Limited refugia and high velocity range-shifts predicted for bat communities in drought-risk areas of the Northern Hemisphere

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ABSTRACT

Species occupying semi-arid and dry regions around the globe face an uncertain future due to increases in the frequency and severity of droughts. In this study we modelled the potential effect of climate change on bat communities within two high-drought risk regions of the world and assessed the magnitude and direction of the predicted shifts in climatic suitability, locating climate change refugia and identifying species at greatest risk of population declines. To do this, we compared climate suitability models for 43 species using three global climate models and three emissions scenarios for current (1950–2000) and future (2061–2080) climates within two regions where droughts are predicted to increase, the Western Palaearctic and Western North America. Our models predicted an overall reduction in bat richness with future climates. Areas projected to support high species richness in the current climate coincided with greatest predicted species loss and greatest future drought risk. For species with the potential to extend their range, high velocity range shifts would be required to keep pace with these changes, particularly in the Western Palaearctic, where additional barriers to movement include seas and areas of high human population density. Predicted refugial zones were limited and occurred in similar areas across continents (montane and high latitude with some coastal areas). The area of climate suitability was predicted to contract for around half of study species, with nine identified as species of conservation concern due to low overlap between current and future modelled ranges. The best-case scenario for bat diversity in semi-arid and dry regions in the future is likely to be reduced species richness, with many species facing rapid range expansion over challenging landscapes to access climatically suitable areas. Conservation of bats in high drought risk

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regions will likely depend on protection of identified refugia and networks of water sources, as well as global measures to protect biodiversity and human wellbeing, such as reduction in global carbon emissions.

1. Introduction

Semi-arid areas around the world are experiencing more frequent, intense, and longer periods of drought as a result of declining levels of precipitation and an increase in atmospheric evaporative demands (Trenberth et al., 2014). Water shortages in already drought prone regions of the world are likely to dramatically impact ecosystems and cause a reduction in biodiversity (Kingsford, 2011), potentially forcing mobile species to shift or contract their ranges (Prudhomme et al., 2015). Even when drought conditions end, the recovery of many species is negatively impacted by anthropogenic degradation of natural habitats and human demands for water (Bennett et al., 2014). The extent to which changes in the duration and frequency of precipitation will impact the biodiversity of semi-arid ecosystems is still unclear as the majority of climate studies focus on more temperate regions (Felton et al., 2009; Watson et al., 2017).

Within drought-prone regions of the world, bats are a diverse and ubiquitous taxa with variable dependencies on water (Russo & Jones, 2003; Sirami et al., 2013; Lisón & Calvo, 2014; Blakey et al., 2017; Monadjem et al., 2018). Bat reproduction has been shown to decline dramatically with the onset of drought (Adams, 2010; Amorim et al., 2015) as dependency on water is heightened during reproduction, particularly for lactating females (Adams & Hayes, 2008). While all bats need water for metabolic functions, some bat species forage specifically for emergent aquatic prey (Fukui et al., 2006), or fish (Bordignon, 2006) or specialise in foraging near to or from the surface of water (Biscardi et al., 2007; Campbell, 2011), making them especially susceptible to drought conditions. Many bats in drought-prone areas roost near water (Kalcounis-Ruppell et al., 2005), and/or select foraging habitats that are in close proximity to water sources (Lookingbill et al., 2010). While many species have evolved to survive in water-limited landscapes, an increase in the frequency, duration, and severity of drought conditions may result in conditions too harsh for bat populations to persist, and is a threat to the long-term survival of many bat species (Sherwin et al., 2013; Frick et al., 2019).

As bats can be highly mobile, species adapted to long-distance dispersal are predicted to be better suited to shifting their ranges in response to rapid climate change (Jones et al., 2009). Studies across the world have already observed range shifts by bats that have coincided with temperature increases (Willis & Brigham, 2004; Wu, 2015; Ancillotto et al., 2016). Mechanisms underpinning bat range shifts in response to climate are likely to include dependence on water, bat physiology, phenology and roost quality (Jones & Rebelo, 2013) and even direct mortality (O'Shea et al., 2016). In order to plan for predicted changes in climatic suitability for bats across the landscape, studies in Mexico (Zamora-Gutierrez et al., 2018), South America (Aguiar et al., 2016), Southeast Asia (Hughes et al., 2012) and Western Palaearctic (Rebelo et al., 2010; Bilgin et al., 2012) have predicted changes in bat distributions as a result of future climate scenarios, with many range contractions and even extinctions projected for the coming century. However, as recently highlighted in a review by Lisón et al. (2019), studies concerning ecology and conservation of bat communities utilising semi-arid areas are very few and generally focused on single species. This is concerning because these regions often support high levels of bat diversity and species endemism (Myers et al., 2000) but are projected to increase in drought frequency and intensity (Trenberth et al., 2014).

We address this knowledge gap by modelling how future climatic patterns are likely to influence bat distributions and species richness within two regions of the world with significant semi-arid zones where droughts are predicted to worsen: The Western Palaearctic and Western North America. Our objectives were to: 1) assess predicted variability in bat species richness and community turnover across landscapes of high drought risk under different climate scenarios; 2) identify areas that remain climatically suitable for bats between current and future climates (refugia); 3) identify the magnitude and direction of shifts in climatic suitability for bat communities by calculating the velocity of change; and, 4) identify species at greatest risk of population declines and possible extinction. To achieve this, we predict shifts in bioclimatic suitability for 43 species of bat whose current distribution includes semi-arid zones across the Western Palaearctic (24 species) and Western North America (19 species). Presence-only ecological niche models were fit using current and future climates for three Intergovernmental Panel on Climate Change (IPCC) derived greenhouse gas (GHG) emission scenarios, including three Global Circulation Models (GCMs) from the Coupled Model Intercomparison Project (CMIP5) and three future (2061–2080) GHG scenarios, ranging from lowest to highest concentrations (RCP2.6, RCP6.0, RCP8.5).

2. Methods

2.1. Study area

We chose two global regions that are predicted to be impacted by increasing frequency and severity of future drought (Dai et al., 2004) and for which sufficient bat data were available – the Western Palaearctic (Europe and North Africa), and Western North America (Canada, United States of America, and Mexico) (Appendix S1). For these two regions, climate models are

consistent in projecting a continuing decrease in precipitation, stream flow, and water availability throughout the 21st century (Milly et al., 2005; Bates et al., 2008; Dai, 2011).

