



Bat responses to climate change: a systematic review

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ABSTRACT

Understanding how species respond to climate change is key to informing vulnerability assessments and designing effective conservation strategies, yet research efforts on wildlife responses to climate change fail to deliver a representative overview due to inherent biases. Bats are a species-rich, globally distributed group of organisms that are thought to be particularly sensitive to the effects of climate change because of their high surface-to-volume ratios and low reproductive rates. We systematically reviewed the literature on bat responses to climate change to provide an overview of the current state of knowledge, identify research gaps and biases and highlight future research needs. We found that studies are geographically biased towards Europe, North America and Australia, and temperate and Mediterranean biomes, thus missing a substantial proportion of bat diversity and thermal responses. Less than half of the published studies provide

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concrete evidence for bat responses to climate change. For over a third of studied bat species, response evidence is only based on predictive species distribution models. Consequently, the most frequently reported responses involve range shifts (57% of species) and changes in patterns of species diversity (26%). Bats showed a variety of responses, including both positive (e.g. range expansion and population increase) and negative responses (range contraction and population decrease), although responses to extreme events were always negative or neutral. Spatial responses varied in their outcome and across families, with almost all taxonomic groups featuring both range expansions and contractions, while demographic responses were strongly biased towards negative outcomes, particularly among Pteropodidae and Molossidae. The commonly used correlative modelling approaches can be applied to many species, but do not provide mechanistic insight into behavioural, physiological, phenological or genetic responses. There was a paucity of experimental studies (26%), and only a small proportion of the 396 bat species covered in the examined studies were studied using long-term and/or experimental approaches (11%), even though they are more informative about the effects of climate change. We emphasise the need for more empirical studies to unravel the multifaceted nature of bats' responses to climate change and the need for standardised study designs that will enable synthesis and meta-analysis of the literature. Finally, we stress the importance of overcoming geographic and taxonomic disparities through strengthening research capacity in the Global South to provide a more comprehensive view of terrestrial biodiversity responses to climate change.

Key words: bats, climate change, conservation, life traits, physiology, species range.

CONTENTS

I. Introduction	2
II. Methods	3
(1) Literature search	3
(2) Articles screening and classification	3
III. Results	5
IV. Discussion	8
(1) Bat responses to climate change	9
(2) Gaps in the literature and future research	9
V. Conclusions	11
VI. Acknowledgements	11
VII. References	12
VIII. Supporting information	15

I. INTRODUCTION

Climate change is currently recognised as one of the main threats to global biodiversity (Schmittner & Galbraith, 2008; Wolkovich *et al.*, 2014) with impacts expected to become more severe before the end of the century (Urban, 2015). Yet research efforts on wildlife responses to climate change fail to deliver a representative overview because studies are taxonomically and geographically biased (e.g. Pacifici *et al.*, 2015; Scheffers *et al.*, 2016; Winter *et al.*, 2016; Feeley, Stroud & Perez, 2017), often focus on particular species (e.g. Lane *et al.*, 2012; Tafani *et al.*, 2013; Plard *et al.*, 2014), or are primarily based on correlative modelling approaches (e.g. Warren *et al.*, 2018). The threats that stem from climate change are diverse and multifaceted, resulting in complicated direct and indirect effects on wildlife. Anthropogenically driven climate change has already resulted in increased temperature, changes in precipitation patterns and increased intensity and frequency of extreme events, such as heatwaves, droughts, or wildfires (Allan *et al.*, 2021); all are factors that strongly influence wildlife by increasing mortality, reducing reproductive success, or

altering species–environment relationships and biotic interactions, among other effects (Montoya & Raffaelli, 2010; Moreno & Møller, 2011).

Bats (Chiroptera) are the second most species-rich taxonomic order of mammals, accounting for one-fifth of global mammalian diversity (>1430 species; Simmons & Cirranello, 2021). Bats are globally distributed and inhabit a wide diversity of habitats, spanning from tropical rainforests to arid regions, boreal forests, and oceanic islands (Altringham, 2011). As bats occur in a diverse range of environmental conditions, they represent an excellent study system for assessing the effects of climate change on vertebrates. Bats display a variety of dietary adaptations including insectivory, carnivory, nectarivory and haematophagy (Altringham, 2011), thus playing key roles in ecosystems and providing ecosystem services such as suppression of pest populations, seed dispersal, pollination, enhancement of soil fertility and nutrient distribution (Kunz *et al.*, 2011; Ramírez-Francel *et al.*, 2021).

Globally, over 16% of bat species are classified as threatened by the IUCN *Red List* (2022). However, the

conservation status of many bats is unknown, with 18% classified as data deficient and 57% with unknown population trends, a higher proportion than other mammals and birds (Frick, Kingston & Flanders, 2020). Bats are especially threatened by habitat loss (43% of species) and bushmeat hunting (33%; IUCN, 2022). New threats have emerged in recent years, including wind energy installations (Frick *et al.*, 2017), emerging infectious diseases (O'Shea *et al.*, 2016), climate change (Sherwin, Montgomery & Lundy, 2013) and increased frequency of heatwaves and fires, resulting in mass mortality events (Welbergen *et al.*, 2008; Ward *et al.*, 2020).

Bats are expected to be particularly sensitive to climate change because they are prone to dehydration due to high surface-to-volume ratios caused by their generally small body mass and their large wing and tail membranes (Korine *et al.*, 2016). Moreover, their slow, *K*-selected reproductive strategy (e.g. Famoso, Hopkins & Davis, 2018) makes them more susceptible to extinction under rapid environmental changes (Frick *et al.*, 2020; O'Grady *et al.*, 2004). Understanding how bats are affected by and cope with climate change is thus key to informing more accurate conservation assessments and management strategies from the global to the local level.

Here, we present a systematic review of bat responses to climate change to provide an overview of the current state of knowledge, identify research gaps and biases, and highlight future research needs. First, we identified studies focusing on the impacts of climate change on bats and classified them based on the methods used, studied taxa and evidence of response to climate change. Second, we summarised the evidence of bat responses to climate change from the individual to the assemblage levels and their response type, from behavioural to evolutionary, and quantified taxonomic and geographic biases. Finally, we tested for associations between the studied climate change events and the observed bat responses.

