The score attributed to species did not vary between NERC species and the remainder ($F_{1,384} < 0.01$, $P = 0.99$), but did vary with taxonomic group ($F_{16,384} = 3.38$, $P < 0.0001$). The lowest scores, indicating the greatest proportion of species at risk from climate change, were for bryophytes ($n = 14$), with the highest scores for ants ($n = 13$) and wasps ($n = 13$), the majority of which were classed as having a high opportunity from climate change (Figure 4).

There was no significant variation overall between habitats in the frequencies of NERC species allocated to different risk categories ($\chi_{25}{}^2 = 33.86$, $P = 0.11$). However, upland was the only habitat with a majority of species (75%) regarded as being at risk of a decline in the area of projected suitable climate (Figure 5), which contrasted significantly with average of 40% of species across the remaining habitats when lumped together ($\chi_5{}^2 = 15.59$, $P = 0.008$).

For the majority (314) of species in the full assessment, confidence was poor, for 86 it was medium and good for only two. Confidence scores differed significantly between taxonomic groups ($\chi_{16}{}^2 = 57.23$, $P < 0.0001$), driven primarily by a greater level of confidence for bird assessments (35% of 82 assessments were accorded medium or good confidence) than for other species, where 18% of 320 assessments were classed as having medium confidence, and none good.

3.3. Simplified v Full Risk Assessment

There was a strong association between the scores using the simplified and full approaches for species assessed by both ($F_{1,398} = 955.56$, $P < 0.0001$; $S_F = -0.33\ (\pm 0.089) + 0.91\ (\pm 0.029)\ S_S$, where S_F is the full assessment score and S_S the simplified assessment score). The scores from the two frameworks had a close to 1:1 relationship, but the intercept shows that the full assessment on average produced a lower (higher risk or lower opportunity) score by 0.33 (or one third of a category).

4. Discussion

Here we present a national-level assessment of species' vulnerability to climate change, covering 3048 species across 17 taxonomic groups. Consistently for both B1 and A1B scenarios, we found that there was a greater number of species for which potential range is projected to increase as a result of climate change than it is projected to decrease. This was particularly the case when considering the outputs for the simplified framework for all species, where over 50% were classified with a medium or high opportunity from climate change (Table 2), but also applied to 43% of the subset of species run through the full risk assessment framework, compared with projected negative range impacts for 35% (Table 3). This also concurs with the previously published results of the full risk assessment methodology for butterflies in GB, which used an A2 climate change scenario intermediate between the B1 and A1B scenarios used here (Thomas et al., 2011). Of 58 butterfly species, three were regarded as at high risk from climate change, three at medium risk, 10 likely to have a medium opportunity, 14 a high opportunity and 27 limited impact. If turned into rank scores and added to the results of our study, this would place butterflies intermediate between coccinelid beetles and craneflies, with a mean score of 0.52 (Figure 4). Our findings are also consistent with recently observed trends across multiple taxa in the UK where more species are regarded as being impacted positively by climate change than negatively, at least in the short-term (Burns et al., 2016).

It could be argued that by indicating that a greater number of taxa are likely to have an opportunity for range expansion in response to climate change than be at risk of range contraction, our analysis suggests that climate change will have a positive impact upon UK biodiversity. However, before considering this, it is worth noting how our findings may result from both underlying methodological constraints and inherent biological processes.

It was not possible to undertake assessments for 13% of species because there were insufficient data to generate a bioclimate model, and for a further 29% of remaining species there was insufficient information to produce effort-corrected observed trends. Given latitudinal gradients in observer (recorder) effort within the UK, with more recorders in the south than the north, it is likely that a greater proportion of unassessed species were northerly-distributed and may include species more likely to be at risk of adverse climate change impacts than to benefit. However, by selecting species from England, but using data from across GB for their assessment, this enabled us to include more northern and upland species than we otherwise would have done had we undertaken the assessment with distribution data from England alone. In addition, it is possible that more localised and specialised species, which may be species less likely to benefit from climate change (e.g. Warren et al., 2001), were more likely to be data deficient and excluded. We did observe a significant difference between the scores of conservation priority species (many of which are rare and specialised) and others in the simplified assessment, but there was no such difference in the full assessment.

