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The role of climate, water and biotic interactions in shaping biodiversity patterns in arid environments across spatial scales

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Abstract

Aim: Desert ecosystems, with their harsh environmental conditions, hold the key to understanding the responses of biodiversity to climate change. As desert community structure is influenced by processes acting at different spatial scales, studies combining multiple scales are essential for understanding the conservation requirements of desert biota. We investigated the role of environmental variables and biotic interactions in shaping broad and fine-scale patterns of diversity and distribution of bats in arid environments to understand how the expansion of nondesert species can affect the long-term conservation of desert biodiversity.

Location: Levant, Eastern Mediterranean.

Methods: We combine species distribution modelling and niche overlap statistics with a statistical model selection approach to integrate interspecific interactions into broadscale distribution models and fine-scale analysis of ecological requirements. We focus on competition between desert bats and mesic species that recently expanded their distribution into arid environment following anthropogenic land-use changes.

Results: We show that both climate and water availability limit bat distributions and diversity across spatial scales. The broadscale distribution of bats was determined by proximity to water and high temperatures, although the latter did not affect the distribution of mesic species. At the fine-scale, high levels of bat activity and diversity were associated with increased water availability and warmer periods. Desert species were strongly associated with warmer and drier desert types. Range and niche overlap were high among potential competitors, but coexistence was facilitated through fine-scale spatial partitioning of water resources.

Main conclusions: Adaptations to drier and warmer conditions allow desert-obligate species to prevail in more arid environments. However, this competitive advantage may disappear as anthropogenic activities encroach further into desert habitats. We conclude that reduced water availability in arid environments under future climate change projections pose a major threat to desert wildlife because it can affect survival and reproductive success and may increase competition over remaining water resources.

KEYWORDS

bats, desert biogeography, global change, interspecific competition, invasive species, niche overlap, species distribution modelling, water resources

1 | INTRODUCTION

Deserts and arid regions (annual precipitation/potential evapotranspiration <0.20; UNEP, 2009), together referred to herein as arid environments, are commonly perceived as low productivity ecosystems of low biodiversity value, and as a result have been neglected in terms of conservation resource allocation and underrepresented in the scientific literature. Yet they contain surprisingly high levels of biodiversity, including a quarter of terrestrial vertebrate species, high rates of endemism and species of highest conservation concern (Brito et al., 2014; Durant et al., 2012, 2014). The combination of high ambient temperatures, strong solar radiation, low humidity, limited and unpredictable precipitation and restricted water availability exert strong selective pressures on desert biota, leading to behavioural and physiological adaptations to cope with the harsh environmental conditions (Muñoz-Garcia et al., 2016; Noy-Meir, 1974; Randall, 1993). Precipitation, in particular, is an important driver of variation in selection across animals and plants globally, affecting fecundity, survival and selection on morphological traits, and therefore, variability in precipitation under future climate change may lead to changes in selection regimes (Siepielski et al., 2017). As such, desert biodiversity holds the key to understanding the genetic and physiological adaptations required to tolerate extreme temperatures and water stress under future climate change (Durant et al., 2014). However, the velocity of future temperature change is predicted to be particularly high in the desert biome (Loarie et al., 2009), and these already water-limited ecosystems are predicted to suffer from reduced water availability due to increased aridity (IPCC, 2014). Therefore, threats to desert biodiversity, and in particular desert-obligate species with low adaptive capacity, are only likely to increase (Vale & Brito, 2015).

Although deserts tend to display low alpha diversity, they can exhibit high beta diversity, and total number of species and mechanisms underlying community structure can vary widely among geographic regions (Kelt, Rogovin, Shenbrot, & Brown, 1999). Desert community structure is influenced by different processes acting at different spatial, temporal and taxonomic scales, ranging from broadscale biogeographic to fine-scale density-dependent processes. Across the deserts of North America, temperature is the main variable predicting desert bat phylogenetic community structure at the broadscale and in areas experiencing harsher climatic conditions (Patrick & Stevens, 2016). This corresponds to the general scale-dependent effect of environmental factors, whereby, climatic variables limit species ranges, while habitat variables and biotic interactions determine species distributions at finer spatial scales (Pearson & Dawson, 2003). As a result, studies addressing species distributions across regional or continental spatial scales often focus primarily on climatic variables (e.g., Munguía, Townsend Peterson, & Sánchez-Cordero, 2008), but this scale is insufficient to address patterns of habitat use within species ranges. Hence, studies combining a range of spatial scales are essential for understanding the ecological processes governing the distribution and diversity of desert biota.

Biotic interactions in the form of interspecific competition can limit the number of species that can stably coexist (Schoener, 1974) and are therefore thought to shape species' distributions and community assemblage not only at the local but also at the regional and even global scale (Wisz et al., 2013). The role of interspecific competition in structuring communities may be particularly pronounced in arid environments due to the scarcity of food and water resources (Noy-Meir, 1974). Interspecific competition was shown to play a major role in structuring garnivorous rodent communities in the deserts of North America (Bower & Brown, 1982) and to affect the density and patterns of habitat use of gerbils in the deserts of Israel (Abramsky, Rosenzweig, Elbaz, & Ziv, 2005). However, the influence of competition on species' distributions is reduced when species are able to coexist through specialisation on different resources (Godsoe, Murray, & Plank, 2015).

Species distribution models (SDMs; also known as ecological niche models) offer a robust framework for incorporating the effect of processes and variables acting at different spatial and temporal scales on limiting the potential distribution of species (Guisan & Thuiller, 2005). SDMs can help identify patterns of species richness in under-studied areas and therefore should be used to guide conservation priorities in arid environments where comprehensive survey efforts are often hampered by limited accessibility (Brito et al., 2014). This approach is particularly relevant for understanding distributions, biogeography and patterns of diversity of bats because their nocturnal behaviour hinders detectability and identification in flight, and as a result, occurrence data for many species are sparse, in particularly outside accessible regions and developed countries (Herkt, Barnikel, Skidmore, & Fahr, 2016). Yet bats have been underrepresented in early modelling studies, and despite wider adoption of these approaches in recent years, studies are still heavily biased towards Europe, where bat diversity is lower, but bat survey efforts are more extensive (Razgour, Rebelo, Di Febbraro, & Russo, 2016).