Overall, our review was guided by the following hypotheses and associated predictions.

- (1) Bats are long-lived mammals that may show a time lag in their functional responses to climate change, and therefore may require long-term (e.g. >20 years) studies to identify responses to climate change. Given the lack of long-term monitoring programmes of bats across the world, we predicted that there will be limited concrete evidence in the literature for bat responses to climate change.
- (2) Given the expected sensitivity of bats to climate change due to their high surface-to-volume ratios we hypothesised that bats will predominately show negative responses to climate change, in the form of population declines and range contractions.
- (3) Given the well-documented mass mortality events of bats, in particular pteropodids, under heat waves (Welbergen *et al.*, 2008), we hypothesised that bat responses to extreme events will be more negative than

their responses to temperature and rainfall changes. We predicted that the family Pteropodidae will show particularly negative responses in the form of population declines and range losses in response to extreme events.

II. METHODS

(1) Literature search

We followed the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) protocols (Page *et al.*, 2021). We searched the *Web of Science* and *Scopus* databases using the following search string: 'Chiroptera' OR 'bat*' AND 'climate change*' OR 'global warming' OR 'drought*' OR 'extreme event*' OR 'windthrow' OR 'fire*' OR 'mortality' OR 'extreme temperature*'. We also searched for relevant grey literature, using the same search terms and the advanced search features in Google, to identify additional papers that had been missed, however, no new documents were identified through our Google search. Searches were performed in English, Spanish, Portuguese and Polish. The final search was carried out in August 2020.

(2) Articles screening and classification

The review team consisted of 17 reviewers who held regular meetings to set the inclusion criteria, establish a common review protocol, and discuss any possible divergences in the relevance of some studies. To ensure consistency among reviewers, 46% of the documents were independently reviewed by at least two reviewers. If the reviewers disagreed about whether the paper should be included, they discussed the paper, and if opinions were still divergent, the paper was reviewed by a third reviewer. All reviewers were given clear protocols to follow with detailed descriptions of the inclusion criteria and practice papers to assess consistency among reviewers.

We first screened the title and abstract of the studies retrieved in our search and excluded documents that did not study the impacts of climate change on bats. Specifically, we interpreted as an impact of climate change any measured change, whether positive (e.g. range expansion, population increase), negative (e.g. range contraction, population decrease) or neutral (e.g. no change or unclear trend), in response to climatically driven pressures. We included impacts that were either explicitly observed and measured or predicted based on modelling approaches. We then read the full text to assess its relevance according to the following four criteria, at least one of which had to be fulfilled for the study to be included in the review: (C1) the paper focused on assessing bat responses to the effects of climate change, including predictive modelling studies (speculative studies without fact-based evidence were excluded); (C2) the paper reported quantitative data on morphology, behaviour, colony size and location or hibernation in relation to climate

change; (C3) the paper clearly mentioned before–after, control–impact experiments or a long-term monitoring design to tease apart the effects of climate change from the other confounding factors; (C4) the paper reported the impacts of a single extreme event putatively linked to climate change.

Because our aim was to establish a baseline on the overall current state of knowledge on bat responses to climate change, our retained studies reported myriad exposures (increase in temperature, changes in precipitation, etc.) and/or multiple outcomes (spatial, demographic, physiological, etc.) based on different methodological approaches (empirical, model-based, etc.). Hence, our studies were not homogenous and sample sizes for each response were too low to allow systematic extraction of quantitative data that could be summarised as standardised effect sizes for a meta-analysis (Gurevitch *et al.*, 2018). This would require a narrower, more focused question that

could direct the literature search and data extraction, and prior identification of common metrics reported across several studies to address that question. We instead report our findings as a qualitative synthesis. From each retained paper, we extracted information on the bat species investigated, the geographic scope of the study, study type, evidence level, methods, temporal period, climate change events, bat responses and interaction with other drivers (see online Supporting Information, Table S1). Chi-squared tests were used to test our predictions and identify associations between the studied climate change event, study type, recorded responses and the studied biome.

Where possible, we also assessed whether the observed responses were positive or negative. Changes in diversity or community structure, as well as individual behaviour, are difficult to evaluate in terms of their conservation implications. Thus, this classification was applied only to studies reporting demographic and spatial responses. We considered as positive

