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Testing consistency of modelled predictions of the impact of climate change on bats ☆☆☆★☆☆†††††

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ABSTRACT

Species Distribution Models (SDMs) are a cornerstone of climate change conservation research but temporal extrapolations into future climate scenarios cannot be verified until later this century. One way of assessing the robustness of projections is to compare their consistency between different modelling approaches, placing more confidence on consistent rather than inconsistent predictions, especially if they are consistent with recent population trajectories. We compared predicted climate change impacts on nine bat species throughout their European ranges (using SDMs) and their activity (using GLMMs) within Ireland as a focal study region. Five species (*N. leisleri*, *P. nathusii*, *P. pipistrellus*, *P. pygmaeus* and *P. auritus*) were predicted to have stable ranges throughout the 21st century with projected increases in activity consistent with recently observed population increases. *M. daubentonii* and *R. hipposideros* are also likely to have stable European ranges throughout the 21st century but models predicted a negative impact of climate change on activity in Ireland, contrasting with a stable population trend in *M. daubentonii* and an increasing trend in *R. hipposideros* over recent decades. *M. nattereri* was predicted to maintain its range extent while *M. mystacinus* was predicted to undergo range contraction by the end of the 21st century under a high greenhouse gas emissions scenario. We propose there is utility in comparing predicted trajectories from climate change impact models using different parameters (e.g. range versus activity). Our predictions should inform government and conservation organisations when creating future climate change conservation policy.

1. Introduction

Modelling the impact of projected climate change on a species, or biodiversity more generally, can be achieved using various techniques, commonly including but not limited to: Species Distribution Models (SDMs) that project a species' environmental niche space [1,2], mechanistic models that link species physiology to environmental tolerances [3-5] and agent-based or process-driven simulations that ex-

PLICITLY include behaviour such as dispersal or migration [6-7]. Easily downloaded freeware (for example, Maxent) and the availability of on-line spatially explicit GIS (Geographical Information Systems) datasets mean that SDMs have become a cornerstone of climate change conservation research and policy [8]. As a demonstration of the ubiquity of these approaches, during April 2021, a search of the Web of Science (<https://wok.mimas.ac.uk>) suggested that 1,555 papers explicitly mentioned the phrase "Species Distribution Model" with 4,308 using "Max-

☆ <https://wok.mimas.ac.uk> (accessed 20th April 2020).

☆☆ <https://www.gbif.org/species/734> (accessed 13th November 2020).

★ www.batconservationireland.org (accessed 13th November 2020).

★★ <https://www.worldclim.org/data/worldclim21.html> (accessed 16th November 2020).

† https://www.worldclim.org/data/v1.4/cmip5_10m.html (accessed 16th November 2020).

†† <https://www.ichec.ie> (accessed 13th November 2020).

††† <https://land.copernicus.eu/pan-european/corine-land-cover/clc2018> (accessed 13th November 2020).

†††† http://biodiversityinformatics.amnh.org/open_source/maxent (accessed 13th November 2020).

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ent". As a result, SDMs have become an 'insert species data and crank the handle' approach, proliferating predictions of the impact of climate change on environmental suitability for species occurrence. However, few (if any) studies using SDMs compare or contrast their predictions with alternative modelling approaches using data sources other than species locational records. Thus, there may be utility in comparing future projections of species environmental suitability and/or distribution from SDMs, with models of other parameters, for example, species activity (relative abundance), to provide some assessment of the consistency of predicted trajectories under future climate change scenarios.

In response to changes, principally in temperature, many species are predicted to undergo poleward shifts in their distribution, which in the northern hemisphere may result in range contraction from their southern range edge margin and range expansion of their northern range edge margin with the opposite pattern in the southern hemisphere [6,9,10]. The suitability of each region or area within a species' range is, therefore, likely to undergo turnover. If a species is sufficiently mobile and capable of dispersal or migration that keeps pace with climatic change, it may be expected that, whilst their range shifts position globally, they may be able to maintain their range extent with little decrease in the average suitability of conditions within the new extent [4,6]. Northern regions (Arctic and subarctic regions 50°N or above) are projected to experience greatest warming, especially during winter [11] with species in such regions disproportionately vulnerable to the impacts of climate change [12]. Generally, we might expect range turnover to be greatest at suboptimal range edge extremes than in more optimal conditions within range centres [6,9]. In addition to latitudinal and range edge effects, changes in regional temperatures and precipitation patterns may result in some species being predicted to undergo elevational upslope shifts in distribution. They are predicted to retreat from lowlands and extend upward to higher altitudes, resulting in decreasing range extent and increasingly patchy or disjunct distributions due to local extirpations where insufficient suitable territory remains [9,13,14]. Where climate conditions become less suitable and a species' range contracts, it might be expected that, for example, relative activity or abundance, i.e. population size, would also decline due to the lower suitability of occupied regions. Thus, it might be expected that trajectories in range size and population should be largely consistent.

Bats (Chiroptera) are the most diverse, widespread and highly mobile terrestrial mammals, responsible for vital ecosystem service delivery including biological pest control, pollination and seed dispersal [15–17]. The impact and implications of climate change on bats have been reviewed [18] with effects on individual species and diversity modelled (e.g. [9,19,20]). For common, widespread European Microchiropteran species, such as *Pipistrellus pipistrellus*, annual percentage change in population indices have been positively correlated with summer temperatures at a temporal lag of one year and projected to increase with increasing temperatures in Ireland [21]. Such change is likely to be context-dependent, with activity of *P. pipistrellus* and *Nyctalus leisleri* predicted to increase in southern regions and decrease in northern regions of Ireland, whilst *Pipistrellus pygmaeus* activity is predicted to increase in coastal margins [22]. The highly mobile, migratory species, *Pipistrellus nathusii* has already exhibited phenological change by appearing earlier in spring in its summering range [23] and shifting north and eastward, colonising new areas in which it had not previously been recorded (e.g. [24–26]) with colonisation patterns captured by climate change data [19]. Generally, European bat ranges have been predicted to be largely robust to climate change up to the mid-century though may decline by the end of the century under worst case, high greenhouse gas (GHG) emissions scenarios; community species richness, however, is predicted to increase in northern regions e.g. in Great Britain and Scandinavia [9].

This study aimed to quantify the impact of projected climate change on a community of bat species throughout their range (Europe) and within a focal study area (Ireland). The main objective was to compare predictions from Species Distribution Models in terms of change in distribution (number of potentially suitable grid cells) derived from

species occurrence data with entirely independent models of bat abundance (relative activity or roost counts). Whilst modelling approaches can be tested synchronous with model construction by withholding a randomly selected test dataset, their temporal extrapolations into the future will remain unverified until later this century, depending how global climate change progresses. Our goal was to assess the degree of consistency of predictions between two distinct modelling approaches using different datasets to evaluate the utility of either approach in isolation and whether future predicted trajectories were consistent with recent observed changes in population size.

2. Methods

2.1. Bat species records and activity

Ireland represents the extreme north-western range edge margin of nine bat species: Daubenton's bat (*Myotis daubentonii*), whiskered bat (*M. mystacinus*), Natterer's bat (*M. nattereri*), Leisler's bat (*Nyctalus leisleri*), common pipistrelle (*Pipistrellus pipistrellus*), soprano pipistrelle (*P. pygmaeus*), Nathusius' pipistrelle (*P. nathusii*), brown long-eared bat (*Plecotus auritus*) and lesser horseshoe bat (*Rhinolophus hipposideros*).