Bats are important contributors to mammalian biodiversity in arid environments (Carpenter, 1969). In some regions, such as the deserts in Israel, insectivorous bats comprise the most diverse group of mammals (Mendelsson & Yom-Tov, 1999). Their flight ability, adaptability and diversification into several trophic and ecological niches enabled bats to expand their distributions across much of the world's terrestrial ecosystems (Kunz & Pierson, 1994). However, within their ranges, bats are sensitive to the availability of suitable roosting and foraging habitats (Fenton, 1997). In arid environments, bat activity and diversity concentrates near water resources and their associated vegetation (Korine, Adams, Russo, Fisher-Phelps, & Jacobs, 2016). Despite physiological adaptations for reduced evaporative water loss rates (Muñoz-Garcia et al., 2016), access to free water and roosting are thought to be the main factors driving bat activity and reproductive success in arid environments (Adams & Hayes, 2008; Williams & Dickman, 2004). Yet thus far arid regions have been under-represented in studies examining the use of water resources by bats (Salvarina, 2016).

We investigate patterns of bat biogeography and conservation requirements in arid environments across spatial scales, using

a combination of species distribution modelling and statistical approaches. Focusing on the insectivorous bat community of the deserts of southern Israel, we compare the role of environmental variables and water availability versus interspecific competition in structuring broad and fine-scale patterns of distribution, diversity and activity. We hypothesised that the importance of climatic versus water and habitat variables varies with spatial scale.

First, at the broadscale, given that water is a limiting resource in arid environments (Noy-Meir, 1973) and that the activity of desert bats tends to concentrate near water bodies (Korine et al., 2016), we predicted that the distribution of bats in arid environments is determined not only by climate but also by the availability of water resources.

Second, we predicted that at the broadscale open-space foragers will be less affected by land cover variables than species that forage near vegetation or water resources.

Third, at the fine scale, we predicted that water and habitat characteristics will play more important roles than climate, and therefore, bat diversity and abundance will increase with pond size, water availability and vegetation density.

Fourth, we predicted that bat diversity will be higher in natural habitats, where desert-obligate species are more likely to be found, but bat abundance will be higher in anthropogenic sites because of the reliance of mesic bats on artificial water resources.

Finally, as interspecific competition was shown to affect local bat activity patterns in arid environments (Razgour, Korine, & Saltz, 2011), our second hypothesis was that interspecific competition plays an important role at both fine and broad spatial scales. We focus on competition between mesic bat species that recently expanded their distribution into arid environments following anthropogenic land-use changes, and desert bat species. First, we predicted that at the broadscale desert-obligate species will be more closely associated with more arid environments, while the distribution of mesic species will concentrate around water resources and anthropogenic habitats. Second, at the fine scale, we predicted that, when sympatric, competing bat species coexist through spatial resource partitioning, and therefore will be associated with different water body characteristics. Through testing these predictions, we aim to understand how the expansion of nondesert species can affect the biogeography and conservation of desert biodiversity.

2 | METHODS

2.1 | Study area

The study was carried out in the deserts of Israel in the Eastern Mediterranean, the Negev desert, the southern Judean desert and the Arava Rift Valley (Supporting information Figure S1). This area was identified as a hotspot of bat diversity in the Eastern Mediterranean, where the effects of future climate change are predicted to be most severe (Bilgin, Keşişoğlu, & Rebelo, 2012). The study area is bordered by the more mesic Mediterranean zone to the North and excludes the Gaza Strip, located to the north-west of the Negev desert along the Mediterranean coast. Land cover across the majority of the area is classified as bare based on global land cover maps (http://maps.elie.ucl.ac.be/CCI/viewer). Sparse vegetation cover is found along dry riverbeds (wadis) and around oases containing permanent springs and ponds, where both herbaceous and woody vegetation can be found year round. Rapid and extensive land-use changes have occurred in the deserts of Israel since the 20th century as a result of human population increase, redirection of water resources and the building of roads, towns and military installations (Yom-Tov & Mendelssohn, 1988).

The Negev desert includes several villages, surrounded by agricultural fields, and larger towns. Rainfall occurs mainly during winter with large temporal and spatial differences in total precipitation and its distribution, ranging from 70 to 220 mm in the Negev Highlands to 30–50 mm in the more arid south (Evenari, 1981). The Arava Rift Valley connects the Dead Sea to the Red Sea. It is a more arid desert with mean annual rainfall <50 mm (UNESCO, 1963). Scattered small villages with irrigated gardens and agricultural fields exist along the entire length of the valley. To the north of the Arava lay the mountainous terrain of the southern Judean desert, around the south-western shores of the Dead Sea. These two deserts are together referred to herein as the Arava desert.

2.2 | Broadscale analysis

The broadscale data set includes location records for 16 insectivorous bat species collected from 192 locations across the study area (Supporting information Figure S1), using a combination of acoustic recordings (methods described below) and trapping with mist nets, and based on data from the Israel Biodiversity Information System (www.biogis.huji.ac.il/). The data set includes records collected over different land cover types, including water bodies, dry river beds, urban areas and agricultural lands. The majority of our sampling efforts concentrated on the summer period because this is the period of highest bat activity and the breeding season (when bats are pregnant and lactating), and therefore the most important period for the bats. Consequently, our models primarily represent the summer, and to a lesser extent the spring distribution of the bats, with the exception of one species (*Pipistrellus rueppellii*) for whom most of the records were collected in the autumn. Although the locations were spread relatively evenly throughout the study area, to account for limited sampling in some areas, we included a bias layer, generated in ARCGIS 10.3.1 (ESRI) through creating 10 km buffers around all sampling locations. Species with a low number of location records ($N < 10$) were excluded from the study, resulting in a data set of 12 species, including desert-obligate species (found exclusively in deserts across their geographic range, as described in the IUCN Red List www.iucnredlist.org/), species found in both desert and temperate regions and species found in deserts and subtropical regions (Table 1). The echolocation calls of one of the study species, *Hypsugo ariel/bodenheimeri* (herein *Hypsugo ariel*), cannot be distinguished from the calls of *Pipistrellus pipistrellus*, a mesic species that was only recorded outside our study area, East of the Rift Valley (Benda et al., 2010), but