2.2. Species records

For this study we took species occurrence records from the Global Biodiversity Information Facility (GBIF, 2014) as well as NatureServe, and state heritage databases (WA, OR, CA, NV, AZ, NM) for Western North America and private databases (Russo et al., 2014), peer-reviewed publications (Dondini & Vergari, 2000; Hanak et al., 2001; Nagy & Szántó, 2003; Benda et al., 2006, 2010; Baron & Vella, 2010; Gukasova & Vlaschenko, 2011) and the 3rd Italian EU Habitats Directive reporting (www.sinanet.isprambiente.it/Reporting_Dir_Habitat) for the Western Palaearctic. We acknowledge that there are significant spatial and temporal biases within these databases (Fourcade et al., 2014; Fisher-Phelps et al., 2017; Smeraldo et al., 2018), for example, in dry areas bat species are regularly captured near water, however these biases are likely to be reduced at the scale of our study (5 arc-minute grainsize). We took several additional steps to improve the quality and comparability of the species records included in our study. First we filtered out fossil records that were indicative of potentially different historical climates, as well as taxonomically or regionally spurious records (outliers). Next, we followed Heap & Culham's (2010) approach to ensure that the uncertainty of the species points was smaller than the spatial resolution of the environmental predictors we used. This involved retaining only species occurrences with at least two decimal places and identifying the resolution of gridded data by visually inspecting for equidistant patterns and inspecting metadata of species records. In this way, we excluded all records with an uncertainty >10 km. We selected bat species with range centroids within the two target regions (Appendix S1) which left 77,402 and 56,692 original occurrence records for the Western Palaearctic and Western North America respectively.

To model current and future climates, we used 17 widely-used climate variables from WorldClim at 5 arc-minute (9.26 ×9.26 km ≈ 86 km^2 at the equator) resolution (Hijmans et al., 2005). As recommended by Andersen & Beauvais (2013), we removed two variables (bio8 - mean temperature of wettest quarter, bio9 - mean temperature of driest quarter) that show an artificially abrupt spatial shift in their values and replaced them with two new variables: mean temperatures of northern hemisphere winter and summer. To avoid uninformative background points as a result of overly large spatial extents (Barbet-Massin et al., 2012) we clipped all climate layers to a minimum convex polygon containing all the species occurrences with a buffer of 50 km for each of the two regions (Western Palaearctic and Western North America) (dashed polygons, Appendix S1). This meant including parts of the Western Palaearctic and Western North America that are not currently considered semi-arid. However, for the purposes of modelling the direction and extent of potential range shifts we considered including this wider geographical area as beneficial for the study. We then removed highly correlated variables for each region based on a Pearson's correlation coefficient threshold of 0.7 (Dormann et al., 2013), retaining variables among correlated sets that were predicted to be most relevant to predicting bat distributions. The remaining seven variables included: bio1 – annual mean temperature (both regions), bio2 – mean diurnal range (Western Palaearctic), bio3 – isothermality (Western North America), bio7 – temperature annual range (both regions), bio9_JJA – mean summer temperature (June – August; Western Palaearctic), bio12 – annual precipitation (both regions), bio15 – precipitation seasonality (both regions), bio17 – precipitation of driest quarter (Western Palaearctic), bio18 – precipitation of the warmest quarter (Western North America).

We reduced spatial autocorrelation between occurrence records as this can violate the assumption of independence leading to type I errors and poor model interpretation (Dormann et al., 2007). We achieved this by reducing clusters of points (points within a 15 km buffer distance) to a single point where climate heterogeneity was similar. We calculated climate heterogeneity by first reducing our seven climate variables to three orthogonal principal components describing the majority (>90%) of the variability in climate, using Principal Components Analysis (PCA). We then used these three components to calculate a climate heterogeneity raster using the SDMToolbox (Brown, 2014) within Arc GIS v 10.2. We then reduced the climate heterogeneity surface into five classes and where points were within 15 km of each other and also fell within the same climate heterogeneity class, they were reduced to a single point (Brown, 2014). We used the buffer size of 15 km as a compromise for the widely variable home range sizes of the bats in the study areas. Spatial autocorrelation reduction left us with 11,221 occurrence records for the Western Palaearctic and 5312 records for Western North America.

To characterise current climates, we averaged our seven climate variables across the years 1950–2000. We selected the 2061–2080 time period for future climates, because it was sufficiently soon to be relevant to conservation management recommendations. We considered a subset of available global climate models (GCMs) from the Coupled Model Intercomparison Project (CMIP) including CCSM4, HadGEM2-ES and MIROC-ESM (Taylor et al., 2012). For each GCM, we considered three future emissions scenarios, ranging from lowest emissions (RCP2.6) to highest emissions (RCP8.5), with RCP6.0 intermediate (Moss et al., 2010). We elected to use Global Climate Models, rather than Regional Climate Models to reduce the effects of spatial biases in the dataset which are intensified at finer grain sizes (Fourcade et al., 2014).

2.3. Bioclimatic modelling of present (1950–2000) and future (2061–2080) climates

We used Maxent software (Phillips et al., 2006, 2015) to model relationships between current and future climates and bat distributions because of its predictive performance and suitability to presence only data (Elith et al., 2006, 2011). We modelled present climatic suitability of the landscape (rather than known distribution) of separate bat species (*n* = 101; 29 Western Palaearctic, 72 Western North America) in the following steps. First, we evaluated model fit using cross validation, running five separate Maxent models with 80% of the bat presence data randomly selected each time as training data and the remaining 20%

used as testing data, with the 7 climate variables as predictors, using the autofeatures option to select appropriate functions (Merow et al., 2013). Fixed values of maximum interactions (2000), prevalence (0.5) and regularisation multiplier (1) were considered in all the runs to allow model comparisons between species. From these models, we calculated five measures of the Area Under Curve (AUC), averaging them to obtain an overall measurement of model ability to discriminate between climatically suitable and unsuitable cells for the bat species being modelled. AUC values ≥0.7 were judged as having high discrimination performance (Elith et al., 2006) and where our models had discrimination performance lower than this threshold, we did not consider the species further. Next, we used the full datasets to re-run models for the remaining species ($n = 43$), again using current climate data and then used these models to predict probability of occurrence of each bat species across their study region (Western Palaearctic and Western North America) based on climate suitability. We then used the same modelled relationships (between current bat probability of occurrence and the seven climate variables) to predict climate suitability for each species across 6 future climate layers (3 RCPs for each of 3 GCMS). Next, we converted probability of occurrence across the 7 climate suitability maps for each species (1 current climate suitability, 6 future climate suitability) from a continuous range to a measure of presence or absence using maximum training sensitivity plus specificity logistic threshold values (MTSS) proposed by Liu, White, & Newell (2013). As bats are known to travel long distances (e.g. >200 km during migration, Krauel & McCracken, 2013), we assumed an unlimited dispersal scenario (that species can inhabit any suitable habitat anywhere in the study area) (Bateman et al., 2013). While we acknowledge that dispersal barriers exist (e.g. Jones & Rebelo, 2013), in the absence of reliable information on dispersal patterns for the majority of study species we felt this more conservative approach was the best option (Moussy et al., 2013). Next, we compared environmental similarity of current and future climate surfaces using Multivariate Environmental Similarity Surfaces (MESS) (Elith et al., 2010). We did this to spatially quantify confidence in our ability to predict climate suitability in areas where climates fall outside of the climatic range of the training data (Elith et al., 2010). This process resulted in 7 raster files (5 arc-minute grid cells) for each of the 43 species showing predicted climate suitability for present climates (1950–2000) and for future climates (2061–2080) for three GCMs and three emissions scenarios. Finally, we combined the three GCM layers for each RCP scenario, taking a consensus approach by summing the three GCM layers together and taking as climatically suitable only pixels where the majority (at least 2 of 3) of GCM models predicted species presence (Araújo & New, 2007). This approach aims to reduce the 'noise' associated with individual model errors and uncertainties so that the signal of interest, in this case climate suitability, can emerge (Araújo & New, 2007).