Locational records for all nine species throughout their European ranges were downloaded from the Global Biodiversity Information Facility (GBIF; <https://www.gbif.org/species/734>). Funded by the Irish Government's National Parks & Wildlife Service (NPWS), the conservation charity, Bat Conservation Ireland (BCIreland; www.batconservationireland.org), manages Ireland's national bat monitoring programme. The programme contains a series of annual bat surveys throughout Ireland; namely the Car-based Bat Monitoring Scheme, Daubenton's Bat Waterways Monitoring Scheme, and Lesser Horseshoe Bat Roost Monitoring Scheme (Online Supplementary Material; Fig. S1) as well as a Brown Long-eared Bat Roost Monitoring Scheme. Car-based Bat Monitoring covered 28 survey squares (each 30 × 30km) distributed throughout Ireland, within which were 15 separate 1.6km line transects. Transects were driven at 24km/hr usually between 9pm and 3am during the survey night with an acoustic time expansion bat detector clamped to the open passenger door window. Where possible, surveys were conducted once during July and repeated in August annually from 2003–2017. Species identification was derived from analysis of recorded sonograms. *Myotis* spp. could not be differentiated acoustically and were recorded as a single genus grouping. For this reason, they were excluded from the current study. The Daubenton's Bat Waterways Monitoring Scheme covered up to 255 separate 1km walked line transects throughout Ireland placed along waterways, each comprising 10 point transects placed 100m apart. Transects were monitored annually from 2006–2017 between 9pm and 3am on two independent nights in August with a heterodyne bat detector and torchlight. During both the Car-based and Waterways Bat Monitoring Surveys bat activity was quantified as the total number of bat passes/transect. The Lesser Horseshoe Bat Roost Monitoring Scheme typically involved dusk emergence counts or daytime internal counts at >100 summer roost sites. Counts were expressed as the number of individuals present annually from 1992–2017. For full details of the methodology of each scheme see Aughney et al. [21]. The Brown Long-eared Bat Roost Monitoring Scheme was not included in this study. A total of 661,065 GBIF species locational records were collated with 16,439 BCIreland records (Table S1) covering the nine focal species (Fig. S2). A second GBIF download included >1.5M species records covering all 45 bat species known to occur throughout Europe which were used as a proxy of bat survey effort (see Section 2.4 below).

2.2. Climate data

Climate at the extent of Europe was characterised by data downloaded from Worldclim (<https://www.worldclim.org/data/worldclim21.html>) at a 10° grid cell resolution (~15 × 15km). Of the nineteen bioclimatic variables available, eight were selected based on their perceived relevance to bat biology (Table S2; Fig. S3). Bats are

small with a high metabolic rate and with a large surface area-to-volume ratio lose heat easily [27], thus mean temperature (bio1), the diurnal temperature range (bio2), temperature seasonality (bio4), minimum temperature of the coldest month (bio6), and mean temperature of the warmest quarter (bio10) were selected as potentially relevant to homeostasis, foraging, and hibernation. Precipitation (bio12), precipitation seasonality (bio15), and precipitation of the driest quarter (bio17) were selected as potentially relevant to flight conditions, foraging, and aerial insect (prey) activity [28–29]. Future climatological projections used the HadGEM2-ES model which is a coupled Earth System developed by the UK Met Office Hadley Centre for the World Climate Research Programme (WCRP) Coupled Model Intercomparison Project Phase 5 (CMIP5) centennial simulations. HadGEM2-ES was chosen as it incorporated high levels of climatic complexity, including a coupled atmosphere-ocean configuration and a well-resolved stratosphere with atmospheric chemistry, ocean biology, and dynamic vegetation. Future projections were downloaded for the mid-century 2050s (averaged for 2041–2060) and late century 2070s (averaged for 2061–2080) for both an intermediate greenhouse gas (GHG) emissions scenario or Representative Concentration Pathway (RCP4.5 where emissions are assumed to peak around 2040 and then decline) and a high emissions scenario (RCP8.5 where emissions are assumed to continue to increase throughout the 21st century). Future climate data are available at https://www.worldclim.org/data/v1.4/cmip5_10m.html.

Climate at the extent of Ireland has been simulated at high spatial resolution using the Consortium for Small-scale Modelling-Climate Limited-area Modelling (COSMO-CLM; v5.0) Regional Climate Model [30,31] by the Irish Centre for High End Computing (ICHEC; <https://www.ichec.ie>). The following Coupled Model Intercomparison Projection Phase 5 (CMIP5; [32]) Global Climate Model (GCM) datasets were dynamically downscaled: the UK Met Office's Hadley Centre Global Environment Model version 2 Earth System (HadGEM2-ES) configuration GCM [33]; the EC-Earth consortium GCM [34]; the CNRM-CM5 GCM developed by the Centre National de Recherches Météorologiques-Groupe d'études de l'Atmosphère Météorologique (CNRM-GAME) and the Centre Européen de Recherche et de Formation Avancée (Cerfacs) [35]; the Model for Interdisciplinary Research on Climate (MIROC5) GCM developed by the MIROC5 Japanese research consortium [36]; and the MPI-ESM-LR Earth System Model developed by the Max Planck Institute for Meteorology [37]. Of the twenty-two variables available, we selected four on their perceived relevance to bat biology (Table S2; Fig. S4). In addition to temperature and precipitation, we selected variables not available via Worldclim including humidity and wind speed $\leq 10\text{m}$ above ground level as potentially relevant to aerial insect activity and flight conditions. Gridded climate datasets for Ireland, both historical (1976–2005) and future (2021–2100), were generated at temporal and spatial resolutions of 3 hours and $4 \times 4\text{km}$, respectively. Values were averaged for the 6-hourly 9pm to 3am period on each date on which a bat survey had been performed, allowing conditions at the point of survey to be quantified (Survey_{*t*}). Seasonal and temporally lagged weather and climate effects may also influence bat activity so average nightly values for the focal summer (Jun-Jul-Aug) of each bat survey (Summer_{*t*}), the immediate preceding Spring_{*t*} (Mar-Apr-May) of the same year (*t*) and four seasons in the preceding year (*t*₋₁): Winter_{*t*}-1 (Dec-Jan-Feb), Autumn_{*t*}-1 (Sep-Oct-Nov), Summer_{*t*}-1, and Spring_{*t*}-1, were also generated. To account for the uncertainty arising from the estimation of future global emissions of greenhouse gases and changing land use, downscaled GCM simulations based on two Representative Concentration Pathways: RCP4.5 and RCP8.5 [38] were used to simulate the future climate. For a full description of the RCM configuration and an overview of validations and projections see Nolan et al. [39] and Nolan & Flanagan [40].

2.3. Habitat data

Habitat data were downloaded for CORINE Land Cover 2018 from the European Environment Agency (EEA, 2020;

<https://land.copernicus.eu/pan-european/corine-land-cover/clc2018>) and summarised at a 10° grid cell resolution ($\sim 15 \times 15\text{km}$) throughout Europe and a $4 \times 4\text{km}$ grid cell resolution throughout Ireland to match the two climate datasets. Spatial manipulation of habitat data used ArcMap 10.8 (ESRI, California, USA). Individual CORINE land codes were aggregated and collapsed to derive simplified, ecologically relevant habitat classifications (Table S2), including: grassland, crop, heterogeneous agriculture, broad-leaved and mixed woodland, coniferous forest and agroforestry, scrub, sclerophyllous vegetation, sparse vegetation, bog and marsh, moor and heath, freshwater, urban and Simpson's Diversity Index (SDI) of habitat patches (Figs. S3 and S4). Sclerophyllous vegetation consisted of xerophytic plants, characteristic of Mediterranean arid regions and was included in models at the European extent only to cover southerly regions but was excluded from models at the extent of Ireland as the habitat was not present. The landscape of Ireland is predominately grassland with lower habitat diversity and smaller habitat patch extent than that of Europe.