TABLE 1 Results of the species distribution models for the 12 bat species in the Negev and Arava deserts, including species classification based on their geographical range (IUCN range: D = desert-only, D-ST = desert and subtropical, D-Te = desert and temperate), number of location records included in the models (*N*), AUC scores, percent of the study area predicted to be suitable for the species (% area), and the percent contribution of the different environmental variables (Dist. = distance to variables)

Species	IUCN range	*N*	AUC train	AUC test	% area	Annual rainfall	Max summer temp	Temp cold quarter	Dist. water	Dist. wadis	Dist. urban	NDVI spring	Geology	Land cover	Land cover type
Asellia tridens	D	18	0.92	0.90	23.8	0.0	15.3	**52.8**	2.4	0.6	10.4	1.1	0.4	**17.0**	Water + sparse
Eptesicus bottae	D	75	0.88	0.83	15.0	4.5	**13.9**	0.4	**62.6**	12.6	1.5	0.3	4.1	0.0	
Hypsugo ariel	D	47	0.93	0.89	19.5	1.0	**26.3**	8.3	**49.9**	10.7	3.0	0.8	0.0	0.0	
Otonycteris hemprichii	D	53	0.88	0.83	8.9	4.1	0.3	**5.9**	**78.1**	3.2	4.7	0.1	3.3	0.2	
Plecotus christii	D	60	0.86	0.80	7.8	7.0	**8.1**	0.1	**74.4**	2.1	2.8	1.4	3.6	0.3	
Pipistrellus rueppellii	D-ST	39	0.91	0.87	21.1	6.5	12.3	**15.6**	**56.6**	6.4	1.0	0.0	0.9	0.7	
Rhinolophus clivosus	D-ST	55	0.86	0.81	24.9	2.0	0.1	1.4	**65.8**	3.3	1.1	**20.9**	5.2	0.1	
Rhinopoma hardwickii	D-ST	49	0.88	0.85	16.7	1.5	**29.0**	14.5	**27.8**	8.2	11.8	2.2	2.8	2.1	Sparse + bare
Rhinopoma microphyllum	D-ST	29	0.89	0.79	27.4	1.4	**23.6**	14.0	**41.4**	5.4	14.0	0.1	0.0	0.1	
Pipistrellus kuhlii	D-Te	81	0.84	0.79	8.4	2.4	1.6	2.6	**80.8**	3.1	**6.0**	0.8	1.5	1.1	All excluding bare
Rhinolophus hipposideros	D-Te	29	0.92	0.82	14.4	6.1	7.0	1.0	**57.3**	**28.1**	0.1	0.0	0.2	0.1	
Tadarida teniotis	D-Te	67	0.83	0.80	9.1	6.9	2.7	0.0	**53.8**	6.7	**22.1**	0.2	3.5	4.1	All excluding bare

Variables that have the strongest effect on model gain and contributed most to the model are highlighted in bold.

the two species can be easily distinguished morphologically. Even though *P. pipistrellus* was never recorded in our study area despite decades of bat captures, we took the precautionary approach and only included in the models capture location records for *H. ariel*.

To address our hypothesis that at the broadscale the distribution of bats in arid environments is determined not only by climate but also by water availability, we generated Species distribution models (SDMs) with the programme MAXENT 3.3.3k (Phillips, Anderson, & Schapire, 2006) to determine the potential distribution and ecological requirements of bats in our study area. Model resolution was set at 30 arc sec (~1,000 m). Models included a combination of climatic (downloaded from WorldClim: www.worldclim.org/), geological (obtained from Ben-Gurion University GIS resources) and land cover variables. Land cover variables included a land cover map (GlobCover2009 map, www.due.esrin.esa.int/globcover), reclassified into seven broad categories (arable, mosaic cropland, native vegetation, sparse vegetation, urban, bare, water bodies). Fine-scale habitat shape files of water bodies (including natural springs and artificial water bodies), wadis and urban areas (obtained from Ben-Gurion University GIS resources and Survey of Israel Mapping and GIS Publications: www.mapi.gov.il) were converted into distance variables in ARCGIS. Wadis are dry riverbeds covered with sparse vegetation throughout the year, but only contain running water in winter and early spring during occasional short flash floods and temporary ponds during spring. We also included seasonal Normalised Difference Vegetation Index (NDVI) variables for the spring period, when temporary ponds are present (March–May), and the dry, summer period (July–September). The NDVI variables were generated from the MODIS/Terra Vegetation Indices Monthly L3 Global 1 km (MOD13A3; downloaded from USGS https://lpdaac.usgs.gov/) through averaging layers from the years 2007 to 2010, corresponding to the period when most location records were collected. We removed correlated variables ($R > 0.75$, tested with ENMTOOLS 1.3 (Warren, Glor, & Turelli, 2010)) and variables that did not contribute to the models across species. The final models were run with three climatic variables, three distances to habitat variables, one vegetation index, a land cover and a geology variable (Table 1).

SDMs were run with 1,500 iterations using the cumulative model output. Model parameterisation (regularisation multiplier value and number of parameters) was tested using ENMTOOLS, based on Akaike Information Criterion corrected for small sample sizes (AICc). The best fit model across species included five features (linear, quadratic product, threshold and hinge) and a regularisation multiplier of 2. SDM performance and model fit were evaluated using fivefold cross-validations based on the Area Under the Receiver Operator Curve (AUC), a measure of model ability to distinguish between presence locations and background/pseudoabsences. Model AUC scores were compared to those of 100 null models, generated through resampling the annual rainfall layer in ENMTOOLS, to determine whether SDMs performed significantly better than random (Raes & ter Steege, 2007).