2.4. Assessing changes in climate suitability

For each species and future projection (43 species × 3 RCPs) we mapped predicted niche contraction or loss (*L*, areas climatically suitable for the present conditions but not for the future), areas of potential climate niche expansion or gain (*G*, regions predicted to be uninhabitable for the current conditions but suitable for the future) and persistence or stable areas (*S*, predicted suitable conditions for both the present and for the future) (Loehle & LeBlanc, 1996). The species suitable area net change was then calculated as the difference between predicted climatic niche gain and loss (G–L).

We calculated species richness by summing each of the current and future occurrence layers across all species in each pixel for each emissions scenario for both study areas (Western Palaearctic and Western North America). We also quantified the rate of predicted incoming or outgoing species turnover in each pixel as a consequence of a changing climate using an adjusted turnover metric based on the metric used by Broennimann et al. (2006). For each emissions scenario and pixel, we summed local gains (G_{sum}) and local losses (L_{sum}) separately across all species. Then, the difference between G_{sum} and L_{sum} was divided by the overall current species richness ($SR_{current}$) plus G_{sum}, according to the following equation (Eq. 1):

$$T(\%) = 100\text{X}(G_{sum} - L_{sum})/(SR_{current} + G_{sum}) \tag{1}$$

This turnover index has a lower limit of −100%, that indicates a predicted complete loss of species and an upper limit of +100% that indicates a predicted full income of species where none previously occurred (independently from the original number of species). A turnover equal to zero indicates no predicted variation in the number of species (though the species assemblage may have changed).

2.5. Identification of potential climate refugia

We identified potential climate refugia for bats (defined as areas where bioclimatic suitability was maintained between past and future climate conditions) in three emission scenarios using two approaches: identifying areas that a) had the greatest number of species that retained climatic suitability and b) retained climatic suitability for the full complement of species present currently. A pixel was considered to retain climatic suitability for a species if that species was recorded in that pixel for both current climate conditions and predicted future climate conditions.

2.6. Analysis of the direction and magnitude of projected range shifts

We computed the centroid (two-dimensional midpoint of the species' simulated distribution) of modelled current and future distributions for each bat species (VanDerWal et al., 2013) to understand and quantify the direction and the magnitude (distance and velocity) of predicted range shifts (shifts in climatic suitability) under changing climate. We used the *SDMToolbox* (Brown, 2014) for ArcGIS v10.2 to connect vectors between centroids of current and future occurrence and calculated the

geodesic distance and the azimuth: the bearing relative to North (0°) at which the geodesic path departs from the initial point, representing the direction of the shift from the present to the future centroid (Huntley et al., 2008). We estimated the velocity of predicted range shifts (rate of range centroid shift in km year^{-1}, Loarie et al., 2009) by dividing the estimated range centroid distance shift by 95 (the number of years between the baseline, 1950–2000, and the period of future projections, 2061–2080, Huntley et al., 2008).

2.7. Identifying species at greatest risk of population decline

Species were deemed more vulnerable to population declines and extinction when little overlap was observed between predicted current climatically suitable areas and future climatically suitable areas (Rebelo et al., 2010). We measured the predicted variation in occupied area by comparing the amount of predicted contraction or expansion of the modelled distribution between present and future conditions as a percentage. Percentage values of variation in occupied area range from −100% to >100% where −100% indicates a complete loss of climatically suitable area and positive values indicate increases in favourable area. Remaining suitable area is the percentage of the suitable area that is predicted to be preserved between current and future predictions (overlap), values range from 0 to +100%, where low percentage values indicate that the suitable area is predicted to contract or shift in the future, while +100% indicates that the entire suitable area is predicted to remain unvaried over time.

3. Results

3.1. Climate drivers of bat occurrence in high drought-risk areas

Climate drivers of predicted bat species distributions differed between continents and were dominated by temperature variables in the Western Palaearctic (temperature outranked precipitation in 21 of 24 models) and precipitation variables in Western North America (precipitation outranked temperature in 10 of the 19 models) (Table 1). The strongest temperature variables predicting bat species occurrence were annual temperature range (Western Palaearctic), isothermality (Western North America) and annual mean temperature (both study areas) (Table 1). Top precipitation predictors were precipitation in the driest quarter (Western Palaearctic), precipitation in the warmest quarter (Western North America) and annual precipitation (both study areas) (Table 1). Overall, the best predictive temperature variables explained more variance (Western Palaearctic: 40%, Western North America: 34%) than precipitation variables (Western Palaearctic: 20%, Western North America: 30%).

3.2. Predicted changes in bioclimatic suitability for bat communities in drought-risk areas

All future emissions scenarios led to an overall reduction in predicted bat richness in both continents by 2080 (Fig. 1). In the Western Palaearctic, high negative turnover was predicted in coastal areas of Europe and North Africa, which support greatest current species richness (18–24 spp.) (Fig. 1). In Western North America, a loss of species from low elevation areas of southwestern US and Mexico were predicted (Fig. 1). For both the Western Palaearctic and Western North America, positive turnover was predicted in higher latitude and montane areas, indicating that species may move into these areas where feasible (Fig. 1). Reductions in bat richness were predicted to be more extensive for higher emissions scenarios, with 36% of the study area predicted to have lower future richness in RCP 2.6, increasing to 43% for RCP 6.0 and 48% for RCP 8.5.

3.3. Identification of potential refugia

Areas where the greatest number of species were predicted to retain climatic suitability included montane areas (Portugal, northern Spain, northern Italy in Western Palaearctic; Sierra Madre mountains of Mexico and montane areas of Arizona and New Mexico in Western North America) as well as western coastal areas (Western France and Southern England in Western Palaearctic; coastal California and Mexico in Western North America) (Fig. 1). At the highest emissions scenarios, very few lower latitude areas retained their full complement of species (Fig. 2). In the Western Palaearctic <1% of areas below 45°N and in Western North America <6% of the area below 30°N were expected to retain their full complement of species (Fig. 2).