2.4. Species distribution models

Species Distribution Models were constructed using maximum entropy with the programme Maxent 3.4.4 (accessible via: http://biodiversityinformatics.amnh.org/open_source/maxent). To minimise spatial autocorrelation and to prevent drawing duplicate records from the same cell during a given model run, species records were reduced in resolution to match that of input environmental data reducing sample sizes ($n=30,529$ species records in Europe and $n=2,047$ records in Ireland; Table S3).

Species records represented presence data and, whilst absence data were available for surveys conducted in Ireland, they were unavailable for GBIF records throughout Europe. Therefore, to account for some degree of survey effort across Europe, background points (pseudo-absences) were not drawn at random from throughout the model extent, but instead were confined to cells in which any of the 45 bat species that occur in Europe had been recorded i.e. we could be confident an observer predisposed to submitting a bat record was present in the cell but failed to report the focal species being modelled. Thus, background points more closely approximated true absence data than if randomly selected from throughout the extent of Europe.

Species records were split into model training datasets (75% of records chosen randomly) and test datasets (25% chosen randomly) with four replicate model runs (with bootstrapping) such that every record had a roughly equal chance of being selected once as a test record. Model outputs across the four replicate runs were averaged. To minimise model overfitting, hinge and threshold responses were excluded with only linear and quadratic curves fitted to create smoothed (ecologically plausible) response curves for each input variable. A Jackknife analysis of variable importance to test gain was used to assess the contribution of variables to model predictive success.

The most used SDM evaluation metric is the Area Under the Curve (AUC value) of the Receiver Operating Characteristic (ROC) curve [41]. AUC can be problematic when using presence-only data as it must distinguish between presence and true absence [42,43]; however, our restriction of background points, whilst imperfect, will have gone some way to minimising false negatives. AUC is heavily influenced by the extent of model prediction; if the extent is large and the species range restricted, then AUC values will be artificially inflated [43,44]. Thus, alternative metrics of predictive success are recommended including: sensitivity (proportion of presences predicted correctly), specificity (proportion of absences predicted correctly), True Skill Statistics (TSS; measure of model performance, incorporating both sensitivity and specificity) and omission rate (probability of presences misclassified as absences) among others. All metrics range from 0 to 1 (except TSS, which ranges from -1 to 1), with higher AUC, sensitivity, specificity and TSS values, and lower omission rate values best. Traditionally, AUC values ≥ 0.7 are considered good [45].

Table 1

Species Distribution Model average sample sizes (training, test and background points) per run (x4 replicate runs) and average model evaluation metrics \pm S.E when tested against the maximum test sensitivity plus specificity (MaxTSS) threshold.

Species	Sample size (n)			Maximum test sensitivity plus specificity (MaxTSS) threshold				
	Background	75% training	25% test	AUC	Sensitivity	Specificity	Omission rate	TSS
<i>Myotis daubentonii</i>	3,791	1,263	12,525	0.640 \pm 0.017	0.606 \pm 0.064	0.673 \pm 0.044	0.394 \pm 0.064	0.279 \pm 0.034
<i>M. mystacinus</i>	2,075	691	11,372	0.757 \pm 0.018	0.855 \pm 0.024	0.658 \pm 0.037	0.145 \pm 0.024	0.513 \pm 0.035
<i>M. nattereri</i>	2,325	774	11,524	0.762 \pm 0.009	0.793 \pm 0.038	0.731 \pm 0.028	0.207 \pm 0.038	0.524 \pm 0.019
<i>Nyctalus leisleri</i>	1,444	481	10,954	0.784 \pm 0.007	0.852 \pm 0.057	0.716 \pm 0.044	0.148 \pm 0.057	0.568 \pm 0.014
<i>Pipistrellus nathusii</i>	1,413	471	10,025	0.590 \pm 0.015	0.625 \pm 0.085	0.556 \pm 0.105	0.375 \pm 0.085	0.181 \pm 0.029
<i>P. pipistrellus</i>	3,996	1,331	12,617	0.769 \pm 0.006	0.836 \pm 0.043	0.701 \pm 0.040	0.164 \pm 0.043	0.537 \pm 0.011
<i>P. pygmaeus</i>	2,802	933	11,832	0.746 \pm 0.007	0.845 \pm 0.037	0.647 \pm 0.024	0.155 \pm 0.037	0.492 \pm 0.014
<i>Plecotus auritus</i>	2,966	988	11,931	0.723 \pm 0.009	0.774 \pm 0.026	0.671 \pm 0.032	0.226 \pm 0.026	0.445 \pm 0.018
<i>Rhinolophus hipposideros</i>	2,060	686	11,315	0.742 \pm 0.006	0.894 \pm 0.030	0.590 \pm 0.021	0.106 \pm 0.030	0.484 \pm 0.012
Mean \pm S.E	2,541	846	11,566	0.725 \pm 0.045	0.788 \pm 0.045	0.662 \pm 0.041	0.212 \pm 0.045	0.447 \pm 0.021

Heatmaps of the continuous probability of species presence (hereafter, referred to as 'suitability') were binarised into greyscale maps of likely suitable conditions (hereafter, referred to as 'range') using the Maximum Test Sensitivity plus Specificity (MaxTSS) threshold which optimises models using their ability to predict test rather than training data.

Models were extrapolated into future climatological conditions assuming low (RCP4.5) and high (RCP8.5) emissions.

All species models adopted a standard structure and identical fitting procedures with one exception: the SDM for *P. nathusii*. All the other eight bat species are typically (though not strictly necessarily) resident within their ranges and thus were assumed to be at equilibrium (i.e. their current range was assumed to be mostly historically static). Unlike the other species, *P. nathusii* is actively migratory each year and is well-documented in the published literature to have undergone an active range expansion driven by recent climate change (see Section 1). Thus, as the only species known to be in non-equilibrium, the model for *P. nathusii* was built, not across the total extent of Europe, but within the 95% kernel of its species records (explicitly excluding 5% of outlying records, mostly in the extreme south of its range in Iberia, extreme north of its range in Scandinavia and northern Scotland, and low density records in Eastern Europe), restricting the extent of the environmental envelope and background points for model building i.e. explicitly excluding conditions in its range edge margins likely to have experienced flux in recent decades (Fig. S5). The *P. nathusii* model was extrapolated spatially from its 95% kernel range to the full extent of Europe under current conditions and, like the other species models, extrapolated temporally into future climatological conditions. This approach was adopted to ensure the model for this species did not violate SDM assumptions of equilibrium and, thus, explicitly attempted to account for potential disequilibrium due to recent range expansion.

Changes in range (suitable/unsuitable cell counts) were assessed between current and each future climate scenario using $2 \times 2 \chi^2$ Contingency tests. Percentage change in range was calculated between current conditions and future climate scenarios for each species.