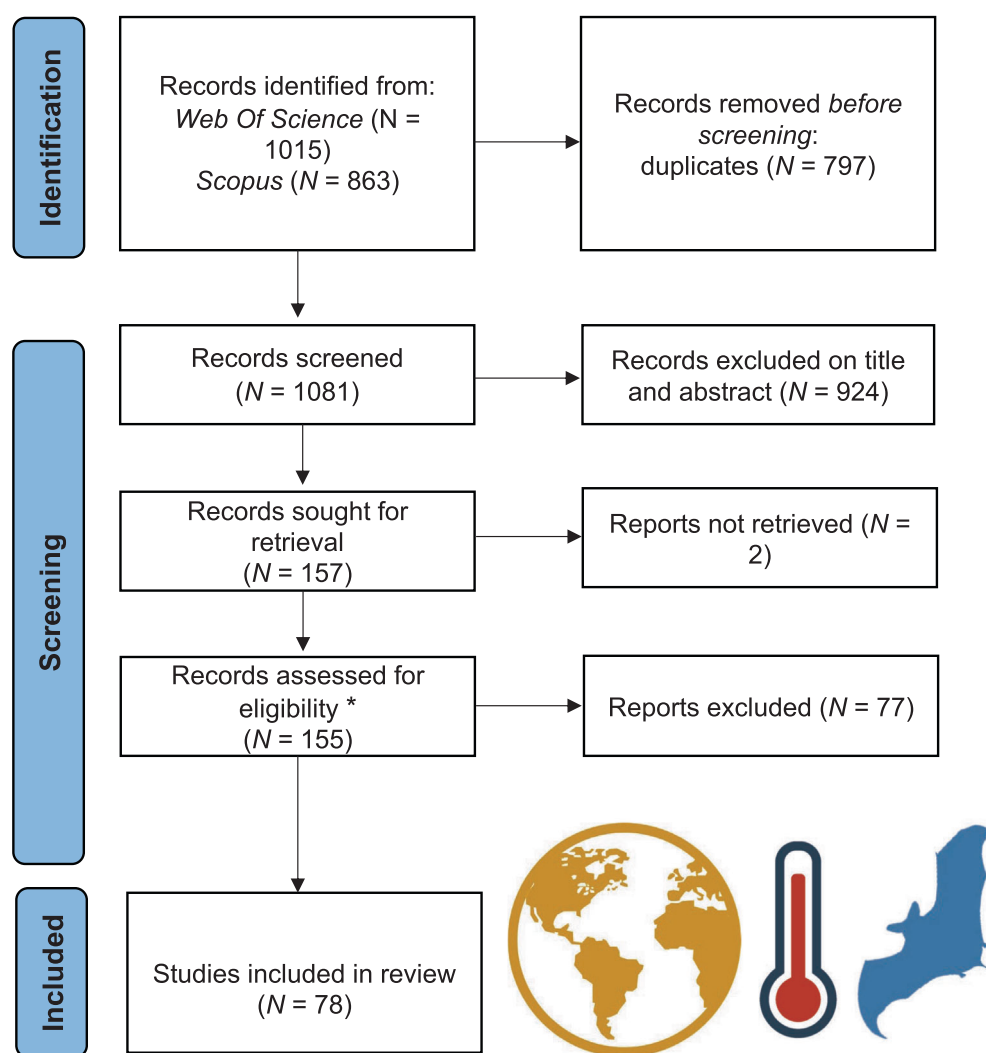


Fig. 1. PRISMA flow diagram illustrating the systematic review process for studies investigating bats and climate change. *Inclusion criteria: (1) paper focuses on assessing bat responses to climate change; (2) paper reports quantitative data on bats in relation to climate change; (3) paper reports evidence from long-term monitoring or field experiment; (4) paper reports on the impacts on bats due to single extreme events putatively linked to climate change.

those responses that potentially, but clearly, favour the long-term persistence of populations or species (e.g. range expansions, increased population size, increased reproductive success, decreased mortality), and as negative those responses that can lead to local or global extinction (e.g. range contractions, decreased population size, decreased reproductive success, increased mortality). Mixed or ambiguous responses were classified as no change or unclear.

III. RESULTS

We retrieved 1081 papers, 926 of which were rejected based on their title and abstract or because they could not be

accessed (two books and one unidentified reference). Of the remaining 155 papers, 77 were excluded after reading the full text because they did not satisfy at least one of our inclusion criteria. The final data set included 78 papers (Fig. 1; Table S2). See Table S3 for a list of excluded studies, with reasons for exclusion.

The retained papers were published between 1932 and 2020, but the majority (>80%) were published during the last 10 years (Fig. 2B). Most studies relied on species distribution modelling (26%), field experiments (24%) and field observations (23%), with other types of approaches representing a minor portion of the published evidence (Fig. 2G). The type of evidence retrieved was mainly observational (72% of papers), followed by experimental approaches (26%). In terms of the level of evidence (Fig. 2H), 44% of papers