3.4. Magnitude and direction of predicted range shifts

There was an overall trend towards species shifting their ranges towards the N-NNW in both the Western Palaearctic (mean = 352°) and Western North America (mean = 340°) (Fig. 3). Predicted range shifts were greater in distance and velocity on average in the Western Palaearctic, compared to Western North America. Mean distances of predicted range shifts in the Western Palaearctic across species ranged from 394 km ± 6 (RCP 2.6) to 719 km ± 14 (RCP 8.5), shifting at a rate of 41 km/decade ± 0.7 (RCP 2.6) to 76 km/decade ± 1.0 (RCP 8.5). Predicted range shift distances were shorter and slower in Western North America, ranging from 272 km ± 23 (RCP 2.6) to 436 km ± 22 (RCP 8.5), at a rate of 29 km/decade ± 2.4 (RCP 2.6) to 46 km/decade ± 2.3 (RCP 8.5). Greatest range shifts were predicted for *Eptesicus isabellinus* (1673 km, 176 km/decade NE) and *Pipistrellus nathusii* (1474 km, 155 km/decade NE) in the Western Palaearctic and *Euderma maculatum* (1950 km, 205 km/decade) and *Idionycteris phyllotis* (712 km, 75 km/decade) in Western North America. Shifts predicted for *E. maculatum* should be treated

Table 1

Results of Maxent models relating 8 climate variables and elevation to occurrence of 43 bat species in Western Palaearctic and Western North America, identifying the most important climate variable for model prediction and its contribution to modelled variability.