2.5. Species activity models

Bat activity (total number of bat passes/transect or summer roost counts) was modelled as the independent variable in a suite of species-specific Generalised Linear Mixed Models (GLMMs). Models assumed a Poisson distribution (for count data), with Transect_ID per year fitted as a Random Factor to account for multiple replicate surveys per year with the analysis weighted by the total number of surveys (not all transects/roosts were surveyed the same number of times). Max-ent accommodates multicollinearity in SDMs, adjusting species response curves for correlations between input variables. However, linear modelling techniques, including GLMMs, are vulnerable to model leverage due to multicollinearity. Climate variables and habitat variables were highly collinear and could not be fitted together in the same model

without violating model assumptions. Such was the degree of collinearity that removal of significant bivariate left few variables for inclusion and was not an adequate solution. Thus, the set of climate and habitat variables were each reduced in separate Principal Component Analyses (PCA) to create orthogonal axes. Only axes with an Eigenvalue >1 were retained for inclusion in analysis [46]. GLMMs fitted climate PCA axis scores for the 6-hourly 9pm to 3am conditions at the point of Survey_t and seasonal effects covering Summer_t and Spring_t, as well as temporally lagged effects covering Winter_{t-1}, Autumn_{t-1}, Summer_{t-1} and Spring_{t-1} of the preceding year. Habitat PCA axis scores were simultaneously fitted. Projections of each species were made using future climatic conditions under low (RCP 4.5) and high (RCP 8.5) carbon scenarios for each spatially explicit survey location. Predicted values were averaged across individual transects within each 30km survey square and mapped using ArcMap to illustrate likely spatial patterns in temporal changes of species detected during the Car-based Monitoring Survey. Spatially explicit predictions for the Daubenton's Bat Waterway Scheme and Lesser Horseshoe bat Summer Roost Scheme, which did not use the same survey structure, were interpolated using the Kriging function in the Spatial Analyst toolbox of ArcMap to produce spatial patterns in temporal changes for *M. daubentonii* and *R. hipposideros* respectively.

Predicted values for activity were compared between current and each future climate scenario using paired t-tests. Percentage change in predicted bat passes/transect or summer roost counts was calculated between current conditions and future climate scenarios for each species and compared to percentage change in suitability and range from SDMs to assess the consistency in modelled predictions. We also report percentage change in observed population indices for each species throughout Ireland during the early 21st century as reported by Aughney et al. [21] to determine whether future predicted trajectories in range and activity are consistent with recent past population change.

3. Results

3.1. European SDMs

Bat SDMs at the extent of Europe had good predictive power with mean AUC and sensitivity >0.7 , specificity >0.6 , TSS typically between 0.4 and 0.5 and omission rate typically <0.2 (Table 1). The model for *P. nathusii* had lowest AUC, specificity and TSS, and one of the highest omission rates but comparable sensitivity to other models.

Jackknife analysis suggested the contribution of each variable to test gain and the shape of variable response curves were species-specific (Figs. S6 and S7). Averaged (mean) test gain was contributed to most by bio6 (min. temperature of coldest month), bio4 (temperature seasonality), bio15 (precipitation seasonality), bio1 (mean temperature), and bio17 (precipitation of driest quarter). Although contributing less than a third than most climate variables, grassland was the highest single contributing habitat variable when averaged across all species (Fig. S6). Except for *P. nathusii*, the top contributing variables to each species

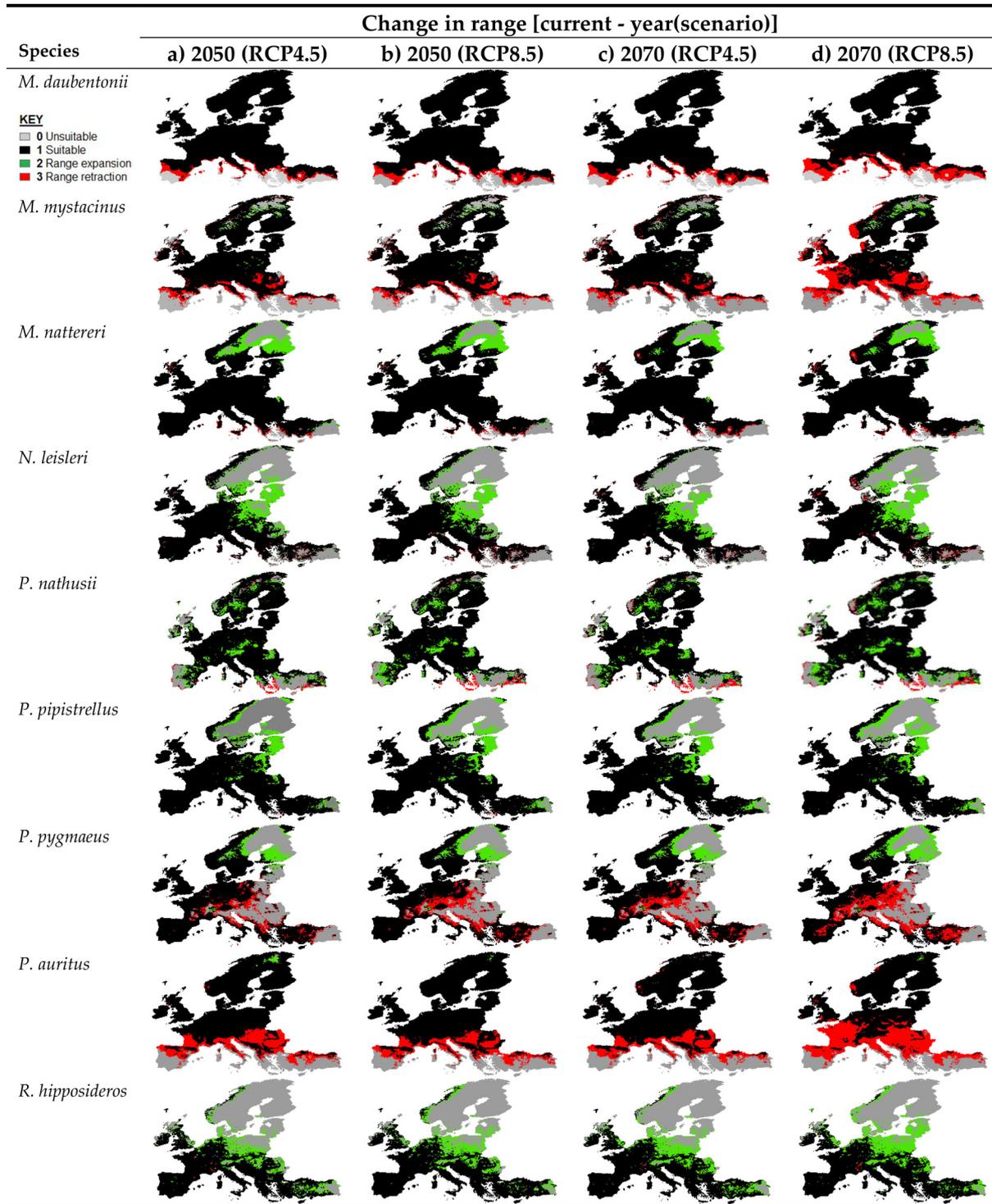


Fig. 1. Maps of change in predicted distribution (cell suitability) throughout Europe, using the MaxTSS threshold, between current conditions and a) 2050 (RCP4.5), b) 2050 (RCP8.5), c) 2070 (RCP4.5) and d) 2070 (RCP8.5) for each bat species present in Ireland showing range contraction (red) and/or expansion (green).

model were climatic, not habitat. The single greatest contribution to test gain for *P. nathusii* was the extent of urban land cover (Fig. S6) with which it had a positive relationship (Fig. S7).