Model outputs were converted into binary maps, using the thresholding method that maximizes the sum of sensitivity and specificity. This thresholding method is particularly suitable for presence-only data and was found to outperform other methods in terms of its discrimination ability (Liu, White, & Newell, 2013). Individual species' maps were combined to identify patterns of bat diversity across the study area. We also compared individual species' models to test our predictions that open-space foragers will be less affected by land cover variables and desert-obligate species will be more closely associated with more arid regions.

To address the role of interspecific competition at the broad spatial scale, we calculated range and niche overlap between morphologically similar species thought to be potential competitors (Razgour et al., 2011), the nondesert (mesic) species, *Pipistrellus kuhlii*, and two desert species *Pipistrellus rueppellii* and *Hypsugo ariel*. *P. kuhlii* is thought to have recently expanded its distribution into the desert following human settlements (Yom-Tov & Mendelssohn, 1988). These three species are referred to as the *Pipistrellus* species because *H. ariel* was up until recently classified under the *Pipistrellus* genus (Benda et al., 2008). The phylogeny of western Palaearctic vespertilionid bats constructed by Mayer, Dietz, and Kiefer (2007) based on the mitochondrial DNA ND1 region places *Hypsugo ariel* and the *Hypsugo* genus as a sister group to the *Pipistrellus* genus, forming together a separate clade. In the Negev and Arava deserts, *H. ariel* shares the same foraging guild as *P. kuhlii* and *P. rueppellii* (Korine & Pinshow, 2004). The three species have similar diets consisting predominately of Diptera and Lepidoptera (Feldman, Whitaker, & Yom-Tov, 2000), have similar wing morphology and forage in similar habitats (Korine & Pinshow, 2004; Yom-Tov, 1993). Extent of range overlap between species was calculated in ARCGIS. We used Schoener's D index in ENMTOOLS to calculate niche overlap, and the niche identity test to determine whether species distributions are ecologically significantly different based on 50 randomised pseudo-data sets.

2.3 | Fine-scale analysis

To test the effect of water availability versus climate on bat diversity patterns at the fine spatial scale, we recorded bat activity over 63 natural and artificial water bodies (ponds) in the Negev and Arava deserts (Supporting information Figure S2) using acoustic detectors (AnaBat II, Titley Electronics, Australia). Ponds were sampled for a full night during spring (March–June), when temporary water bodies are still available, and summer (July-September), when all temporary water bodies have dried out. Of the 63 ponds, 34 were sampled in both seasons, 18 were only sampled during spring and 10 during summer. We recorded several environmental variables: pond type (natural or artificial), presence of water in the pond, presence of artificial lights around the pond, pond length, width, depth and area (measured following Razgour, Korine, & Saltz, 2010), vegetation cover around the pond (measured based om visual estimations, following the index in Korine & Pinshow, 2004), altitude, and minimum and maximum ambient temperatures (measured ±1°C with a dry mercury thermometer in a sling psychrometer [Bacharach]).

Acoustic recordings were analysed with ANALOOK (3.3f, Titley Electronics), using the available literature to identify calls to the

species level (Benda et al., 2008, 2010). We measured the number of bat species present, the activity of each species (number of passes over the entire night period, whereby a pass is defined as a sequence of bat calls), and overall activity (total number of passes of all bat species over the pond throughout the sampling night).

To identify the environmental variables affecting overall bat activity and species richness over ponds, we used generalised linear mixed effect models (LME4 1.1-12, R package; Bates, Maechler, Bolker, & Walker, 2016) with negative binomial and poisson distributions, respectively, to account for the repeat sampling of sites over the two seasons. After removing auto-correlated variables, we consecutively included environmental variables and tested their effect on model performance. The best fit models were selected based on AIC values, and variable significance ($p < 0.05$). Analysis of Variance (ANOVA) tests were used to determine whether AIC values of competing models were significantly different.

To test our prediction that, when sympatric, competing bat species coexist through spatial resource partitioning and therefore will be associated with different water body characteristics, we analysed separately the activity of the two desert *Pipistrellus* species and one nondesert *Pipistrellus* species that are thought to be potential competitors. Due to potential call overlap between *H. ariel* and *P. pipistrellus* (which was never captured in the study area), when analysing the *H. ariel* data set, we only included ponds within 10 km of known capture records of this species, as well as all ponds where the species was not recorded. We compared the analysis based on this reduced data set to an analysis based on the full data set and obtained identical results. This analysis was performed using generalised linear mixed effect models (LME4 1.1-12) with negative binomial distribution, following the same procedures as for bat activity and species richness.

To further test the effect of environmental variables, bat activity and the activity of potential competitors over the sampling ponds were plotted using the Canonical Correspondence Analysis (CCA) ordination method in PAST 3.11 (Hammer, Harper, & Ryan, 2001). We tested for significant differences between bat community composition over ponds grouped based on season, pond type, presence of water or desert (Arava versus Negev), using the one-way Analysis of Similarities (ANOSIM) test in PAST. The Bray–Curtis similarity index was used with 10^4 permutations to obtain significance values.

3 | RESULTS

3.1 | Broad-scale patterns of distribution and diversity

All SDMs had good model fit (AUC_{train} = 0.83–0.93, $AUC_{crossvalidations}$ = 0.79–0.90) and performed significantly better than random (null models AUC range: 0.55–0.74). The main environmental variables affecting habitat suitability for bats were distance to water bodies and maximum summer temperatures, but the latter was only important for some of the desert-obligate and desert-subtropical bats. Distance to wadis was an important variable in the *Rhinolophus hipposideros* model, while spring vegetation density was important for *Rhinolophus clivosus*. Distance to urban areas was an important variable for *Tadarida teniotis* and *P. kuhlii*. *Asellia tridens* was the only bat for whom habitat suitability in the study area was primarily determined by temperature variables, rather than the presence of water. Overall, habitat suitability for the majority of bats increased with proximity to water and at medium- to-high temperatures (Table 1; Supporting information Figures S3–S5).