| Family	Species	IUCN status	Population trend	Top Precip	% Top Precip	Top Temp	% Top Temp	AUC
Western Palaearctic								
Miniopteridae	*Miniopterus schreibersii*	NT	decreasing	Annual precipitation	9.6	Annual mean temperature	45.4	0.87
Molossidae	*Tadarida teniotis*	LC	unknown	Annual precipitation	11.0	Temperature annual range	39.3	0.88
Rhinolophidae	*Rhinolophus blasii*	LC	decreasing	Precipitation seasonality	57.8	Annual mean temperature	16.4	0.92
Rhinolophidae	*Rhinolophus euryale*	NT	decreasing	Annual precipitation	12.6	Annual mean temperature	52.2	0.88
Rhinolophidae	*Rhinolophus ferrumequinum*	LC	decreasing	Annual precipitation	11.7	Annual mean temperature	44.2	0.83
Rhinolophidae	*Rhinolophus hipposideros*	LC	decreasing	Annual precipitation	14.3	Temperature annual range	49.3	0.83
Rhinolophidae	*Rhinolophus mehelyi*	VU	decreasing	Precipitation driest Q	12.6	Annual mean temperature	39.7	0.95
Vespertilionidae	*Barbastella barbastellus*	NT	decreasing	Precipitation driest Q	20.8	Temperature annual range	49.6	0.85
Vespertilionidae	*Eptesicus isabellinus*	LC	unknown	Precipitation driest Q	42.6	Annual mean temperature	13.0	0.98
Vespertilionidae	*Eptesicus serotinus*	LC	decreasing	Annual precipitation	21.8	Temperature annual range	47.9	0.81
Vespertilionidae	*Myotis bechsteinii*	NT	decreasing	Precipitation driest Q	23.9	Temperature annual range	40.9	0.84
Vespertilionidae	*Myotis blythii/oxygnathus*	LC	decreasing	Annual Precipitation	15.6	Temperature annual range	34.4	0.85
Vespertilionidae	*Myotis capaccinii*	VU	decreasing	Precipitation seasonality	8.2	Mean summer temperature	32.0	0.92
Vespertilionidae	*Myotis emarginatus*	LC	stable	Annual precipitation	15.3	Temperature annual range	39.7	0.85
Vespertilionidae	*Myotis escalerai*	LC	decreasing	Precipitation driest Q	12.0	Temperature annual range	26.3	0.95
Vespertilionidae	*Myotis myotis*	LC	stable	Annual precipitation	12.2	Temperature annual range	51.8	0.81
Vespertilionidae	*Myotis punicus*	DD	decreasing	Precipitation seasonality	57.6	Temperature annual range	29.1	0.98
Vespertilionidae	*Nyctalus lasiopterus*	VU	decreasing	Precipitation driest Q	8.3	Temperature annual range	51.4	0.89
Vespertilionidae	*Nyctalus noctula*	LC	unknown	Precipitation driest Q	27.2	Temperature annual range	44.4	0.83
Vespertilionidae	*Plecotus austriacus*	LC	unknown	Precipitation seasonality	10.0	Temperature annual range	39.3	0.86
Vespertilionidae	*Plecotus auritus begognae*	NE	unknown	Precipitation driest Q	16.6	Temperature annual range	32.8	0.98
Vespertilionidae	*Pipistrellus kuhlii*	LC	unknown	Annual precipitation	14.5	Annual mean temperature	38.8	0.87
Vespertilionidae	*Pipistrellus nathusii*	LC	unknown	Precipitation seasonality	23.2	Temperature annual range	47.4	0.86
Vespertilionidae	*Pipistrellus pipistrellus*	LC	stable	Annual precipitation	16.3	Temperature annual range	62.7	0.81
Western North America								
Molossidae	*Eumops perotis*	LC	decreasing	Precipitation warmest Q	26.7	Isothermality	28.9	0.94
Molossidae	*Nyctinomops femorosaccus*	LC	stable	Annual precipitation	13.7	Isothermality	48.5	0.94
Molossidae	*Nyctinomops macrotis*	LC	unknown	Annual precipitation	29.5	Isothermality	26.4	0.89
Molossidae	*Tadarida brasiliensis*	LC	stable	Precipitation seasonality	15.3	Isothermality	42.7	0.81
Phyllostomidae	*Choeronycteris mexicana*	NT	unknown	Precipitation seasonality	14.6	Isothermality	53.8	0.95
Phyllostomidae	*Leptonycteris nivalis*	EN	decreasing	Precipitation warmest Q	14.5	Isothermality	53.4	0.95
Phyllostomidae	*Leptonycteris yerbabuenae/sanborni*	NT	decreasing	Precipitation seasonality	21.2	Isothermality	58.0	0.95
Phyllostomidae	*Macrotus californicus*	LC	stable	Annual Precipitation	36.2	Annual mean temperature	43.8	0.96
Vespertilionidae	*Antrozous pallidus*	LC	stable	Precipitation warmest Q	37.7	Isothermality	20.9	0.82
Vespertilionidae	*Corynorhinus townsendii*	LC	stable	Precipitation warmest Q	56.5	Annual mean temperature	23.1	0.81
Vespertilionidae	*Euderma maculatum*	LC	stable	Precipitation warmest Q	32.0	Annual mean temperature	25.2	0.91
Vespertilionidae	*Idionycteris phyllotis*	LC	stable	Annual precipitation	37.7	Annual mean temperature	28.2	0.92
Vespertilionidae	*Lasiurus blossevillii*	LC	unknown	Precipitation seasonality	50.9	Annual mean temperature	13.0	0.93
Vespertilionidae	*Lasiurus xanthinus/ega*	LC	stable	Precipitation warmest Q	30.1	Annual mean temperature	20.1	0.93
Vespertilionidae	*Myotis californicus*	LC	unknown	Precipitation warmest Q	45.8	Isothermality	18.0	0.84
Vespertilionidae	*Myotis occultus*	LC	stable	Annual Precipitation	18.4	Isothermality	53.8	0.89
Vespertilionidae	*Myotis thysanodes*	LC	stable	Precipitation warmest Q	29.2	Annual mean temperature	28.0	0.83
Vespertilionidae	*Myotis velifer*	LC	stable	Precipitation seasonality	30.2	Annual mean temperature	36.0	0.88
Vespertilionidae	*Parastrellus hesperus*	LC	stable	Annual precipitation	29.7	Annual mean temperature	21.8	0.88
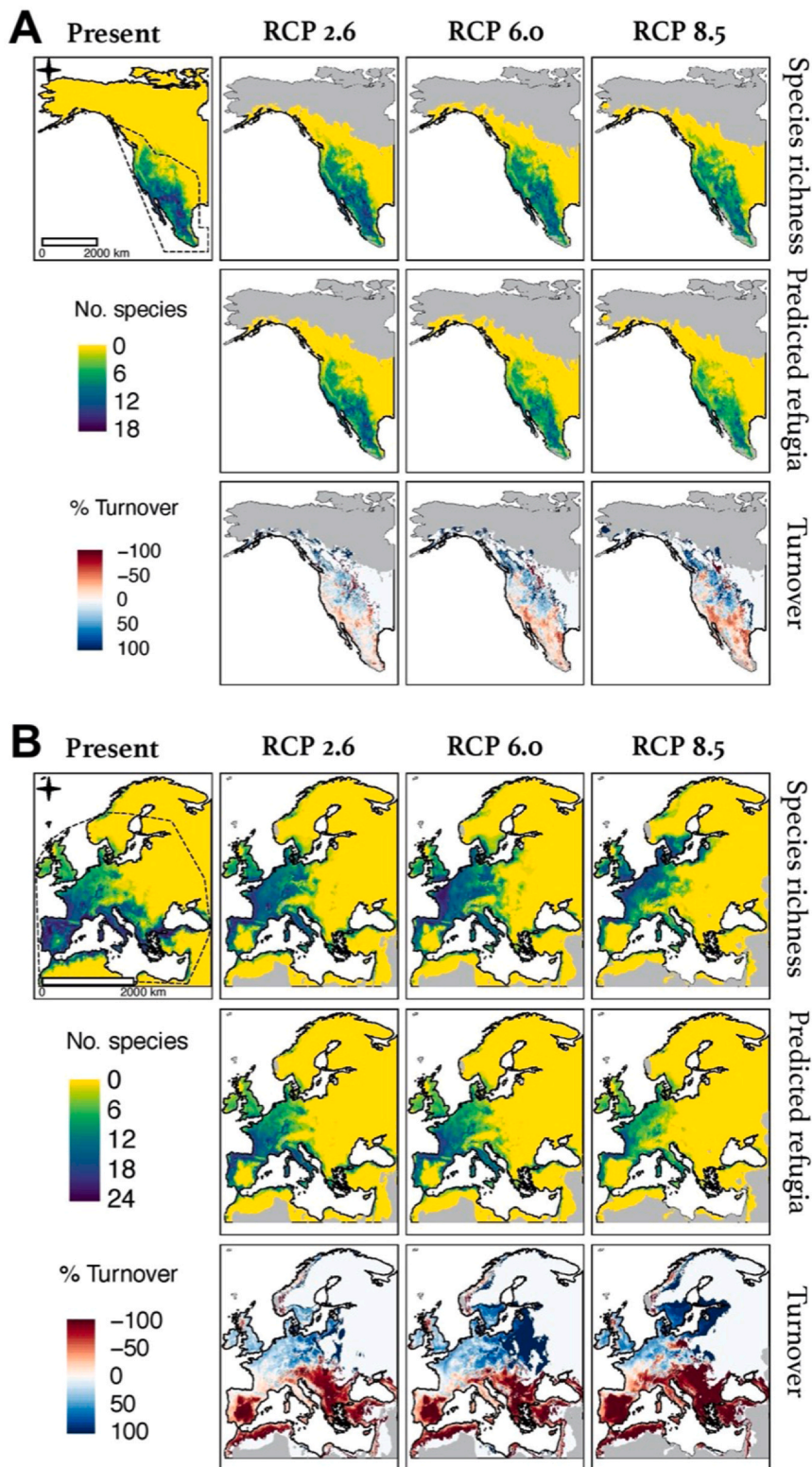
Fig. 1. Predicted current and future species richness, with predicted refugia (darker colours show where a greater number of species remained within their current range) and percent turnover of species (relative gain or loss of species, expressed as a percentage of total current richness at the location) in (A) Western North America and (B) Western Palaearctic study areas. Predictions are based on Maxent Species Distribution Models of presence-only bat occurrence data trained on current climate data and projected to three future climate scenarios from low to high emissions (RCP 2.6, RCP 6.0, RCP 8.5) for the 2061–2080 time period. Dashed polygons show study areas, comprising the minimum convex polygon containing all species occurrences with a buffer of 50 km.
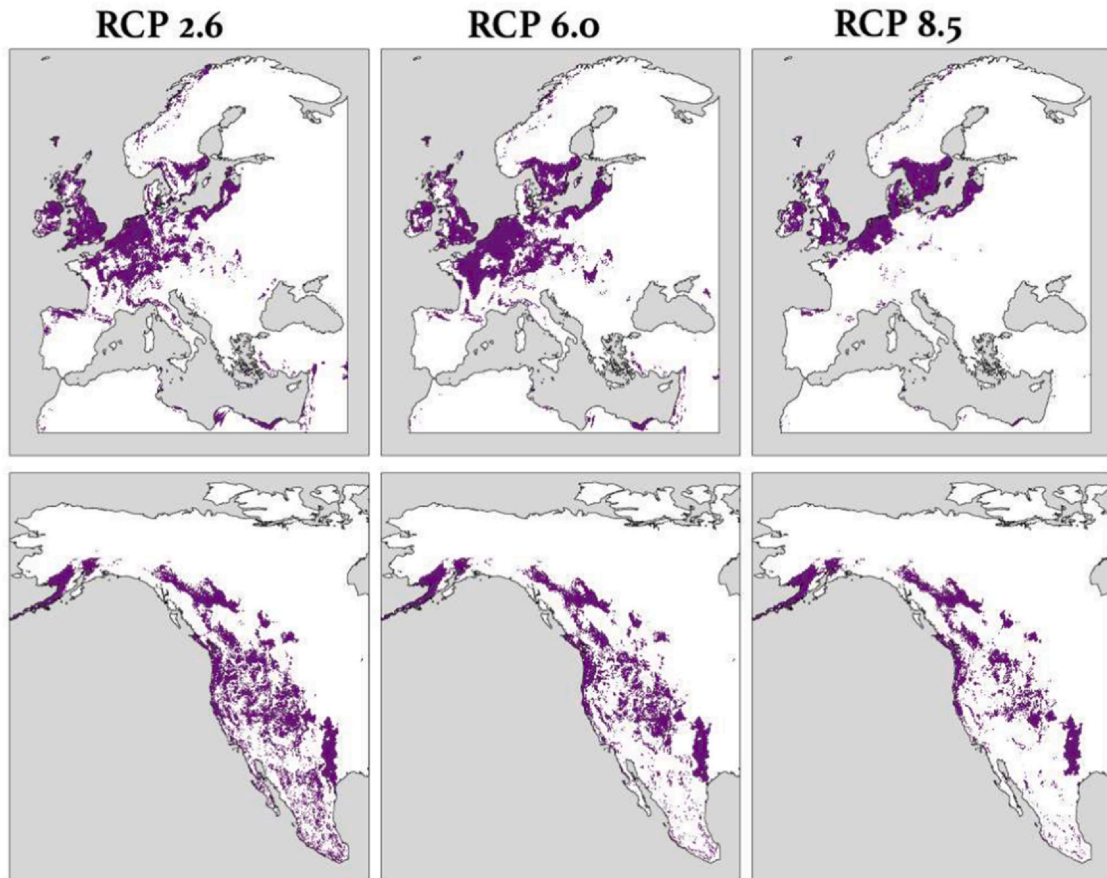
Fig. 2. Refugial zones where all species occurring in current climate (1950–2000) retain climatic suitability in 2061–2080 in the Western Palaearctic and Western North America for three emissions scenarios (RCP 2.6, RCP 6.0, RCP 8.5).