Change in the suitability of grid cells was species-specific (Fig. S8) but all species showed a significant ($p < 0.001$) change in the number of potentially suitable cells (those above the MaxTSS threshold) throughout mainland Europe (Table S4) with varying spatial patterns of range retraction, stability or expansion predicted as the 21st century progresses under low and high emissions scenarios (Fig. 1). Southerly range retrac-

tion was predicted for *M. daubentonii* and *P. auritus* in Mediterranean regions with little change elsewhere throughout their range. Southerly range retraction was also predicted for *M. mystacinus* and *P. pygmaeus* but accompanied with some degree of northerly range expansion, extending into Scandinavia including higher elevations in the Scandinavian interior. Little range retraction was predicted for *M. nattereri*, *N. leisleri*, *P. pipistrellus* and *R. hipposideros* with range expansion likely in northern and eastern parts of their range. Predictions for *P. nathusii* suggested no overall directional change in range edge margins, however,

Species	Climate												Habitat					
	PC1 (wet, unsettled)						PC2 (warm, dry)						PC1 (complex marginal landscapes)	PC2 (anthropogenic landscapes)	PC3 (wooded riparian habitats)	PC4 (rural agriculture)		
	Survey _t	Summer _t	Spring _t	Winter _{t-1}	Autumn _{t-1}	Summer _{t-1}	Spring _{t-1}	Survey _t	Summer _t	Spring _t	Winter _{t-1}	Autumn _{t-1}					Summer _{t-1}	Spring _{t-1}
<i>M. daubentonii</i>												*	*	*		**	***	***
<i>N. leisleri</i>						***		**				*			***		***	
<i>P. nathusii</i>		***					***		***			***						
<i>P. pipistrellus</i>				***	***	***	***	***	*	*				***	***	***		***
<i>P. pygmaeus</i>			***		***	**			*	***	**				***		***	***
<i>P. auritus</i>							**											
<i>R. hipposideros</i>	*	***			***		***	***	***				***	***	***	*	***	***

Fig. 2. Summary of the effects of climate (at various seasonal temporal lags: t and $t-1$) and habitat (each captured as principal component axis scores; for details see Tables S5 & S6) on activity for each bat species (number of bat passes except for *R. hipposideros* represented by summer roost counts).

patchy range expansion was predicted, filling in gaps in its current distribution around its northern and western range edge (Scandinavia, Iberia and Ireland) and consolidation of its range in Eastern Europe with very marginal range contraction in the extreme south-east (Greece and Anatolia). Changes in range were largely consistent between Great Britain and Ireland (Fig. 1; Table S4). All cells in Ireland remained above the MaxTSS threshold as potentially suitable for occupation such that there was no major range change predicted for *M. daubentonii*, *M. nattereri*, *P. pipistrellus*, *P. pygmaeus* and *P. auritus* under any future scenario (Table S4; Fig. S9). *M. mystacinus* was the only species predicted to undergo range contraction in Ireland, most notably by 2070 under the high emission scenario, retreating from the west (Fig. S9). Nevertheless, most of the island (62%) remained suitable for the species by 2070 under RCP8.5. Whilst the model for *R. hipposideros* was predictively good at the European extent (AUC = 0.742, sensitivity = 0.894, TSS = 0.484 and omission = 0.106), it failed to capture the range restricted nature of the species' distribution in Ireland (limited to the south-west; Fig. S1c) with most of the island predicted as generally suitable (Fig. S9). Nevertheless, the model predicted Ireland may become marginally more suitable under future climate change (Fig. S9). *P. nathusii* was the only species predicted to undergo substantial range expansion in Ireland (Fig. S9). Notably, predictions for *P. nathusii* exhibited spatial variation with some cells predicted as being lost and neighbouring cells predicted as being gained as predicted suitability throughout Ireland was very close to the MaxTSS threshold, but the general trend was markedly positive.

3.2. Irish activity models

Climate variables and habitat variables were highly collinear with the former reduced to two Principal Component Axes and the latter to four (Tables S5 and S6). GLMMs of bat activity were highly species-specific (Tables S7-13) but generally had good predictive power (average adjusted $r^2 = 0.703$). However, the model for *R. hipposideros* (adj. $r^2 = 0.546$) was notably poor (excluding this species average adj. $r^2 = 0.729$). Climate and habitat variables had varying species-specific effects (Fig. 2). *P. nathusii*, *P. pipistrellus*, and *R. hipposideros* were significantly influenced by weather conditions on the night of Survey_t but were related to different PCA axes in differing ways with the pipistrelles positively related to climate PC2 (warm, dry conditions) but *R. hipposideros* negatively related to climate PC1 (wet unsettled conditions).

All bat species were significantly influenced by climate at various seasonal lags (Fig. 2). Generally, species that were significantly related to climate PC1 of the previous autumn (*P. pipistrellus*, *P. pygmaeus*, and *R. hipposideros*) and the previous summer (*N. leisleri*, *P. pipistrellus*, and *P. pygmaeus*), were negatively affected by wet unsettled conditions. Other climatic relationships varied markedly between species (Fig. 2). For detailed specific-specific Results and Discussion see Online Supplementary Materials. All species' activity was influenced by habitat except *P. nathusii* and *P. auritus*. The latter was notable as the only species whose activity was significantly influenced by just one variable, being negatively related to climate PC2 (warm, dry conditions) during Summer_t (Fig. 2).

Activity levels were predicted to change significantly ($p < 0.001$) for all species between current and all future conditions (Table S14). Activity of all species was predicted to increase by 2050 and further by 2070 under low emissions and even more under high emissions scenarios except for *M. daubentonii* and *R. hipposideros*, which were both predicted to decline markedly by 2050 even under the low emissions scenario though with some recovery of the former by the late 21st century under high emissions (Fig. S10). Spatial patterns in predicted change in activity throughout Ireland varied between species. Whilst it was difficult to generalise, increases typically exhibited a south-west to north-east cline with greater gains in the south and south-west (Fig. 3).

3.3. Population, range and activity trajectories

Five species (*N. leisleri*, *P. nathusii*, *P. pipistrellus*, *P. pygmaeus* and *P. auritus*) exhibited largely consistent positive trajectories in recent population trends (extracted from [21]) and predicted future change in suitable range and activity throughout Ireland by the late 21st century under a high greenhouse gas emission scenario (Table 2). The range of *P. auritus* was predicted to decline significantly ($p = 0.007$) by 2% (Table S4) but this seems unlikely to be ecologically meaningful given that no change was predicted during the 2050s under both RCP4.5 and RCP8.5 emissions scenarios or during the 2070s RCP4.5 (Fig. S9). *P. nathusii* had the highest increase in population indices in recent decades and its range was predicted to increase by 31% and activity by many orders of magnitude by the late 21st century under high emissions. The very large increase in predicted activity of *P. nathusii* can be attributed to it being currently rare but widespread with a very low detection rate ($0.030 \pm$