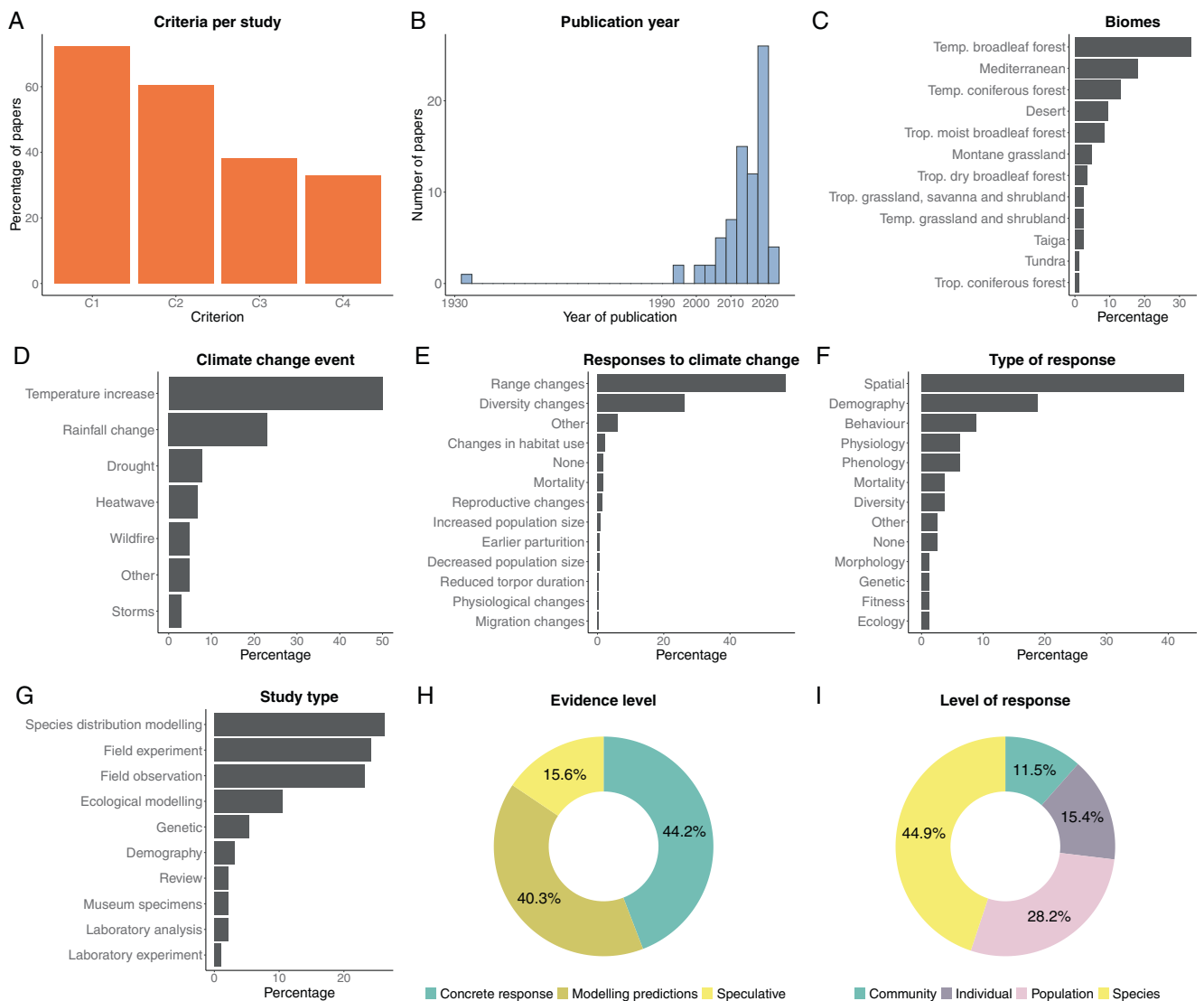


Fig. 2. Summary of published evidence for the impacts of climate change on bats, according to (A) inclusion criterion (see Section II.2); (B) year of publication; (C) biome investigated, Temp., temperate; Trop., tropical; (D) climate change event studied; (E) observed specific response by bats; (F) general category of type of response (note that mortality here refers to mass mortality events, usually in response to extreme events); (G) type of study; (H) evidence level; and (I) level of response.

reported a concrete response (i.e. recorded a phenotypic or behavioural response to climate change through either field or laboratory experiments or field observations), while 40% reported a response based only on model predictions [predictive species distribution models (SDMs) or demographic simulations]. Around 15% of studies were classified as speculative, i.e. they interpreted observed changes as responses to climate change without supporting evidence (Fig. 2H).

The reviewed studies reported evidence of the impact of climate change on 396 bat species (see full list in Table S4), 93% (370 species) of which were studied using SDM approaches, 52% using field observations (206 species), 11% using experimental approaches (43 species), and less than 1% (three species) using genetic methods. More than a third of the species studied (151 species, 38%) were only studied using SDM approaches, and only 38 species (<10%) were featured in more than three papers (Table S4). The most frequently studied species was the North American little brown bat (*Myotis lucifugus*; 10 studies), followed by four European species (*Rhinolophus ferrumequinum*, *Hypsugo savii*, *Myotis daubentonii* and *Pipistrellus kuhlii*) and by *Myotis thysanodes* (all featuring in eight studies each). Of the retrieved papers, 18% covered a time span of less than 1 year (Fig. S1). After removing these short-term studies and two studies dealing with palaeoclimatic data, the median time span of studies was 22 years (range: 1–139), which dropped to 10 years (range: 1–132) after excluding modelling papers projecting climatic conditions under future scenarios (e.g. to 2070). Only nine field studies covered periods >20 years (Fig. S1). The most frequently reported responses by bats were at both the

population (28%) and species (45%) levels and mostly consisted of range shifts (57%), changes in patterns of diversity (26%) and demographic changes (20%) (Fig. 2E, F). Only four papers provided evidence of no response (from 12 species), all dealing with a lack of demographic responses or community changes in relation to climate change. The climatic event reported most frequently as affecting bats was increased mean temperature (50%), followed by change in rainfall regime (23%) (Fig. 2D). The most studied continents were Europe (40%, 27 studies), North America (27%, 18 studies) and Oceania (19%, 13 studies), while the least studied were South America and Africa (two and three studies, respectively) and Asia (6%, four studies; Fig. 3). Correspondingly, the most studied biomes were temperate coniferous and broadleaf forest (47%) and Mediterranean (20%) (Fig. 2C).

We found significant associations between the studied climate change events and the identified responses ($\chi^2 = 76.35$, $df = 42$, $P < 0.005$). Studies of the effects of heatwaves primarily reported mass mortality events and physiological changes, but not range changes. By contrast, studies of the effects of temperature increase were associated with range changes but not mortality. We also found significant associations between study type and the climate change event examined ($\chi^2 = 52.65$, $df = 36$, $P < 0.05$), whereby the effects of heatwaves and wildfires were primarily examined using experimental studies. Despite the lack of significant associations between biome and study type ($P > 0.05$), only field observations and SDM studies were carried out in the tropics, while experiments were mainly carried out in temperate environments (14 papers, 70% of experimental studies).