with caution, given the majority of predicted range expansion area falls within regions where low environmental similarity was recorded (Appendix S2, S3.35). While directions of range shifts were predominantly in the northern direction, several species shifted in notably different directions (Fig. 3) including *Myotis occultus* (SE), *Macrotus californicus* (NE) and *Leptonycteris nivalis* (W-NW) in Western North America and *E. isabellinus* (E) and *M. myotis* (W-NW) in the Western Palaearctic. Range expansions were predicted for both regions in at least one emissions scenario, with up to 67% species predicted to expand (rather than contract) their range in the Western Palaearctic and up to 58% in Western North America. In the Western Palaearctic, the proportion of species predicted to increase their range increased as for the medium and high emission scenarios. The pattern was opposite for Western North America, where a greater number of species were predicted to increase their range at the lowest emission scenario, while more range contractions were projected for higher emissions scenarios (Fig. 4).

3.5. Identifying species at greatest risk of population decline

Across the three emission scenarios 33–50% of bat species in the Western Palaearctic and 42–53% in Western North America were predicted to contract their ranges as a result of climate change (Fig. 4). Four to six bat species in the Western Palaearctic (*Plecotus auritus begognae, Nyctalus lasiopterus, Myotis escalerai, Eptesicus isabellinus, Rhinolophus mehelyi, Plectotus austriacus*) and 1–3 Western North American bat species (*Antrozous pallidus, Idionycteris phyllotis, Myotis thysanodes*) were predicted to experience range contraction, with limited connectivity (<50% overlap) between current and future climatically suitable areas.

3.6. Model confidence

Species models had high AUCs (Western Palaearctic: mean = 0.88 (0.81–0.98); Western North America: mean = 0.90 (0.81–0.96)), indicating good predictive performance (Elith et al., 2006). MESS maps showed that across most of the study areas, ranges in environmental variables largely overlapped between future and current climates (Supplementary, Appendix S2), adding confidence to the bioclimatic predictions. Part of the study area, namely the southwestern edge of Norway and areas in
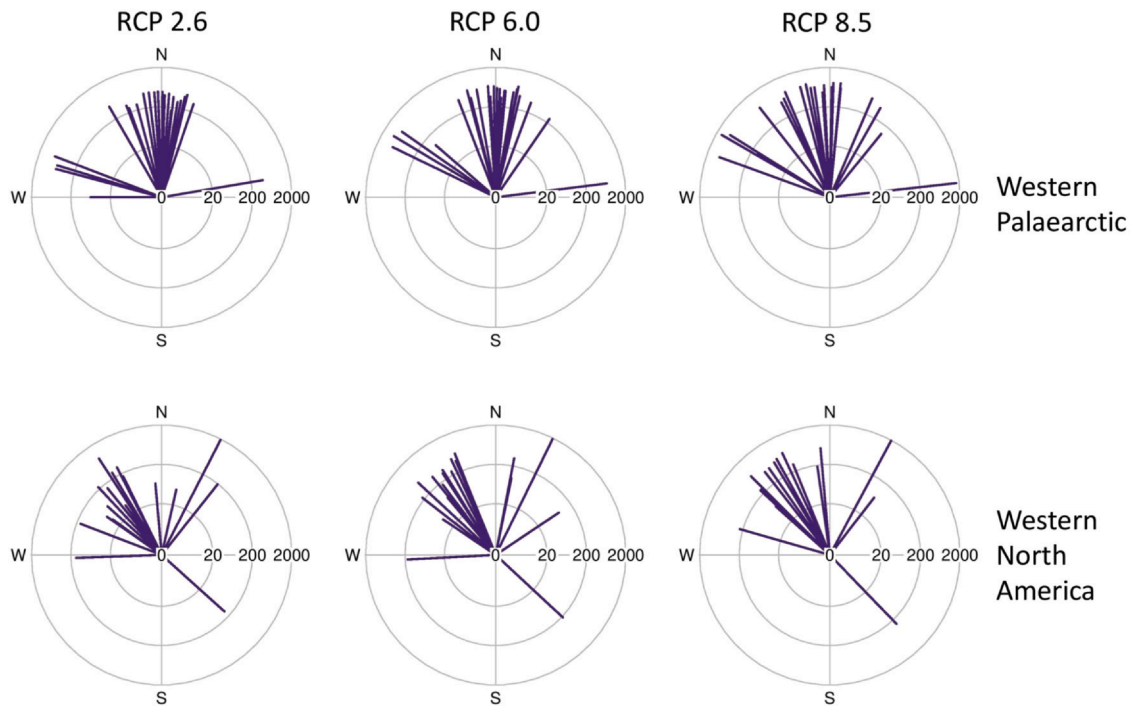
Fig. 3. Polar plots indicating the geographic direction (North (0°), South (180°)) and distance of predicted range shifts (shifts in climatic suitability) for 43 bat species in a) The Western Palaearctic and b) Western North America, calculated by subtracting the centroid of the predicted range from the predicted current range. Predictions are made for three emissions scenarios (RCP 2.6, 6.0 and 8.5) for the time period 2061–2080.

the Middle East and the Sahara for the Western Palaearctic, and the Arctic for Western North America, were included in the analysis because the minimum convex polygons for some widely distributed species extended into these areas. However, these areas were not the emphasis of this study as they are likely to experience novel conditions and as such modelled bioclimatic relationships in these regions should be approached with caution (Appendix S2).

4. Discussion

Key findings of this study were that while a large proportion of bat species occurring in semi-arid and dry landscapes have the potential to expand their range with the changing future climate (up to 67% in Western Palaearctic and 58% in Western North America), high velocity range shifts would be required to keep pace with these changes, with options to remain in refugia limited, particularly in lower altitudes. While our models predict montane and coastal areas in both regions to remain climatically suitable for the majority of bat species it should be noted that these 'refugia' may be influenced by additional climate effects such as sea level rise (coastal areas) and increased incidence and severity of wildfires (montane areas) (Kulp & Strauss, 2019; Bowman et al., 2020).