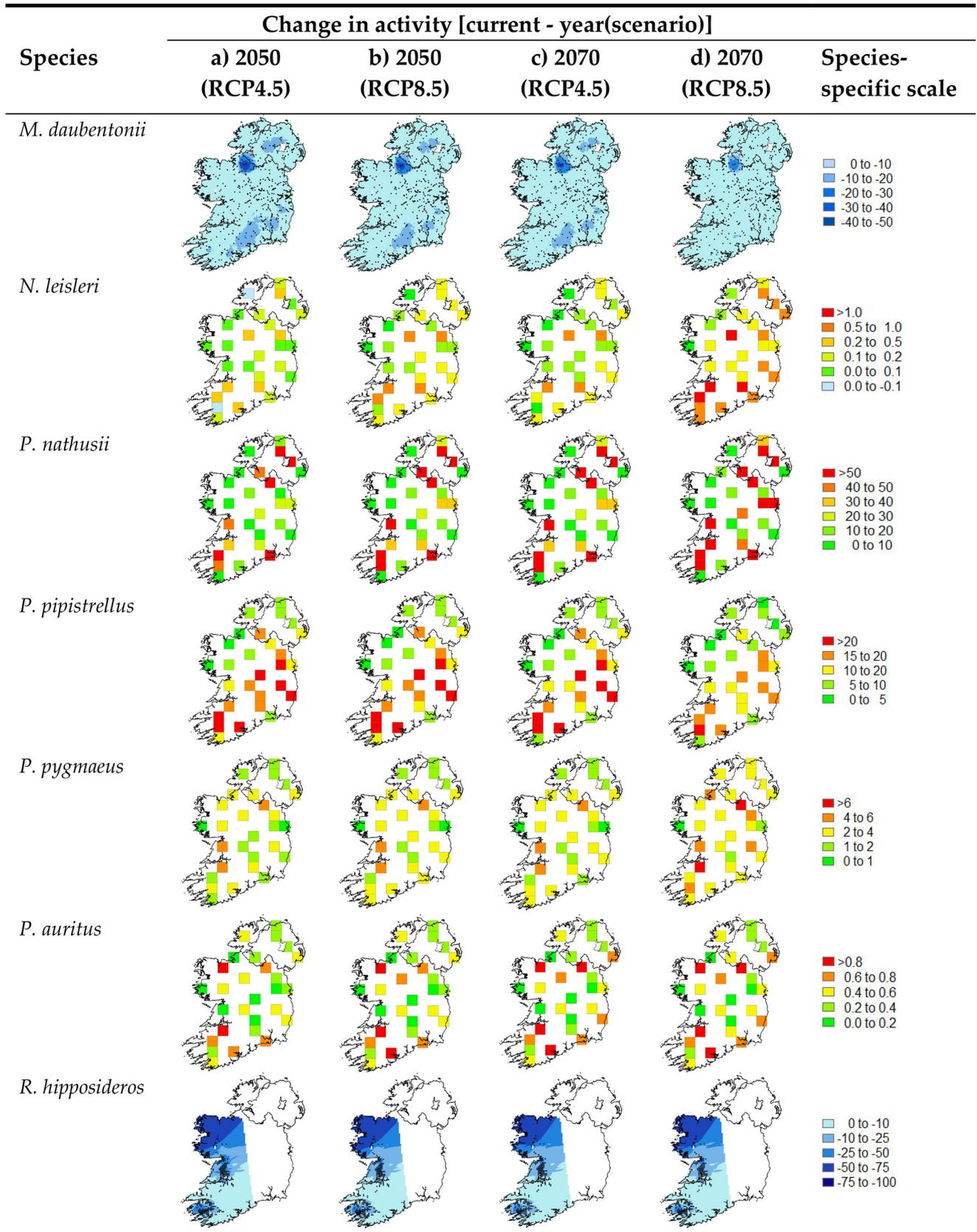


Fig. 3. Spatial patterns of GLMM predicted change in bat activity (bat passes or roost counts) throughout Ireland from current conditions to a) 2050 (RCP4.5), b) 2050 (RCP8.5), c) 2070 (RCP4.5) and d) 2070 (RCP8.5) for each bat species showing decline (light to dark blue) or increase (green to red).

Table 2

A summary of the percentage (%) change in **a)** bat population indices over recent decades throughout Ireland derived from smoothed General Additive Models reported in Aughney et al. [21] where surveys varied in duration: ¹2006-2017 (bat passes), ²2003-2017 (bat passes), ³2007-2017 (based on roost presence) and ⁴1992-2017 (summer roost counts). Predicted percentage change in **b)** SDM range i.e. suitable (above threshold) grid cells and **c)** activity (bat passes/roost counts) by the late 21st century (2070s) under a high GHG emission scenario (RCP8.5). † = significant ($p < 0.05$) positive change, ‡ = significant ($p < 0.05$) negative change and ↔ = no significant ($p > 0.05$) change.

Species	% change		
	Aughney et al. [21]	This study	
	a) Population Index	b) SDM Range	c) GLMM Activity
<i>M. daubentonii</i>	24 ↔ ¹	0 ↔	-8 ‡
<i>M. mystacinus</i>	-50 ↔ ²	-30 ‡	
<i>M. nattereri</i>		-2 ‡	
<i>N. leisleri</i>	109 † ²	-1 ↔	173 †
<i>P. nathusii</i>	512 † ²	31 †	597,852 †
<i>P. pipistrellus</i>	71 † ²	0 ↔	1009 †
<i>P. pygmaeus</i>	170 † ²	0 ↔	484 †
<i>P. auritus</i>	48 † ³	-2 ‡	829 †
<i>R. hipposideros</i>	101 † ⁴	3 ↔	-31 ‡

0.006 s.e. bat passes/transect during surveys), thus, even modest predictions of increase (Fig. S10) led to very large percentage change values (Fig. 4).

M. daubentonii and *R. hipposideros* presented contrasting patterns of recent and future predicted change. Our SDMs predicted that neither species' suitable range should significantly change but their activity (bat passes per transect and summer roost counts respectively) was predicted to decrease significantly by the late 21st century (the former less so than the latter). This result contrasted with observed stable *M. daubentonii* populations and significant increases in *R. hipposideros* population indices in recent decades (Table 2).

The suitable range of *M. nattereri* was predicted to decline significantly ($p=0.007$) by 2% (Table S4), but this is unlikely to be ecologically meaningful (Fig. S9). However, the range of *M. mystacinus* was predicted to decline by 30% by the end century under high emissions (Table 2). Population indices reported by Aughney et al. [21] for *Myotis* spp., whilst having declined by 50% during the early 21st century, showed no statistically significant trend due to the width of associated 95% confidence intervals as detection rates were low on the Car-based Bat Monitoring Survey transects.

4. Discussion

We demonstrate a high degree of consistency in the trajectory of recent bat population trends and future predictions of the impact of projected climate change using both Species Distribution Models (SDMs) to predict range, and Generalised Linear Mixed Models (GLMMs) to predict activity, for five out of nine bat species occurring in Ireland (namely: *N. leisleri*, *P. nathusii*, *P. pipistrellus*, *P. pygmaeus* and *P. auritus*) by the late 21st century. Some of these species have undergone significant increases in population during early 21st century [21] and models predict further increases in relative activity by the mid- to late 21st century under both low and high greenhouse gas emissions scenarios with largely stable or increasing range extents, characterising these species as potential climate change beneficiaries or 'winners'. *P. nathusii* has exhibited earlier migration and arrival in its summering range [23] and has colonised new regions in Northern Scotland, Scandinavia and Eastern Europe [24–26] as well as Great Britain and Ireland in recent decades driven by climate change [19]. In Ireland, there is some indication (albeit with large confidence intervals) that the population increased from 2003 to 2017