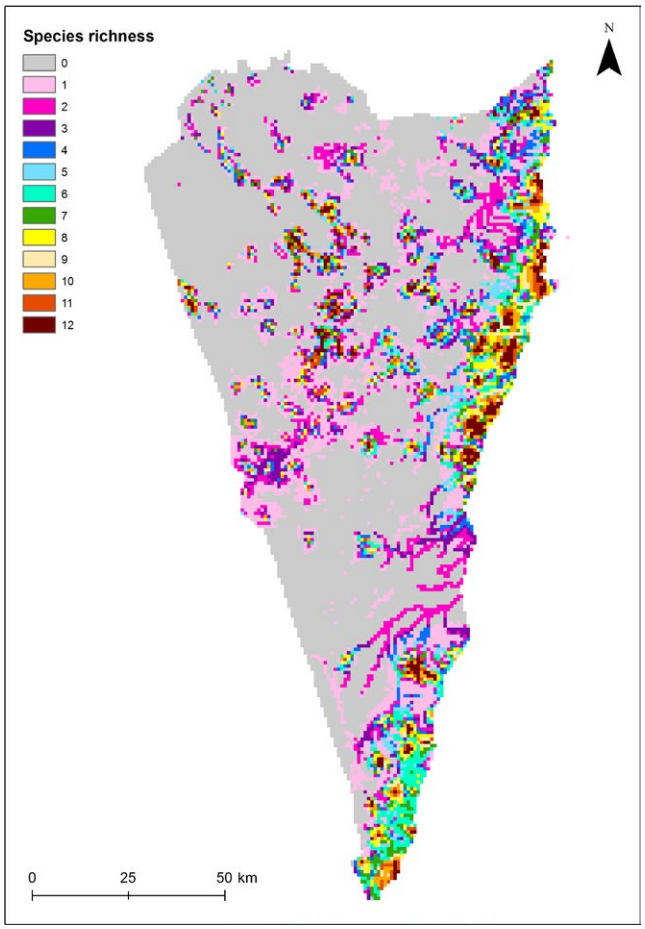

FIGURE 1 Bat diversity hotspots in the Negev and Arava deserts based on aggregated predictions of probability of occurrence based on the species distribution models of 12 bat species

Bat diversity was predicted to be highest along the northern Arava Rift Valley and around the south-western shores of the Dead Sea (Figure 1). This pattern was driven by the strong association of desert-obligate bat species, as well as the desert-subtropical species, *Rhinopoma hardwickii*, with the Arava desert (Figure 2). *Rhinopoma microphyllum* and *Rhinolophus clivosus* were predicted to have the largest extent of suitable area (27% and 25% of the study area, respectively), while *Plecotus christii* was predicted to have the most restricted range, with only 7.8% of the study area being suitable. The two mesic species, *T. teniotis* and *P. kuhlii*, had relatively low percent of suitable areas, and particularly lower habitat suitability along the Arava Rift Valley (Table 1; Figure 2).

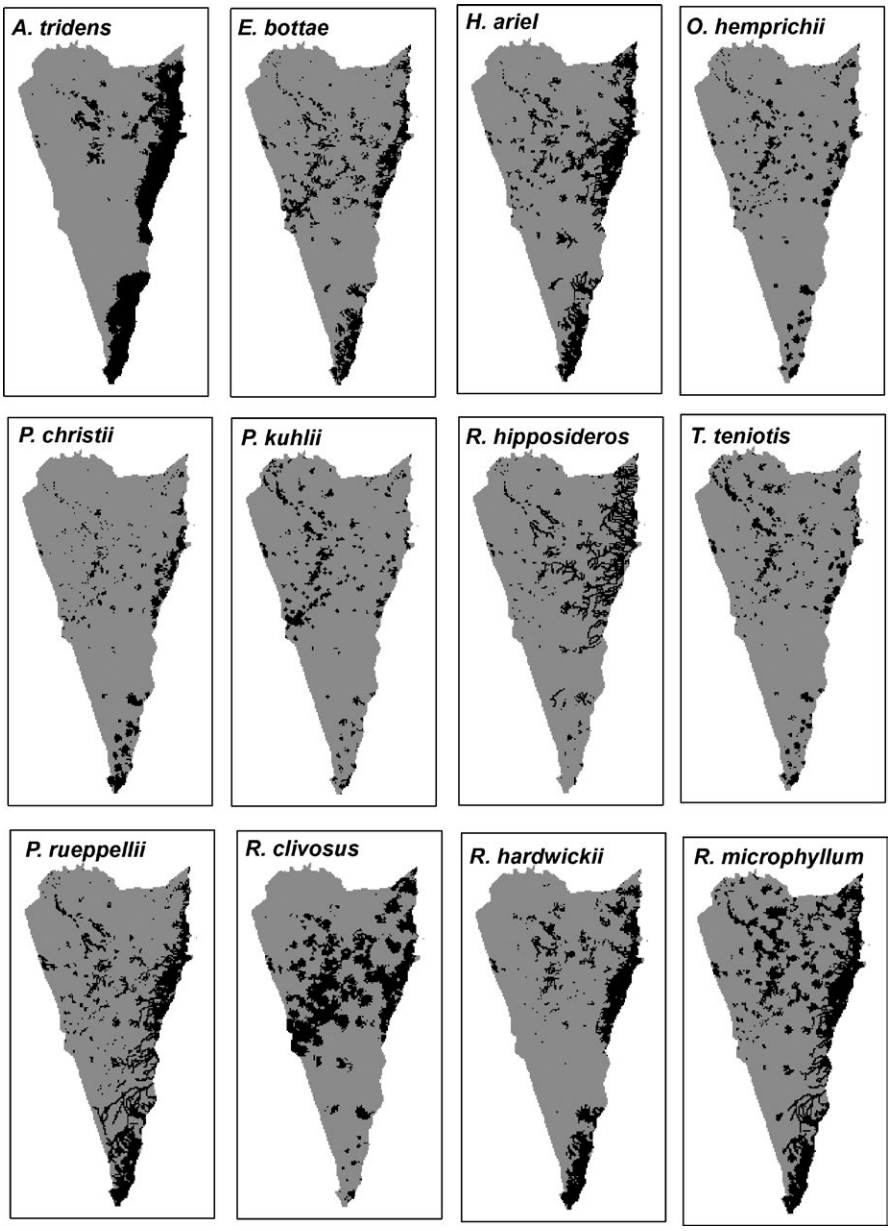

FIGURE 2 Predicted habitat suitability for bats in the Negev and Arava deserts, with grey representing unsuitable areas and black suitable. Starting at top left, the first five species are desert-obligates, followed by the three desert-temperate species, and the last four species are desert-subtropical bats