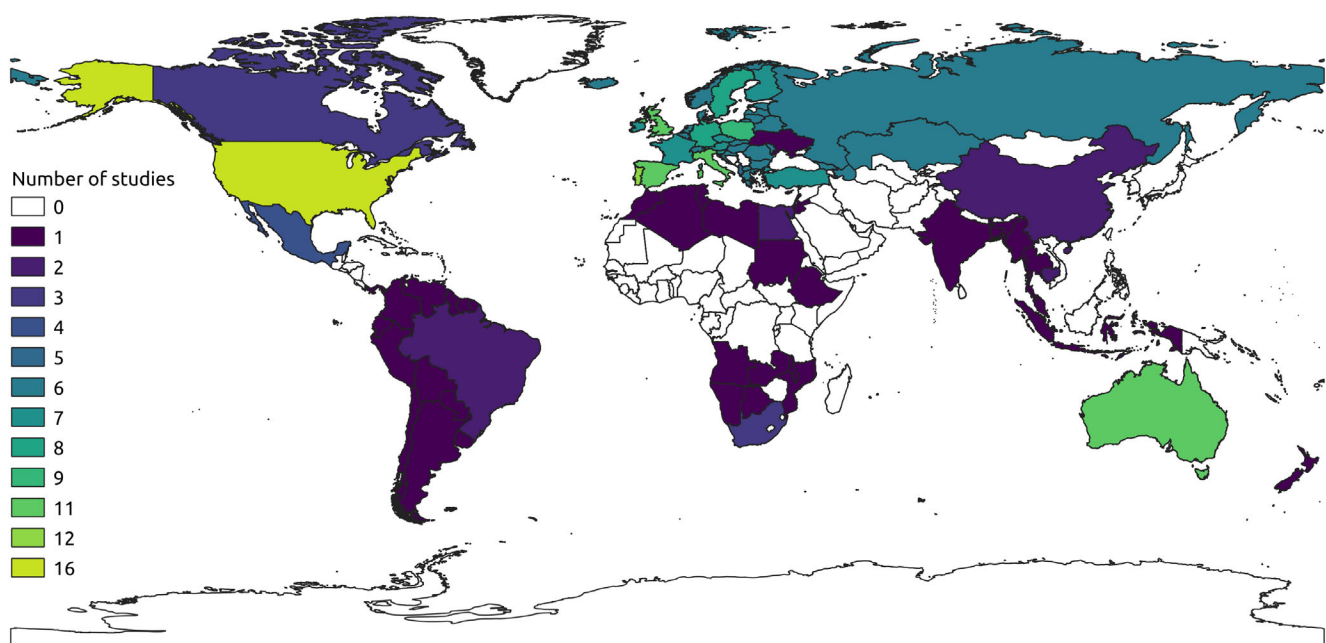
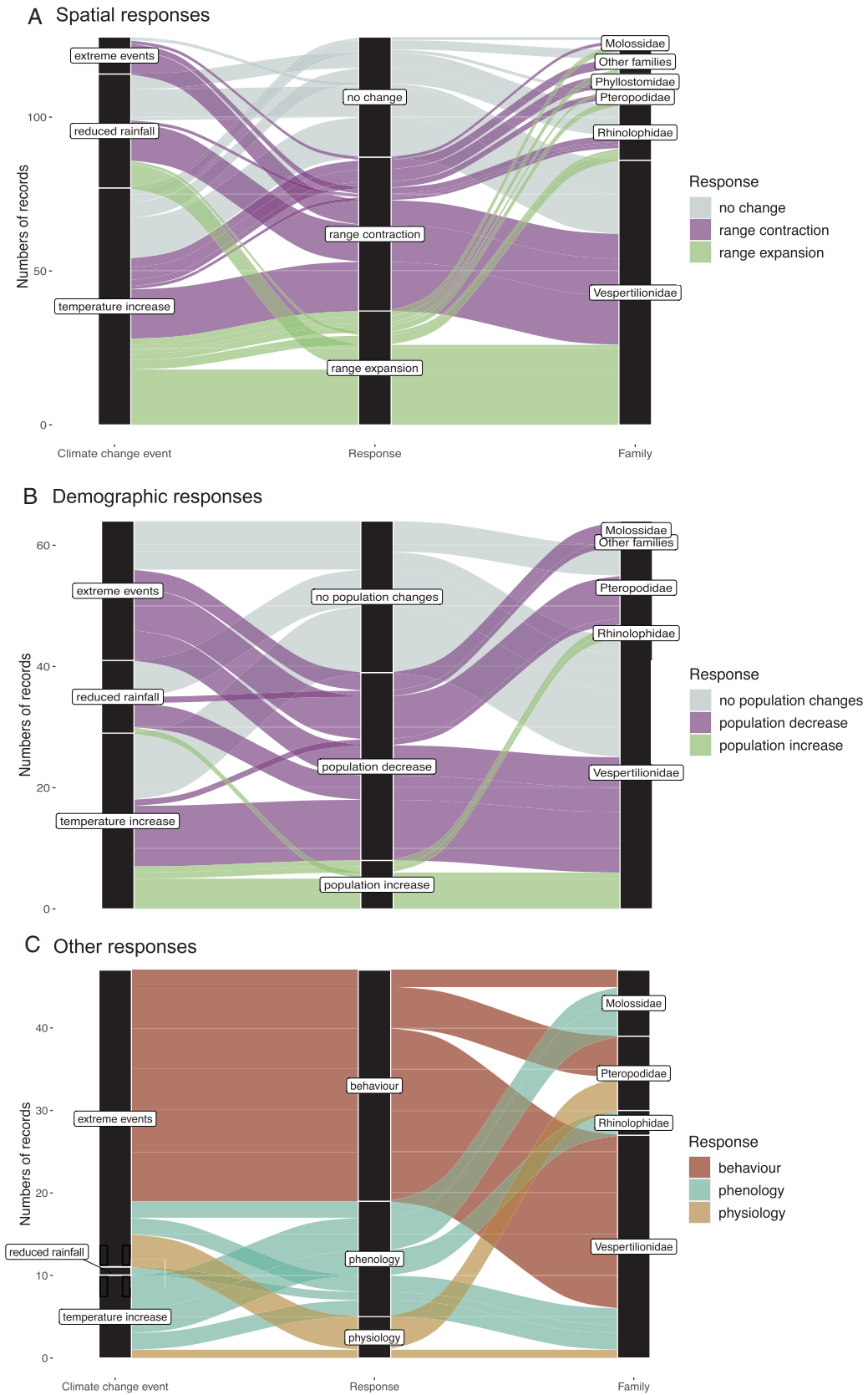


Fig. 3. Global distribution of studies on bats and climate change according to country/region of study. Countries with no studies included in this review are depicted with no colour.



The direction of the reported consequences of climate change on bats varied with the type of response (Fig. 4). A prevalence of negative effects was consistent for reported demographic and spatial responses. Of the demographic responses to all climate change events, 61% were negative, including increased mortality and decreased reproductive success leading to population decline, the remaining 39% included both mixed, neutral and positive effects. Of 160 retrieved spatial responses, 30% reported actual or potentially positive effects (i.e. range expansion), 40% negative (i.e. range contraction), and the remaining 30% provided mixed or unclear evidence. In line with our hypothesis, all responses to extreme events were negative (range contraction or population decrease) or unclear/no change (Fig. 4). In addition, while spatial responses showed high variability in their direction and across bat families, demographic responses were mostly negative, particularly among Pteropodidae and Molossidae. Positive demographic responses (population increases) were identified for only some vespertilionid and rhinolophid bats, mostly associated with temperature increases. Twenty-five papers highlighted that climate change may interact with other drivers potentially affecting bats, the most frequently reported being land-use change and associated habitat fragmentation (40% of papers).