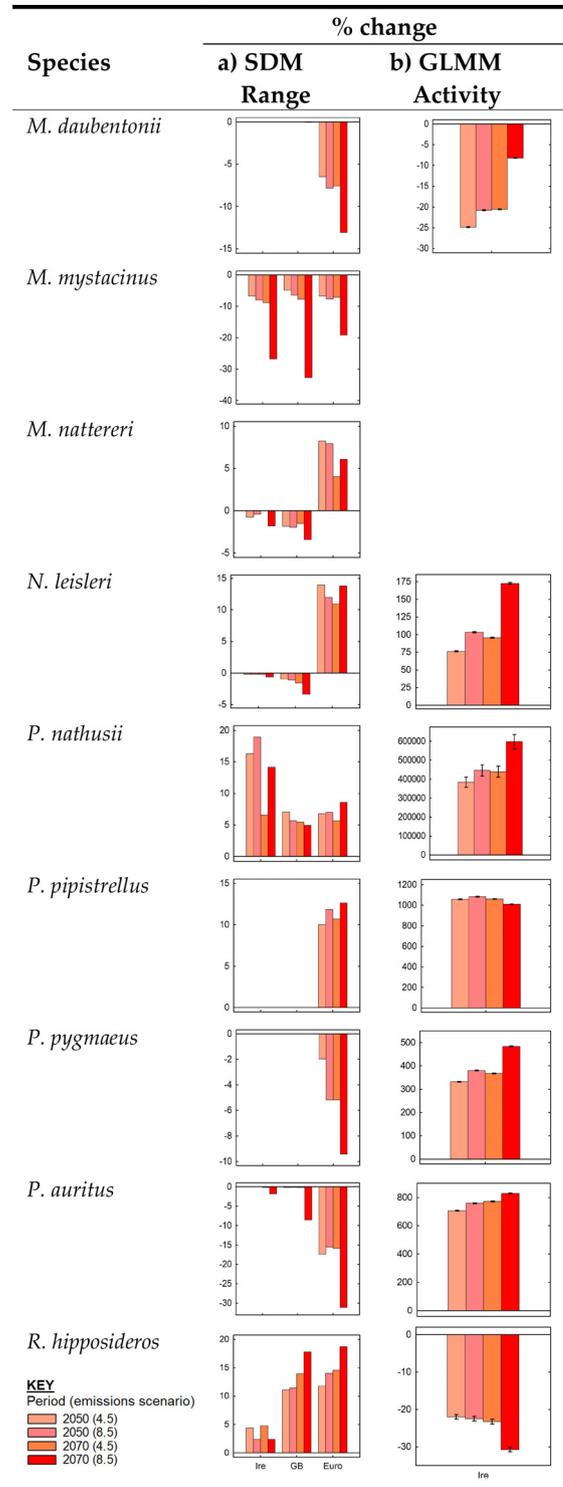


Fig. 4. Summary of predicted percentage (%) change ± S.E. in **a)** predicted suitable range (derived from SDM) for Ireland (Ire), Great Britain (GB) and continental Europe (Euro) contrasted against **c)** activity (derived from GLMM) for Ireland only. Bars show % change between current conditions and future climate change scenarios (left-to-right) from mid- to late-century and low to high GHG emissions (see Key). Note y-axis values are not standardised as some species exhibited substantially higher values than others and the use of a common axis failed to illustrate trends within some species.

[21] and our analyses suggest future climate conditions should result in ongoing substantial increases in its range and activity. Whilst many bat species are capable of relatively long migrations it is not clear whether this behaviour can translate into the active dispersal and colonisation of new regions necessary to shift ranges sufficiently to track their optimal bioclimatic envelope.

Population range, and activity trajectories were potentially inconsistent for four out of nine bat species (*M. daubentonii*, *M. mystacinus*, *M. nattereri* and *R. hipposideros*). Recent population trajectories and predictions of future activity contrasted for both *M. daubentonii* and *R. hipposideros* (the only two species not surveyed by Car-based Bat Monitoring, thus subject to differing data collect methodologies). SDMs predicted that neither species' suitable range should change significantly but their activity (bat passes per transect and summer roost counts respectively) was predicted to significantly decrease by the late 21st century (the former less so than the latter), contrasting with stable observed population trends for *M. daubentonii* and an increasing trend in *R. hipposideros* in recent decades [21]. Notably, however, the range of the latter has decreased in recent years in Ireland [47]. Thus, vigilance and continued monitoring may be required for both species because, whilst their ranges may or may not change, their activity (and by extension population) trajectories may be potentially negatively impacted by projected climate change as the century progresses. Differing data collection schemes (waterway point transects and summer roost counts) were tailored to these species to provide robust data and should have been no less suitable for activity analyses than Car-based Bat Monitoring data. Thus, whilst we cannot rule out that methodological differences could have conceivably led to results for these species being different to that for all other bat species, we think it unlikely that such differences account for inconsistency in predicted trajectories. This result is potentially of conservation management importance since *R. hipposideros* is an Annex II species listed in the EU Habitats Directive (92/43/EEC) and requires special conservation measures to ensure its continued protection. Spatial patterns suggest that the northern-most part of its range in Ireland is likely to be most negatively impacted by climate change.

The suitable range of *M. nattereri* was predicted to decline significantly (but not ecologically meaningfully) by 2% and the range of *M. mystacinus* was predicted to decline by 30% by the end century under high emissions. *M. mystacinus* may, therefore, be a climate change 'loser' with the potential for range contraction (though the majority of Ireland, will nonetheless, remain suitable).

Judging the consistency in predicted trajectories from different parameters (empirically observed recent population changes and future modelled range and activity) provides a more robust basis for inference than any single modelling approach in isolation. It should be noted, however, that our models adopted different dependent variables (presence/absence for SDMs and activity/relative abundance for GLMMs) at different spatial extents (Europe and Ireland) and resolutions (10° and 4km grid cells), with a different set of independent variables (Worldclim climate averaged over decades and Ireland-specific downscaled climate averaged for specific survey nights and seasons with various temporal lags). Any inconsistency in model predictions may, therefore, be explained by the differences in modelling approaches and construction. Ideally, maintaining consistent modelling approaches (in extent, spatial resolution, independent variables etc.) and changing only the dependent variable (presence/absence vs activity) and fitting procedure (binomial vs Poisson) would have provided conditions conducive to assessing the impact of the independent variables on the trajectory of model predictions. However, we aspired to model each dataset with the conditions that conformed to the assumptions of each model, resulting in the most reliable predictions achievable for each dataset whilst retaining the ability to assess consistency between datasets and approaches. Thus, an ideal, statistically consistent approach was sacrificed to optimise real-world predictions for the purposes of species conservation planning.

Activity data from surveys were available only for Ireland necessarily constraining model extent to that region. To restrict SDMs to Ireland only would have failed to capture the full extent of environmental variability tolerated by each species throughout its entire range. As such, projections would have been poor (borne out in early preliminary analyses not presented here) as much of the future climatic envelope, especially during the late century high emissions scenario, would have been outside current Irish conditions used in model building. Thus, assessing changes in range within Ireland required capturing species responses to environmental variables throughout their entire European range. The finest spatial resolution for climate data downscaled for Ireland was 4km and, whilst data were available at a comparative resolution from Worldclim (2.5° grid cells ~ 3-5km depending on latitude), pixel size did not match exactly nor where they spatially aligned. Moreover, computer processing capacity and time meant that using a coarser resolution throughout the full extent of Europe was more expedient as the objective was to assess range which lends itself to being captured at a coarser resolution than activity. Worldclim variables were available as long-term averages e.g. the current period being defined as 1950-2000, with most variables derived from temperature and precipitation only, appropriate for defining species tolerances with respect to likely presence/absence. Ireland-specific downscaled climate variables available from the Irish Centre for High-End Computing (ICHEC) were deemed more appropriate for modelling activity as they were available at 1-hourly intervals historically from 1976-2005, thus mean weather conditions synchronous with the 6-hourly period of bat surveys from 9pm to 3am could be calculated whilst we could also derive nightly averages for each season, including various ecologically plausible temporal lags. Such data were likely to be more predictive of fine-scale spatial and temporal variability in bat activity than the decadal averages available from Worldclim, which were more relevant in defining species occurrence. Moreover, the Ireland-specific climate ensemble provided potentially relevant variables not directly derived from temperature and precipitation, such as humidity and wind speed. Thus, to maximise likely model success *within* SDM and activity models, real-world considerations necessitated adopting different modelling approaches including variations in extent, spatial resolution, and independent variables. Nevertheless, even with the differences in the best available models for range and activity, we might expect some degree of consistency in model projections if they truly captured real-world species responses to weather and climate. Thus, we would argue that the utility of our comparison is because of, not despite, the differences in modelling approaches.