3.2 | Fine-scale patterns of diversity, activity and community composition

The best fit model (AIC = 1,300) showed that overall bat activity increased with pond depth (z = 2.259, p = 0.024) and was higher during summer (z = 3.380, p = 0.0007) and in ponds that contained water (z = 3.564, p = 0.0004; Figure 3; Supporting information Table S2). Bat species richness was found to be highest in the Arava desert (z = −2.417, p = 0.015), in ponds that contained water (z = 2.283, p = 0.022) and at lower altitudes (z = −2.454, p = 0.014, AIC = 443; Figure 3; Supporting information Table S3).

Bat community composition over ponds significantly grouped based on desert (ANOSIM R^2 = 0.664, p = 0.0001). Species were divided along the desert-temperature axis (accounting for 48% of the variation) versus the pond characteristics-season axis (20.5%), with two of the desert-temperature species, *P. kuhlii* and *T. teniotis*, grouping together and all the desert-obligate bats located on the other side of the pond characteristics axis (Supporting information Figure S6).

3.3 | Spatial overlap and partitioning between potentially competing species

At the broadscale, high extents of range overlap were found between *H. ariel* and *P. rueppellii* (83% of *H. ariel*'s range and 77% of *P. rueppellii*'s range), but extent of overlap was lower between these two species and the nondesert bat *P. kuhlii* (Supporting information Table S1; Supporting information Figure S7). Environmental niche overlap was highest between *H. ariel* and *P. rueppellii* (D = 0.832), while the niche of *P. kuhlii* was significantly different from that of its competitors (Table 2).

At the fine-scale, the activity of *P. kuhlii* was higher in ponds that contained water (z = 2.166, p = 0.0303) and increased with

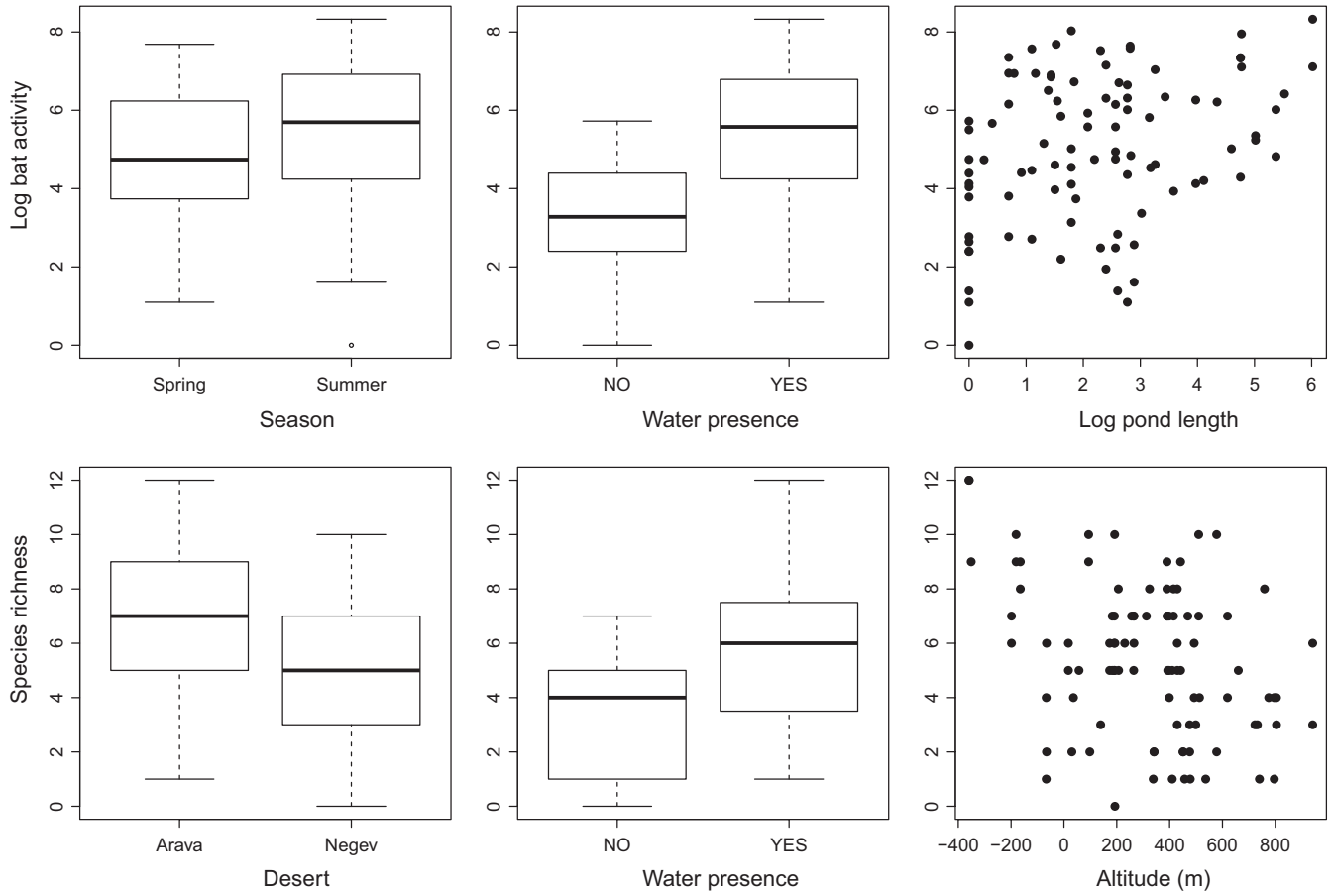

FIGURE 3 Environmental variables affecting bat activity and species richness over water bodies in the Negev and Arava deserts, based on the fine-scale data set. Graphs are only descriptive as they include all sampling sites not accounting for pseudo-replications