Climate drivers of predicted bat species distributions differed between continents, dominated by temperature variables for the Western Palaearctic and by precipitation variables in Western North America. The greater proportion of species in the Western Palaearctic are predicted to expand their range compared to Western North America, where a greater proportion are predicted to contract their range may reflect these different climate drivers. For example, Western North America has highly variable precipitation, increasing the reliance of bat communities on ephemeral water sources and low precipitation can reduce reproductive success, a potential factor in range contraction (Adams & Hayes, 2008; Adams, 2010; Amorim et al., 2015). In contrast, the Western Palaearctic has less variable precipitation, but lower mean temperatures, and rising temperature has been identified as a key driver in recent bat range expansions observed in recent years in Europe (Lundy et al., 2010; Ancillotto et al., 2016). Differences in extent, configuration and geographical location of study areas across continents may influence these relationships.

Our predictions of an overall shift in climatic suitability for bats to higher latitudes and elevations (Figs. 1 and 2) agree with regional predictions in Europe (Rebelo et al., 2010) and Mexico (Zamora-Gutierrez et al., 2018), as well as broader trends in biodiversity response to climate change (Parmesan & Yohe, 2003; Maiorano et al., 2011). Similar to Rebelo et al., (2010) and Bilgin et al. (2012), who predicted a net loss in occupied area by Mediterranean bats in Europe under the highest emission scenarios, our study indicated that up to 50% of Mediterranean bat species in the Western Palaearctic and 53% of Western North America study area are at risk of contracting their distributions due to reduced climatically suitable areas. Importantly, the areas
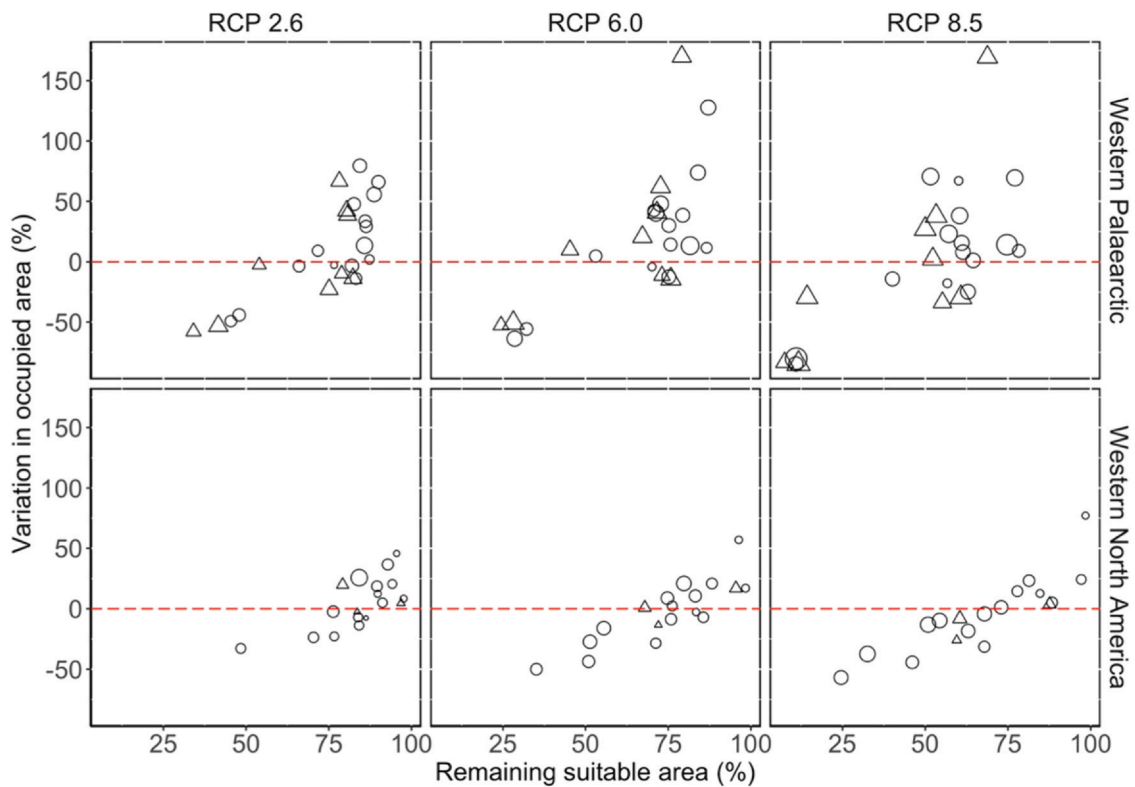
Fig. 4. Relationship between variation in occupied area (the relative amount of potential range expansion and contraction presented as a percentage where −100 predicts a complete loss of suitable habitat and positive values indicate predicted increases in suitable area) and remaining suitable area (the predicted percentage of suitable area that will remain in the same area over time) for three emissions scenarios, predicting for the 2061–2080 time period in the Western Palaearctic (top) and Western North America (bottom). Species listed by the IUCN (12th December, 2019) as least concern (n = 31) are shown in open circles and those with other statuses are triangles (Endangered = 1, Vulnerable = 3, Near threatened = 6, DD = 1, Not evaluated = 1), with size of shapes proportional to distance of predicted range shift. *Euderma maculatum* was not included in this figure, given the majority of predicted range expansion area falls within regions where low environmental similarity was recorded.

in which we predict the highest negative turnover (or loss) of species, coincide with regions where drought risk and water stress are likely to be greatest (Alcamo et al., 2007; Dai, 2011).

The predicted velocities and directions of bat range shifts (shifts in climatic suitability of landscapes) in response to changing bioclimatic niches in the Western Palaearctic are comparable to those forecast for breeding birds (Huntley et al., 2008). Several species in our study were predicted to have very fast range shifts (> 150 km/decade), thought to lead to reduced genetic diversity (Arenas et al., 2012). Additionally, bats of the Western Palaearctic were predicted to undertake farther and faster range shifts, though realising these shifts may be challenging given the landscape contains additional barriers to movement (e.g. seas, greater human population density) compared to Western North America. However, there is evidence that one of the Western Palaearctic species predicted to undergo a fast range shift (*P. nathusii*, 155 km/decade NE) has already moved into novel habitats as a result of increasing temperatures so this species may be well-equipped to continue to shift its range (Lundy et al., 2010; Blomberg et al., 2021).

In the Western Palaearctic study area, 4–6 species of bat were identified as having very little low overlap between current and future suitable areas (Fig. 4) making them extremely vulnerable to population declines and possible extinction. Of these species, two were also identified by a separate climate change risk assessment for European and North-west African bats as at highest risk of extinction (*Rhinolophus mehelyi* and *Nyctalus lasiopterus*) (Sherwin et al., 2013) and are listed as Vulnerable by the IUCN (Table 1) and which may also be threatened by land use change (Lisón & Sánchez-Fernández, 2017). The two *Plecotus* species (*P. auritus begognae* and *P. austriacus*) both have restricted ranges, though *P. auritus begognae* is strongly associated with steep slopes, low temperatures and high precipitation (Santos et al., 2014), making it potentially more vulnerable than *P. austriacus* which inhabits lowland areas (Ashrafi et al., 2011). Our predictions for a contraction of the range of *M. escalerai* (−49 to −85% by 2080) are more extreme than the 18% reduction by 2070 predicted by Razgour et al., (2015) using a high emissions scenario, however both studies indicate that this species is likely to contract its range.