In Ireland, climate change is expected to increase summer day-time temperatures (by 0.7 - 2.6°C) and winter night-time temperatures (by 1.1 - 3.1°C) by 2050 [48,49]. Rainfall is expected to be heavier in autumn and winter months, resulting in more flooding events but summer months are expected to have longer dry spells i.e. greater precipitation seasonality [39,48,50-52]. The number of frost and ice days (minimum temperatures of the coldest month) is projected to halve [48].

Bat SDMs suggested that climatic variables, and not habitat were most important for defining species ranges. It seems more likely that climate is necessary for defining absence (from arid Mediterranean or subarctic Scandinavian regions) than patterns of presence within occupied ranges. Mean annual temperature, minimum temperature of coldest month, temperature seasonality, precipitation of driest quarter and precipitation seasonality were most important in defining species' ranges. These findings are consistent with those of Rebelo et al. [9] who found that temperature and precipitation variables as well as humidity were important predictors of the range of temperate zone bat species. The important variables from this study are likely to define hibernation conditions during winter, emergence conditions in spring, and summer foraging activity. Responses to each variable were highly species-specific indicative of idiosyncratic ecologies. This was further evidenced by species-specific responses in activity within Ireland with each species responding to climatic averages both contemporaneous with surveys and at various seasonal lags. Wet unsettled conditions during the pre-

ceding autumn and summer consistently had a negative effect on the subsequent summer activity of most species (*N. leisleri*, *P. pipistrellus*, *P. pygmaeus*, and *R. hipposideros*) as they are likely to result in reduced foraging success [28,29], lower reproductive success [53] and earlier onset of hibernation [27,54]. Bats choose roosting locations that are thermally stable [55] but climate change may alter roost microclimates, elevating temperatures and making them less suitable due to a risk of hyperthermia. In response, bats are likely to reduce roost fidelity and switch roost sites, favouring those that are cooler, or they may alter roost composition, reducing the number of individuals per roost. Whilst habitat was less important for defining species ranges than climate, most of the species examined occurred throughout central and western Europe, thus, it seems probable that habitat influenced their localised likelihood of occurrence. Indeed, the activity of all but two species (*P. nathusii* and *P. auritus*) in Ireland was influenced by at least one habitat principal component axis. The impact of wooded riparian habitats (freshwater with broad-leaved and mixed woodland i.e. Habitat PC3) had species-specific effects on activity, with some bat species positively (*M. daubentonii*, *P. pygmaeus* and *R. hipposideros*) and others negatively (*N. leisleri*) correlated. Other habitat PCA axes appeared to exhibit more consistent impacts across bat species activity. Anthropogenic landscapes (urban land cover associated with arable crops) and complex marginal landscapes (diverse landscapes composed of wetlands, scrub and coniferous plantations) were generally associated with lower bat activity while rural agriculture (complex cultivation patterns away from urban areas) was generally associated with more bat activity. For a detailed species-by-species interpretation of the impact of projected climate change and species-specific ecology see further Results and Discussion in the Online Supplementary Materials. Whilst some habitats generally had consistent effects across bat species, there may be regional variation in the amplitude of habitat effects. For example, several studies note negative impacts of urbanisation on bat populations [56,57] with impact linked to the degree of urbanisation (e.g. extent of grassland, trees, and parks retained) as well as the adaptability of individual bat species based on morphology and behaviour [56,57].

Predictions from our models contrasted with those of Roche et al. [22] who used the same bat survey dataset for Ireland but modelled bat activity with local weather station data (habitat data were not included) segregating sources of spatial and temporal variation predicting a negative future trend for *P. pipistrellus*, a stable trend for *P. pygmaeus* and increases for *N. leisleri* with increases for *P. pipistrellus* and *N. leisleri* in the south and declines in the north. This highlights that inconsistent predictions can be obtained when using similar data but different analytical approaches, questioning the reliability of any one method and suggesting the need for an ensemble approach.

Our analyses consider the potential impact of climate change only. Whilst spatially explicit habitat variables were included in our models to increase their predictive power, no projections of future land cover change are available nor would they be likely to be accurate given the unpredictable nature of urbanisation, trends in deforestation or afforestation, and changes in food production. Many key factors relevant to bat biology have not, or cannot, be parameterised and predicted for the future. For example, declines in global invertebrates [58,59], including a >75% decline in aerial invertebrates recorded in recent decades in some regions of Europe [58], have undoubtedly reduced bat food resources and, if such trends continue, may further limit future bat fitness. It will not matter if a region, such as Ireland, is climatically suitable to support bats physiologically in the future if suitable habitat or food resources are unavailable. Reductions in prey availability may have disproportionate effects on certain bat species, with generalists able to shift their diet towards more abundant prey items. However, increased inter- and intraspecific competition may limit bat success, regardless of whether they are able to alter their diet according to prey availability; this adaptability will be key to survival [56-57]. Additionally, bats carry parasites and pathogens [60] whose influence on population demography is poorly studied. Climate change is also predicted to affect disease

epizootiology and the impact of pathogens on population dynamics [61-63]. Thus, whilst modelling climate change allows us to estimate its potential impact on limited aspects of species biology (bioclimatic niche space or activity), without the ability to parameterise or predict other vital aspects of their environment (both internal and external) such predictions may not be very meaningful.

5. Conclusions

We demonstrate highly species-specific, nuanced responses of bats to climate and weather conditions, with complex temporally lagged effects likely related to idiosyncratic life histories and ecology. Consistency in recent population trends with predictions of potential range and activity under future climate provides more robust support for inferences than using any one modelling approach in isolation. In the context of Ireland, we conclude that: 1) *N. leisleri*, *P. nathusii*, *P. pipistrellus*, *P. pygmaeus* and *P. auritus* are likely to have largely stable ranges throughout the 21st century and are predicted to increase their activity, most notably under higher emissions scenarios, consistent with recently observed population increases during the early 21st century. *P. nathusii* is likely to be a notable climate change ‘winner’. 2) *M. daubentonii* and *R. hipposideros* are also likely to have largely stable ranges throughout the 21st century but models suggest a potential negative impact of climate change on activity, contrasting with population stability and increases observed in recent decades. This may indicate the potential for a future downturn and further work may be needed on these species to further elucidate the impacts of weather and climate on their relative activity. 3) *M. mystacinus* may be a potential climate change ‘loser’ with models predicting potential range contraction (though most of Ireland, will nonetheless, remain suitable). The range of *M. nattereri* may also decline but only marginally so.

We demonstrate the utility in comparing predicted trajectories from climate change impact models using different parameters. Here we make clear species-specific conclusions about the potential impact of climate change on the bat community of Ireland, which should inform government and conservation organisations when creating future climate change conservation policy. For example, further research on drivers of *M. daubentonii* and *R. hipposideros* activity and more focused monitoring and surveillance of *M. mystacinus* and *M. nattereri* adequate to detect potential range contraction or reduced activity at their western range edge margins could inform conservation actions. In addition, a review of broader bat conservation measures with respect to climate change could be implemented, for example, supporting urban green spaces, protecting variation in roost site provision i.e. veteran trees, caves, and buildings, and the adaptation of bat boxes including their construction materials and positioning to buffer them against higher future temperatures.

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Declaration of Competing Interest

The authors declare no competing interests.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecochg.2021.100011.

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