Species pairs	Niche overlap (Schoener's D)	Niche identity test range	99% CI niche identity test	Significant differences
Ha—Pk	0.690	0.722–0.927	0.806–0.851	Yes
Ha—Pr	0.832	0.709–0.920	0.812–0.853	No
Pk—Pr	0.697	0.699–0.861	0.774–0.814	Yes

TABLE 2 Niche overlap among potentially competing *Pipistrellus* species and the results of the niche identity test for significant differences (Ha: *Hypsugo ariel*; Pk: *Pipistrellus kuhlii*; Pr: *Pipistrellus rueppellii*)

pond depth ($z = 1.968$, $p = 0.049$, AIC = 388; Figure 4). All other variables did not affect its activity (Supporting information Table S4). The activity of *H. ariel* was highest in ponds that contain water ($z = 2.337$, $p = 0.0019$) and it increased with minimum temperatures ($z = 4.059$, $p < 0.0001$) and decreased with altitude ($z = -1.999$, $p = 0.045$, AIC = 337; Figure 4). Other significant variables were desert type and pond length (Supporting information Table S5). The activity of *P. rueppellii* increased with pond length ($z = 3.317$, $p = 0.0009$) and was higher in the Arava desert ($z = -2.121$, $p = 0.034$, AIC = 246; Figure 4). Other variables that significantly correlated with the activity of *P. rueppellii* included pond type, altitude and ambient temperatures (Supporting information Table S6). Unlike its two competitors, *P. rueppellii* was never recorded over ponds without water.

The canonical correspondence analysis separated the three potentially competing *Pipistrellus* species along the two axes in the environmental space. *H. ariel* and *P. rueppellii* were located at the Arava desert end of the temperature-desert axis and *P. kuhlii* at the other, while *H. ariel* and *P. rueppellii* were separated along the pond characteristics axis (Supporting information Figure S6).

4 | DISCUSSION

4.1 | Effect of environmental variables at broad versus fine spatial scales

Using a combination of species distribution modelling and statistical model selection procedures, we identified factors limiting the diversity, distribution and patterns of habitat use of bats in arid environments across multiple spatial scales. At the broadscale, both climate and water availability play an important role in determining bat biogeographical patterns. Habitat suitability for desert bats

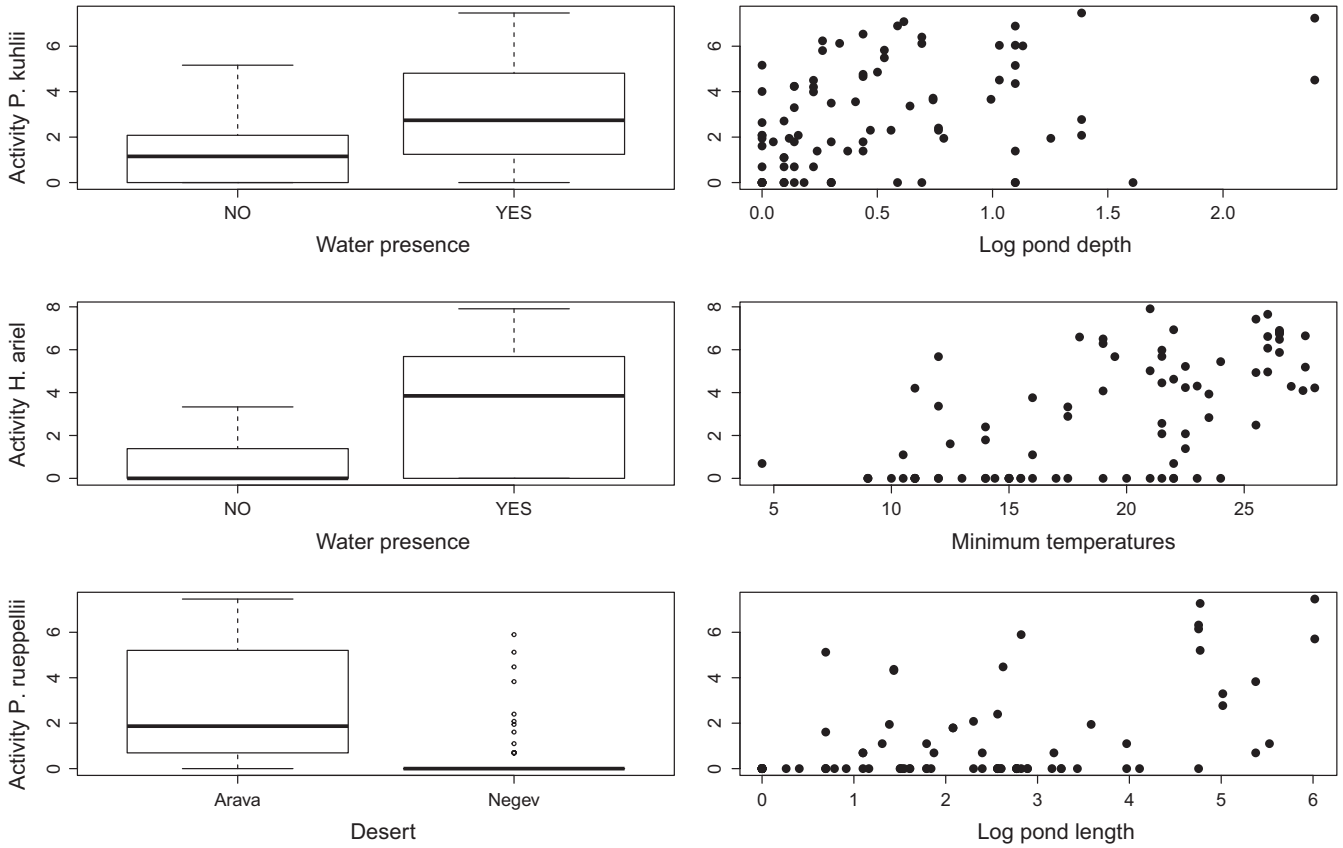

FIGURE 4 Environmental variables affecting the activity of the three *Pipistrellus* species (*P. kuhlii*, *P. rueppellii* and *Hypsugo ariel*), over water bodies in the Negev and Arava deserts. Graphs are only descriptive as they include all sampling sites not accounting for pseudo-replications