Apart from birds and vascular plants, the biodiversity data underpinning the assessment were from GB only, and in most cases our models do not capture the full range of climatically-suitable conditions in which the species can occur. A comparison of models based on GB data vs. GB + European data for birds and vascular plants, suggested that GB-only projections tended to be slightly more pessimistic than those that included European data, although the two were strongly correlated. Thus, the use of GB-only projections for most groups may have slightly inflated the projected magnitude of risk for those groups, although the assessment for vascular plants, one of the groups with the greatest proportion of species regarded as being at risk from climate change, included European data in the assessment. It is also worth noting that by including only species that currently occur in England, we did not consider the potential for new species to colonise the UK from mainland Europe as a result of climate change, which is already happening (e.g. Hiley et al., 2013). Thus our results may exclude a number of potential colonists to the UK for which climate change provides an opportunity. In other words, the outcome of the risk assessment may be scale- and context-dependent; a species projected to be at risk from climate change across mainland Europe may undergo a poleward shift and colonise the UK, where it would be regarded as having an opportunity for range expansion. This emphasises the value of undertaking assessments such as this at a range of spatial scales, which has rarely been done.

We assumed that the species distribution models describe the main relationships between species' occurrence and terrestrial climate. As we employed widely-used bioclimatic variables, this is probably reasonable for most terrestrial taxa, but for some coastal bird species which use the marine environment, where spatial patterns of changes in sea temperature and other climate related variables may differ from those on land, projections are likely to be less certain. We also have not considered potentially detrimental impacts of sea-level rise and storm surges upon vulnerable coastal habitats and species (e.g. Gilbert et al., 2010; Ausden, 2014).

The full assessment that considered ecological factors known to influence observed changes in populations or distributions, or likely constraints on the impacts of climate change, was applied to 402 species only. By excluding these considerations, the simple assessment applied across all species may have over-attributed observed changes to potential impacts of climate change if they were consistent with future projections (such as for farmland birds, crickets, centipedes and millipedes; Eglington and Pearce-Higgins, 2012; Beckmann et al., 2015; Lee, 2015; Burns et al., 2016), or under-estimated the potential magnitude of future climate change impacts if observed changes were opposite to future projections as a result of non-climatic factors. Although both methodologies delivered broadly comparable results, the full assessment did increase the proportion of species projected to experience only a limited impact of climate change, and included a greater proportion of species projected to be at risk.

Finally, there is considerable uncertainty about the likely pace of any distributional shift in response to climate change. Both bird and butterfly communities appear to be lagging behind the rate of warming observed across Europe (Devictor et al., 2012, Massimino et al., 2015); less-mobile groups, such as many of the vascular plants, may well lag even more. The ability of a species to disperse will be an important constraint on the extent to which some species can occupy any new areas of potential range in the future (Barbet-Massin et al., 2012), as will the availability of areas of potentially suitable habitat for colonisation (Thomas et al., 2012; Hiley et al., 2013) and underlying population dynamics (Mair et al., 2014). Although considerable uncertainty remains about the pace of these responses to climate change, these uncertainties were at least partially captured by the full risk assessment, which reduces the likelihood of opportunity as a result of climate change in species with constrained dispersal ability.

Despite the potential methodological constraints, there are good biological reasons to expect more species to be able to expand their range than be at risk of it contracting in response to climate in GB. This is because there are more southern species with potential for northward range expansion in Britain than there are northern species with southern range margins (e.g. butterflies: Asher et al., 2001; vascular plants: Preston et al., 2002; birds: Balmer et al., 2013), with strong latitudinal gradients in species' richness (e.g. Eglington et al., 2015). In combination with largely polewards shifts that are projected to occur in the distribution of a range of taxa, and are already being observed (Mason et al., 2015), this would lead to more species being likely to expand their distributions in GB, than to contract. Observations of recent trends suggest that this is already the case (Massimino et al., 2015, Burns et al., 2016). Although we assessed that fewer species would be at risk of range contraction from climate change than have an opportunity, species of certain taxonomic groups and habitats were identified as being more vulnerable than others. In particular, the full risk assessments completed for those species of conservation concern for which the required data are available suggested that species associated with upland habitat-types, where increasing temperatures might be expected to result in northwards and upwards range contraction, would be particularly vulnerable to climate change. This is consistent with the results of other studies suggesting that northern or upland birds (Green et al., 2008, Pearce-Higgins, 2010), butterflies (Thomas et al., 2011) and plants (Hill and Preston, 2015) may be more vulnerable to climate change than other species. Multi-taxa assessments have found similar patterns (Walmsley et al., 2007; Araújo et al., 2011), and there is already evidence of such impacts being observed (Morecroft and