IV. DISCUSSION

Understanding how bats respond to climate change is key to informing vulnerability assessments and to designing effective conservation strategies, not only for bats but also for other terrestrial vertebrate groups experiencing similar pressures. Our analysis represents the first comprehensive systematic review of the evidence for how bats are responding to climate change, moving our understanding forward from previous work based on predictions and scattered evidence (Jones & Rebelo, 2013; Sherwin *et al.*, 2013). Since those earlier reviews, the number of studies addressing this topic has greatly increased, but only a small proportion provides concrete evidence for bat responses to climate change. Only around 7% of papers and reports published in the last 90 years that mentioned bats and climate change added evidence on the topic, a rather limited body of literature when compared to other topics relating to bats (e.g. López-Baucells, Rocha & Fernández-Llamazares, 2018). Indeed, the overall research effort on bats and climate change is rather low in comparison to other vertebrate groups. For

example, and notwithstanding a total number of species that is nearly an order of magnitude greater than the total number of bats, Möller, Fiedler & Berthold (2010) retrieved >2800 papers dealing with the effects of climate change on birds, compared with our final data set of 78 papers identified as actually addressing this topic for bats. As a consequence of this lower research effort, the available evidence only includes *ca.* 27% of bat species (396 species out of >1430), more than a third of which were only studied using modelling approaches.

Nearly half of the evidence for the effects of climate change on bats comes from modelling studies, primarily based on projections of species distributions under future climate change scenarios. While modelling studies can provide useful estimates for conservation assessments and planning, they inevitably rely on critical assumptions and can have a limited predictive capacity (Sofaer *et al.*, 2018; Venne & Curie, 2021). Thus they do not offer concrete evidence for the effects of climate change, but rather predictions of what could happen provided that the equilibrium assumption holds, the data upon which they were based are representative and sufficient, and all relevant environmental variables are included (Santini *et al.*, 2021). The high proportion of modelling and speculative studies (Fig. 2H) underlines the limited scientific evidence available on the effects of climate change on bats.

Ideally, bat responses to climate change (spatial, phenological, demographic, etc.) should be quantitatively synthesised using a meta-analysis. However, we found that the empirical evidence to date is sparse and not sufficiently homogeneous to derive common effect sizes across studies suitable for a meta-analysis. For example, a meta-analysis addressing the effects of climate change on range and elevational shifts across taxa included 764 and 1367 individual species responses (measured as km/decade), respectively (Chen *et al.*, 2011). Similarly, evidence for elevational shifts in birds (m/year) was synthesised from data for hundreds of species and dozens of studies worldwide (Scridel *et al.*, 2018; Neate-Clegg *et al.*, 2021), whereas phenological shifts (reported as days of advancement/delay per decade) were analysed from a similarly large database (127 studies; Cohen, Lajeunesse & Rohr, 2018). A similar approach is desirable for bat species, yet our review reveals that much of the evidence for the effects of climate change on bats is based on modelling rather than long-term observational studies. We call for increased efforts to design studies that are aimed at understanding bat responses to climate change and for the collection and reporting of results in a standardised manner. Publications

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Fig. 4. Effects of climate change on bats, weighted according to the number of records, for (A) spatial responses, (B) demographic responses, and (C) other responses (behaviour, physiology and phenology). Plots show bat family, reported climate change events, and bat response. In (A) and (B), responses are classified as either positive (range expansion or population increase, in green), negative (range contraction or population decrease, in pink) or neutral (no change, in grey). In (C), climate change events are related to three specific types of response (behaviour, physiology, phenology) due to the more variable nature of these responses and the low number of studies for each category. Note that only responses with $N > 5$ are included in this figure.

should provide sufficient raw data to facilitate their use in future meta-analyses (Radchuk *et al.*, 2019).

We identified geographic biases in the study of bats and climate change. A bias towards the Global North (high-income countries, covering primarily temperate, Mediterranean and boreal biomes) is common in biodiversity research (e.g. Blettler *et al.*, 2018; Titley, Snaddon & Turner, 2017; Winter *et al.*, 2016), likely related to socioeconomic disparities. A large portion of bat diversity is concentrated in the tropics (West Africa, Central and South America, Southeast Asia), with diversity hotspots in tropical forest biomes (Cooper-Bohannon *et al.*, 2016; Myers *et al.*, 2000). Hence, the current evidence base for the effects of climate change on bats is unlikely to represent their full range of responses. Species at higher latitudes may experience different pressures from climate change compared to those in the tropics, for example in terms of the types and intensity of extreme events or changes to weather patterns (Wigley, 2009), and may require different adaptations to compensate accordingly (Pacifci *et al.*, 2015).

(1) Bat responses to climate change

Like other animals, bats may respond to climate change either by moving to different areas, adapting to new conditions, or going extinct. We identified a wide range of responses by bats to different climate change events, including positive, negative and neutral responses. Our review identified a strong prevalence of spatial (range) changes (Fig. 2E, F), including both range shifts and expansions. This may reflect a genuine tendency of bats to move in response to environmental change due to their relatively high mobility, but this may not apply to all species and regions. Evidence for extensive range expansion comes from ecologically plastic species, such as *Pipistrellus nathusii*, *P. kuhlii*, *H. savii* and *Tadarida brasiliensis*, which have expanded their ranges rapidly towards higher latitudes during the past few decades (Ancillotto *et al.*, 2016; Lundy, Montgomery & Russ, 2010; McCracken *et al.*, 2018; Uhrin *et al.*, 2016). By contrast, evidence of range losses was primarily derived from correlative model predictions rather than observational studies (Rebelo, Tarroso & Jones, 2010; Arumogum, Schoeman & Ramdhani, 2019; Razgour *et al.*, 2021).