Within Western North America, a lower number of species were identified having little overlap between current and future suitable areas (1–3, Fig. 4). Our predictions that *M. thysanodes* is likely to lose up to 44% of its range are further supported by a recent simulation study showing that *M. thysanodes* populations could decrease in size by > 90% by 2086 (Hayes & Adams, 2017).

This species uses a wide range of roost structures but is also associated with late seral stage forest attributes in north-western montane regions (Weller, 2008), a limited and declining resource, and lactating females are highly dependent on water sources (Adams & Hayes, 2008). These factors combined indicate elevated conservation concern for *M. thysanodes* from changing climates, and population declines may have already begun, as modelled occurrence probabilities for this species in the Pacific Northwest declined from 2003 to 2010 (Rodhouse et al., 2015).

Specialised nectarivorous bats are also likely to be threatened by future changes in climate. While two of the three nectarivorous species in our Western North America study area (*L. nivalis* and *L. yerbabuenae*) are both migratory and therefore capable of broad-scale movements to new habitats, any range expansion would be reliant on a similar expansion of their food plants (Frick et al., 2018). At present, *L. nivalis* is classified as 'Endangered' by the IUCN due to its continued population decline due to the loss of roosting and foraging habitat (Gómez-Ruiz & Lacher, 2017). Although our study predicts a net range expansion for both species, *L. nivalis* has a highly specialised diet (Agave spp.) and overlap between the distribution of this bat and agave is predicted to reduce by at least 75% by 2050 and > 80% by 2070 (Gómez-Ruiz & Lacher, 2019) – putting any range expansion in doubt. Migratory species and migratory behaviours have been identified as particularly at risk from changes in future climate due to the potential for fragmentation of migratory routes (Wilcove & Wikelski, 2008).

As our models are based only on mean climate variables and elevation and do not consider climate extremes (e.g. heat waves) or indirect effects of climate change (e.g. increasing wildfire incidence and severity) our results must be considered a "best case scenario" (Rebelo et al., 2010). Our study focuses on the potential climatic niche rather than the realised climatic niche, so it is important to remember that many additional factors influence habitat suitability for bats and can potentially restrict bat movement into new areas. In particular, water on the landscape will be critical for survival of species on both continents, particularly during reproduction (Lisón & Calvo, 2014; Salvarina, 2016; Adams & Hayes, 2018; Amorim et al., 2018; Mas et al., 2021). Importantly, the value of water sources to bats are also dependent on anthropogenic disturbance, for example reduced water quality and removal of riparian vegetation (Lisón & Calvo, 2011; Korine et al., 2016; Salvarina, 2016). Climate change can also interact with anthropogenic land use change to affect habitat suitability for bats. For example, a study that combined impacts of climate change with projected future land use changes in Mexico, predicted an average reduction of environmental suitable areas of 51% for bat species by 2050 (Zamora-Gutierrez et al., 2018). In Western North America and the Western Palaearctic, climate change is projected to increase the incidence and severity of wildfires (Bowman et al., 2020), dramatically changing landscape structures and influencing bat assemblages (Blakey et al., 2019; Steel et al., 2019; Ancillotto et al., 2020; López-Baucells et al., 2021). Additional factors that may determine the ability of bats to remain in landscapes with changing climates or colonise new areas include: dispersal barriers (García-Mudarra et al., 2009; Razgour et al., 2015), competition between species (Razgour et al., 2018; Salinas-Ramos et al., 2020; Smeraldo et al., 2021; Hall et al., 2016), prey and food plant availability (Krauel et al., 2015), roost requirements (Loeb & Winters, 2013), habitat fragmentation (Frey-Ehrenbold et al., 2013), disruption of migration phenology (Krauel & McCracken, 2013) and influence of pathogens (Frick et al., 2015). Conversely, many species may be able to withstand changes in climate, for example through flexible use of torpor to regulate body temperature and water loss (Bondarenco et al., 2013), concentration of urine to reduce water loss (Carpenter, 1969) or flexibility in foraging strategy (Frick et al., 2009). The rapid progression of species distribution modelling methods to account for many of these factors (e.g. Razgour et al., 2016; Tikhonov et al., 2017; Lembrechts et al., 2019; Mendes et al., 2020) coupled with establishment of large-scale bat monitoring programmes (Barlow et al., 2015; Loeb et al., 2015) will assist future studies to predict habitat suitability for bats more accurately and at finer scales.

4.1. Conservation recommendations

We recommend that more detailed surveys are carried out in the identified areas of refugia (Figs. 1 and 2) for bat species of the Western Palaearctic and Western North America. Due to the monumental task of protecting species from the effects of climate change, we believe that identifying potential climate refugia is a useful tool to focus conservation efforts. In this way, land managers can prioritise conservation and management activities to enhance existing protected areas and promote connectivity between current and future bat habitats. The refugia maps we have developed are not suitable to identify fine scale refugial habitats, but do correspond in scale with continental natural resource management areas and monitoring programmes. For example, the USDI Bureau of Land Management and USDA Forest Service manage respectively 99 and 68 million ha in the Western US including the majority of the areas identified as refugia in this study. We also recommend the protection of networks of water sources, particularly in environments where drought risk is high (Blakey et al., 2017, 2018; Amorim et al., 2018) and possibly the creation of water sources where the benefits outweigh potential costs (Korine et al., 2016), for example, increases in anthropogenic water sources may allow mesic species to outcompete arid-adapted species (Razgour et al., 2018). As a high degree of uncertainty exists in any predictive modelling, much can be learned from monitoring the leading and trailing edges of species distributions (Amorim et al., 2014), with a priority for the 9 species identified by this study as at being at risk of major range contraction due to climate change (*Plecotus auritus begognae, Nyctalus lasiopterus, Myotis escalerai, Eptesicus isabellinus, Rhinolophus mehelyi, Plectotus austriacus, Antrozous pallidus, Idionycteris phyllotis, Myotis thysanodes*). National and continental bat monitoring programmes, for example the National Bat Monitoring Programme (Barlow et al., 2015) and North American Bat Monitoring Program (Loeb et al., 2015) are at the appropriate scale to test these predictions and are designed to avoid spatial and temporal biases inherent in biodiversity databases (Fourcade et al., 2014; Fisher-Phelps et al., 2017; Smeraldo et al., 2018). Finally, climate change is likely to exacerbate existing anthropogenic threats to bats (Smith et al., 2016; Zamora-Gutierrez et al., 2018), in turn influencing humans by reducing ecosystem services and increasing risk of zoonotic spillover

(Martin et al., 2018; Plowright et al., 2021). Therefore, a commitment by world governments to significantly reduce carbon emissions should be urgently sought in order to avoid further deterioration of bat communities and the important ecosystem services that they provide (Frick et al., 2019).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data accessibility statement

The data that support this study are openly available in the Dryad Data Repository at https://doi.org/10.5068/D12093 (Blakey et al., 2021).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2021.e01608.

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