Speakman, 2015). Whilst many taxonomic groups contain some species likely to be at risk from climate change and others with the potential to expand their distribution, the balance between these two outcomes will vary with the geographical and habitat bias of that group, as well as the ecological characteristics of the species, such as voltinism, diapause strategy, migratory strategy and growth rate (Bale et al., 2002). Other climate-influenced ecological changes will also affect species abundance and distribution in future through altered species interactions (Ockendon et al., 2014).

Geographical differences may partly account for the apparent high sensitivity to future climate change of bryophytes (Figs. 3 and 4), many of which have a northern or north-western distribution, associated with cool and damp conditions. Our analysis suggests that of all the taxonomic groups considered, they are likely to be one of the most at risk from a reduction in areas of suitable climate, conclusions broadly supported by Ellis (2015), who anticipated detrimental impacts of climate change on northern and upland bryophytes, although regarded potential impacts on species associated with oceanic climates as more uncertain. Even though there is some evidence for recent warming being associated with distribution shifts in some bryophytes (Bates and Preston, 2011), there are difficulties in disentangling these changes from decreases in acid and nitrogen deposition from the atmosphere (Roth et al., 2013). The basic assessment also identified vascular plants as containing a high proportion of species at risk from climate change. However climate change may provide more of an opportunity for range expansion in a greater proportion of vascular plants than bryophytes; the full risk assessment suggested 17/51 plants but only 1/14 bryophytes have an opportunity for range expansion from climate change (Figure 4), although it is worth noting that bryophytes probably have greater capacity for colonisation than vascular plants due to their spore-driven dispersal. Conversely the majority of Hymenoptera, particularly ants and wasps, have a southern distribution and were ranked as most likely to experience a high opportunity from climate change. This matches previous studies suggesting that populations of many Hymenoptera increase with warmer temperatures (Pearce-Higgins, 2010, Burns et al., 2016), probably because they are thermophilic species largely constrained by temperature.

It is noteworthy that the majority (78%) of full risk assessments had poor confidence. If this is the case in Britain, which is one of the best studied and data rich parts of the world, climate change risk assessments in other parts of the world are likely to be even more uncertain. This emphasises the need for long-term monitoring and research to document and understand the impacts of climate change on biodiversity, particularly outside well-studied parts of Europe and North America (Ockendon et al., 2014). As a result, nature conservation organisations will have to integrate uncertainty and flexibility into their response to climate change. The taxa for which assessments were most robust were butterflies, where 46% of species assessments had medium or good confidence (Thomas et al., 2011), and birds, for which 35% of assessments were associated with medium or good confidence. These are the two best studied taxonomic groups in Britain with respect to the impacts of climate change on their populations (e.g. Devictor et al., 2012, Morecroft and Speakman, 2015), and therefore the groups where observed changes can be more confidently attributed to climate change, where appropriate. They are also much better monitored than the other groups, with robust distribution change and annual population estimates adding to the confidence of the risk assessment. Practically speaking, the low confidence of most of the species' assessments in this study means that caution must be applied in judging the risk that climate change poses to individual species. Whilst we may have more confidence in the overall patterns of change, and how they vary between broad taxonomic groups and habitats, there are many reasons why an individual assessment for a species may not be borne out in reality. In the absence of further monitoring and research, many individual assessments should be used with an understanding of the confidence they are associated with and the uncertainty involved in projecting the future.

The main tool underpinning this assessment was climate envelope modelling. Although the results of some basic models have been criticised in the literature (see Beale et al., 2008), there is increasing evidence linking climate envelope model predictions to observed bird population changes (Stephens et al., 2016). The choice of statistical model, general circulation model (GCM) and emission scenario can have a significant impact upon the results of climate envelope models (Dormann et al., 2007, Diniz-Filho et al., 2009). Whilst we could therefore be criticised for using only one modelling approach (Beale et al., 2014) and one GCM (HADSM3), and therefore not capturing the potential full range of possible futures, we have tried to select approaches that give the most plausible futures. The Bayesian spatially-explicit GAM used is a significant advance on other modelling approaches, as it accounts for spatially auto-correlated components of a species' distribution (Beale et al., 2014). Furthermore, in studies such as this, Baker et al. (2017) advocate using the most suitable GCM for a particular location, which the HADSM3 is for GB. The use of additional GCMs and modelling approaches could yield alternative projections and assessments of risk as a potential extension of this work. However, these additional models would be unlikely to alter the generality of our conclusions for high-level taxonomic groups or habitats, or reduce the uncertainty of the individual species assessments. Instead, what is required is better validation of climate change risk assessment (Wheatley et al., 2017).