The evolutionary adaptation of wildlife to climate change is hard to quantify because the data necessary to disentangle phenotypic plasticity and evolution are scarce or difficult to collect (Radchuk *et al.*, 2019). Razgour *et al.* (2019) highlighted the role of climate-adapted genotypes in species' responses to climate change. Bats can react rapidly to changing weather patterns by modifying their phenology, as has been documented by several studies. For example, during the last 22 years, *T. brasiliensis* has advanced summer migration and parturition timing by around 2 weeks and begun to overwinter in areas previously occupied exclusively during the summer months, presumably in response to climate change-related temperature increases (Stepanian & Wainwright, 2018). Such changes are common in vertebrates

[e.g. birds (Crick, 2004); amphibians and reptiles (Winter *et al.*, 2016)], particularly in temperate biomes where seasonal environmental conditions are less predictable and species inhabiting these areas may have evolved the flexibility to change their life cycles (Reed *et al.*, 2010). Phenological changes that seem adaptive to climate change in the short term may prove to be ecological traps if mismatches occur between the phenology of the bats and the key resources they rely on (e.g. water, arthropods or fruiting plants), with unpredictable effects on species persistence in a given area (Renner & Zohner, 2018; Stenseth & Mysterud, 2002).

Extinction is the most dramatic response of wildlife to climate change. Several modelling studies predict substantial range contractions, and a consequent increase in extinction risk, for bat species such as the African fruit bats *Epomophorus wahlbergii* and *E. angolensis* (Arumogum *et al.*, 2019) due to the disappearance of suitable habitat soon. Increased and unusual mortality rates have been reported for at least eight species [e.g. *Myotis nattereri* (Reusch *et al.*, 2019) and *Pteropus giganteus* (Dey, Roy & Chattopadhyay, 2015)] in response to extreme events directly associated with climate change, including heatwaves and wildfires. Extreme events can result in the loss of individuals due to direct mortality (e.g. heat stress, roost burning) or resource depletion (e.g. water availability). Such extreme events are not a new stressor for wildlife, but with climate change their frequency and intensity are predicted to increase (Ummenhofer & Meehl, 2017), placing wildlife under stronger selection and with the potential to lead to extinctions of endemic species with narrow or insular ranges (Leclerc, Courchamp & Bellard, 2018). There is increasing evidence that extreme events related to climate change have played a key role in the local extinction of several species, including bumblebees (Rasmont & Iserbyt, 2012) and corals (Sheppard, Sheppard & Fenner, 2020), and even to total extinction, as in the case of the Bramble Cay mosaic-tailed rat, *Melomys rubicola* (Waller *et al.*, 2017). Although the extinction of bat species or extirpation of bat populations due to climate change has yet to be documented, a recent study predicted dramatic population crashes and high extinction risk during the next few decades for the Mediterranean island-endemic Sardinian long-eared bat, *Plecotus sardus* (Ancillotto *et al.*, 2021).

(2) Gaps in the literature and future research

Obtaining more physiological and molecular data on species responses to climate change will be essential for improving the ability of models to predict future changes in distributions and abundance (Bozinovic & Pörtner, 2015; Urban *et al.*, 2016), but both fields are underrepresented in the bat literature. Only three studies included in this review addressed genetic responses to climate change. This reflects the general paucity of studies applying genomic and genetic approaches in climate change research (Pauls *et al.*, 2013). Threats to hotspots of bat genetic diversity under climate change could limit the evolutionary potential of these species and their ability to respond to environmental changes

(Razgour *et al.*, 2013). This highlights the importance of integrating genetic/genomic tools to assess species' long-term viability under climate change. Genomic tools not only provide information on losses of genetic diversity and changes in genetic composition but also on changes in effective population size and genomic vulnerability resulting from maladaptation to changing conditions (Hohenlohe, Funk & Rajora, 2021). Adaptive genetic variation associated with current local climatic conditions can be used to infer the sensitivity of populations to future climatic conditions, and therefore to guide conservation efforts (Razgour *et al.*, 2018). In addition, genomic tools can provide evidence of adaptive responses to climate change (Hoffmann & Sgrò, 2011), which is currently absent from the bat climate change literature. Initiatives to generate genomic databases for bats across the globe such as the Bat1K project (Teeling *et al.*, 2018) will facilitate future research into the genomic responses of bats to climate change.

Similarly, the physiological responses of bats to climate change have been neglected. The available information suggests that bats respond to increasing environmental temperatures by reducing their torpor bout duration (Stawski & Geiser, 2012) and increasing their metabolic rate (Humphries, Thomas & Speakman, 2002); heatwaves leading to heat stress often result in mass mortality (Pruvot *et al.*, 2019). Species are likely to respond differently to climate change based on their mobility and thermal tolerance, and therefore more research is needed on a wider range of bat species. The physiological impacts of climate change have been studied mostly through examining the effects of increased temperature and aridity, while other important factors, such as phenology, are often neglected (Feder, 2010); yet the latter is particularly relevant for bats that enter torpor/hibernation or migrate seasonally in response to changing food availability. Physiological traits can limit species distribution ranges because they influence the survival and reproduction of organisms under specific environmental conditions. Therefore, to predict responses to climate change accurately we need to have a full understanding of their physiological capacities (Chown *et al.*, 2010). The general paucity of data on bat physiological traits, even for well-studied species, is likely to impede our ability to improve model predictions and incorporate mechanistic modelling approaches.

Species-specific life histories associated with environmental constraints, like hibernation, can influence the way climate influences population dynamics. However, the influence of hibernation on responses to climate change is poorly understood. We know little about the plasticity of hibernation behaviours and the capacity of hibernators to respond to climate change. Bats face extreme energetic challenges during the winter period, when the highest mortality rates are recorded (Lentini *et al.*, 2015; Fritze & Puechmaile, 2018). Hibernators may be particularly susceptible to changes in seasonal climate as they have a relatively short activity season in which to reproduce and gain sufficient mass to survive the following winter. Hibernating bats

periodically arouse from hibernation, but arousals are energetically expensive and can account for around 75% of winter energy expenditure (Kayser, 1953). More frequent extreme temperature changes during winter could cause more premature arousals and an increased risk of water loss (Thomas & Geiser, 1997), which can result in dehydration or depletion of critical energy reserves to the extent that the bat is unable to survive the winter. Limited food availability when bats arouse from hibernation can also cause significant mortalities (Jones *et al.*, 2009). An understanding of natural activity patterns and whether and how seasonal climate variability can affect the fitness of hibernators will be essential to understanding bat responses to climate change.

Climate change is causing phenological mismatches between interacting species whose activity is triggered by different environmental stimuli. While this phenomenon has received substantial attention in migrating birds (e.g. Saino *et al.*, 2011; Visser, Holleman & Gienapp, 2006), fleshy-fruited plants (González-Varo *et al.*, 2021) and insect pollinators (e.g. Forrest, 2016; Memmott *et al.*, 2007), we found no studies investigating phenological mismatches in bats. Many tropical bats are nectarivorous and changes in flowering patterns (e.g. due to precipitation regime shifts) may affect their resource use throughout the year. Similarly, for temperate bat species that enter torpor or migrate to avoid thermal stress during the coldest season (Krauel & McCracken, 2013; Meyer, Senulis & Reinartz, 2016), changes in seasonal temperatures may create mismatches between bat emergence from torpor or return from migration and seasonal resource availability.

Changes in interspecific interactions under climate change may alter the ecosystem services provided by animals (e.g. Prather *et al.*, 2013). Whether the ecosystem services delivered by bats (e.g. pest suppression, pollination, seed dispersal) will be affected by climate change is unknown, yet very likely. Models predict that climate change will lead to a more than 75% reduction in the overlap between the ranges of the bat *Leptonycteris nivalis* and the *Agave* plants they pollinate during their annual migration, which may drive the bat to extinction and adversely affect the sexual reproduction and genetic variation of the pollinated plant (Gómez-Ruiz & Lacher, 2019). Similarly, insectivorous bat species are predicted to shift their ranges to higher latitudes to track suitable conditions, such as common pipistrelles in Europe (Smeraldo *et al.*, 2021). Their pest suppression ecosystem service would cease in the abandoned regions, with potentially negative consequences for agriculture, forests and human health. Yet, all these effects are currently hypothetical, and our review reveals the need for empirical studies.

Indirect effects of climate change on bats from interspecific interactions other than resource availability also have been understudied. Climate change may impact other species that naturally interact with bats, like their natural predators, or foster novel interactions with species that did not previously interact with bats. Climate change may modify interspecific competition between bats and other organisms (including other bat species), or generate completely novel competitive scenarios, the outcomes of which are hard to predict (Salinas-Ramos *et al.*, 2020). Impacts on bats from expanding

populations of introduced species (Welch & Leppanen, 2017) may also be exacerbated because many invasive species thrive in altered environments and may exploit conditions related to climate change (Gallardo & Aldridge, 2013).

A critical obstacle in assessing the response of bats to climate change is that reported evidence may represent a response to a short-term process, such as weather fluctuations, rather than to long-term climatic changes. Longitudinal studies reporting actual (field) evidence of responses by bats represent only a minor fraction of the total studies (12%), yet they are extremely valuable to provide clearer insights into the differential effects of short- and long-term fluctuations in environmental conditions. For example, changes in species distributions or phenology, which are critical to understanding and monitoring the effectiveness of adaptation, can be detected only *via* long-term surveys. However, most of the papers in our review that included time-series information consisted of comparisons between the recent or current distribution of bats and predicted changes in climatic suitability in future decades; only a few studies analysed the results of longitudinal studies lasting 10–30 years to investigate how species have already been impacted by climate change. Expanding or establishing systematic monitoring of the abundance and distribution of species and populations is a key priority to validate assessments of species' vulnerability to climate change. Monitoring efforts should be targeted at areas where the effects of climate change are likely to be most prominent to expand empirical knowledge about climate change impacts on wildlife and provide a more solid basis for improving future projections.

There is mounting evidence that the intensity, frequency and duration of extreme weather events are increasing around the globe (Allan *et al.*, 2021). Identifying the populations most at risk is important because such events can have a devastating impact on small populations, in particular for species with low reproductive and population growth rates, like bats. Populations in tropical, subtropical and arid regions are likely to be most at risk because tropical storms and droughts are predicted to become more frequent and severe (Sherwin *et al.*, 2013). O'Shea *et al.* (2016) reported 114 mass bat mortality events from abiotic factors, including heatwaves, droughts, extremely cold weather, flooding and storms, but no data were available from Europe, Africa or South America. We still do not know how heatwaves impact the reproductive success of bats. Collecting data on the effects of extreme weather events will be crucial for mitigating impacts and implementing conservation actions in high-risk areas. For example, creating artificial water sources to provide drinking water and foraging opportunities for bats in arid environments could support populations during drought events (Korine *et al.*, 2016).

V. CONCLUSIONS

(1) Several biological and ecological traits of bats may make them sensitive to climate change, yet there is surprisingly little

evidence on how these mammals respond to this anthropogenic environmental pressure. Our systematic review of published evidence for bat responses to climate change highlights important gaps in the literature and the way we study the impacts of climate change.

(2) The focus on correlative predictive modelling approaches (SDMs), whilst allowing the study of impacts on species at local-to-global scales, does not facilitate an in-depth understanding of behavioural, physiological, phenological and genetic responses.

(3) Longitudinal studies are particularly challenging in long-lived organisms like bats, especially given the short timeframe of most research grants. However, they are essential for tracking species' responses to climate change. Similarly, experimental approaches can provide concrete evidence for species responses but are challenging in long-lived species and species of conservation concern.

(4) Genomic approaches could help bridge the gap by providing a snapshot of both evolutionary adaptations and phenotypic plasticity (e.g. through differential gene expression analysis or epigenetic approaches), although such studies should be performed in addition to investigations of phenotypic responses in the field.

(5) More attention should be given to the interactions between climate change and other drivers that may impact bats, such as land-use change, biological invasions, or perturbations in interspecific and ecosystem-wide interactions between bats and their environment.

(6) Geographic and taxonomic disparities must be overcome to enable a more comprehensive view of biodiversity responses to climate change through strengthening research capacity in the Global South, where a large proportion of biodiversity is found.

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VIII. SUPPORTING INFORMATION

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

Fig. S1. Distribution of study duration (in years) extracted from studies ($N = 46$) about bats and climate change, after excluding modelling and palaeoclimatic works.

Table S1. List of the variables extracted from each paper analysed, with name and description.

Table S2. List of studies that met our inclusion criteria.

Table S3. List of studies excluded from analysis, with reasons for exclusion.

Table S4. List of bat species for which evidence regarding the impact of climate change was reported in the literature.

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