The simplified risk assessment makes use of both observed and projected population and range changes to assess risks and opportunities, allowing assessments to be moderated by the extent to which observed and projected trends are in accordance. The full risk assessment additionally makes use of ecological information on links between population or range changes and climate and on potential exacerbating factors. This information is used to modify the final risk assessment for those species, and to moderate the degree of confidence in the assessment. Evidence for a strong statistical link between distribution and/or abundance and climate, or good evidence that changes are not linked to climate, increased the confidence of the assessment. The quality of evidence around exacerbating factors such as range or population size, interacting species, habitat availability and dispersal, also affected the final assessment of confidence, This combination of climate envelope modelling with ecological information to assess the degree of constraint which species are likely to face in responding to climate change, and comparison with observed trends, is a step forward from the basic climate envelope modelling approach, whilst taking account of some of the potential constraints on a species-by-species basis (Thomas et al., 2011).

4.1. Implications for nature conservation

This analysis provides as near comprehensive an overview of how species ranges may change within a country under climate change as is currently possible. It goes beyond general principles of anticipating species range shift and provides an evidence-based assessment of the extent of change that is likely. The risk assessment indicates that, at a national level, the distributions of most species are liable to change. In the basic risk assessment only 6 out 3048 species were identified as having both low risk and low opportunity, whilst the full assessment classified only 75 of 402 species as having both low opportunity and low risk. This is an important finding for nature conservation planning, suggesting that changing distributions are likely to become the norm, not the exception, in the coming years.

Whilst there are many species that could potentially benefit from an expanding area of potentially suitable climate, these opportunities will not be realised if individuals are unable to disperse. Natural dispersal may be limited by several factors including habitat fragmentation, barriers of unsuitable habitats or low populations sizes and other pressures affecting healthy populations. Facilitating species movement is therefore likely to be a major challenge for future species conservation. Although many taxa have shown evidence of poleward shifts in their distribution in GB (Mason et al., 2015), this has been partly facilitated by a network of protected sites (Thomas et al., 2012), whose continued conservation and expansion becomes even more important in a changing climate.

The study also provides a greater clarity on the extent of threat to some species, particularly highlighting the vulnerability of upland taxa where many species are adapted to cool, wet conditions. For those species at risk of losing areas of potentially suitable climate, conservation actions to increase resilience (Morecroft et al., 2012), including the protection of key sites (Gillingham et al., 2015) and *refugia* (Suggitt et al., 2014), the maintenance of large or functional connected areas of semi-natural habitats within landscapes (Newson et al., 2014, Oliver et al., 2015, 2017) and direct management to promote in-situ persistence (Greenwood et al., 2016) will be important. An example of the latter is the potential to alter the management of vulnerable peatland habitats by raising water levels, likely to benefit plants, invertebrates and birds (Carroll et al., 2011, Bellamy et al., 2012). Reducing other non-climatic pressures on upland species may also increase the ability of their populations to cope with climate change (Pearce-Higgins and Green, 2014).

The confidence assessments emphasise that individual species assessments should be treated cautiously and that conservationists need to draw upon the full range of information available before decisions are made about climate change adaptation and conservation management. Nevertheless for many species this assessment provides the main indication of potential climate change risks and opportunities and, accordingly, it can also highlight where further investigation and monitoring are necessary. It also emphasises the importance of planning to accommodate greater uncertainty about where species will survive and thrive in future. For site managers, this includes being aware of where their site is located in the context of the overall distribution of priority species (most simply, core, leading or trailing edges) and being prepared to adjust management priorities as situations change. To achieve this aim, the nature conservation organisations involved in this study are working to integrate these and comparable findings into their conservation practice, and to make this larger, emerging evidence base more accessible to conservation practitioners.

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Appendix A. Supplementary data

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