during the summer and spring periods, when the great majority of our location records were collected, is primarily a function of proximity to water bodies and high summer temperatures. Temperatures and distance to rivers and sparse vegetation were also identified as the main variables affecting the distribution of mammals in the arid western Sahara-Sahel region (Vale et al., 2016). Similar to our study, Vale et al. (2016) found that most modelled taxa responded in a similar manner to the same set of environmental variables. These analogous responses likely reflect the general concentration of biodiversity around scarce water resources in arid environments (Brito et al., 2014), where water availability plays a major limiting role for flora and fauna (Noy-Meir, 1973, 1974). The importance of water resources in determining the broadscale distribution of bats is not restricted to arid environments. Across Africa, bat species richness was found to increase with proximity to streams and lakes (Herkt et al., 2016).

Despite adaptations for water conservation through reduced evaporative water loss rates (Muñoz-Garcia et al., 2016), bats in arid environments rely on access to open water for both drinking and foraging (Razgour et al., 2010), and consequently, their distribution is closely associated with water resources (Korine et al., 2016). Previous studies highlighted the importance of water bodies and natural vegetation along wadis for bat species richness in the Negev Desert (Korine & Pinshow, 2004), and wadis with dense green acacia stands for bats in the Arava desert (Hackett, Korine, & Holderied, 2013). In the Simpson Desert, Australia, although the activity of all bats regardless of their foraging mode concentrates around water bodies, bats are thought to be more limited by roost availability than water (Williams & Dickman, 2004). This is not likely to be the case in our study area due to the topography of the deserts and the extensive availability of rock crevices where most of the bats roost.

The strong association of the majority of nonmesic bat species with high temperatures is driving the broadscale patterns of bat diversity and the concentration of species richness hotspots along the warmer Arava Rift Valley and Dead Sea shores. These patterns are also mirrored in the eastern bank of the Rift Valley (Benda et al., 2010). The higher predicted bat diversity in the Arava is not surprising given that previous studies recorded 17 bat species around the Dead Sea area (Yom-Tov & Kadmon, 1998) versus only 12 in the Negev desert (Korine & Pinshow, 2004). Only the two mesic species, *T. teniotis* and *P. kuhlii*, have a lower probability of occurrence along the Arava Rift Valley, which is the more arid of the two deserts. Future work can investigate these patterns further through considering temporal (seasonal) variations in species distributions.

At the fine spatial scale, although water availability plays an important role, patterns of habitat use are also determined by broadscale patterns of distribution and climate, with bat activity being highest in the Arava desert and during summer when temperatures

are highest. Bat species richness and activity are highest over ponds that contained water and at deeper ponds, mirroring the strong associations of nearly all species with water resources in the broadscale analysis. Contrary to our predictions, water body type neither affects bat diversity nor activity, highlighting the general importance of scarce water resources in arid environments, regardless of whether they are natural or anthropogenic.

Desert water bodies offer an important source of open free water. Although desert-obligate species have a lower frequency of drinking than mesic species that expanded their distribution into arid environments (Razgour et al., 2010), access to drinking water is still important because it can affect the reproductive success of desert bats (Adams & Hayes, 2008). Many bat species recorded over water resources depend on aquatic prey (Salvarina, 2016). Desert water bodies and their surrounding vegetation host a high concentration of insects and are therefore an important foraging habitat for bats. Many of the nonmesic bats filmed over ponds in the Negev Desert by Razgour et al. (2010) visited ponds to forage rather than drink. Desert bats, including *P. rueppelli*, *H. ariel* and *R. clivosus*, forage over ponds on emerging chironomids (Benda et al., 2010; Feldman et al., 2000), indicating that water availability is also important for the foraging success of bats in arid environments.

4.2 | Relating biogeographical patterns to species ecology

P. christii, a cluttered-space forager that glean prey from the vegetation (Arlettaz et al., 1995), was predicted to have the most restricted suitable range, reflecting its strong associations with the more arid Arava desert and its tendency to forage among vegetation, which concentrates around water bodies and wadis. On the other hand, *R. clivosus*, a widely distributed species that is found over a variety of habitats, from arid to savanna and woodlands (Monadjem et al., 2017), was predicted to have one of the largest suitable ranges.

Of the more mesic species, the distribution of both *T. teniotis* and *P. kuhlii* is closely associated with water bodies and urban areas. Water bodies correspond to the high frequency of drinking in these mesic species (Razgour et al., 2010), in particular in *T. teniotis* that has higher evaporative water loss rates than desert-adapted species (Marom, Korine, Wojciechowski, Tracy, & Pinshow, 2006). Even in more mesic environments, the reproductive success of *P. kuhlii* was shown to increase with availability of permanent water resources (Ancillotto, Tomassini, & Russo, 2016), suggesting that water has a particularly important effect on the distribution of this species. Associations with urban areas reflect the tendency of *T. teniotis* to roost in man-made structures (Dietz, von Helversen, & Nill, 2009) and to mainly forage over artificial habitats, like towns and adjacent agricultural plantations (Hackett et al., 2013). However, in line with our predictions, being an open-space forager that captures moths in flight high above the ground (Norberg & Rayner, 1987), this species is associated with all land cover types, suggesting it is a habitat generalist in arid environments, as has been shown to be the case in the Mediterranean parts of its distribution (Russo & Jones, 2003). Range suitability for the other open-space forager, *R. hardwickii*, was primarily a function of high summer temperatures, rather than land cover or habitat variables, reflecting its distribution along the warmer Rift Valley (Mendelsson & Yom-Tov, 1999), and likely its more limited reliance on access to water bodies for drinking (Vogel 1969).

4.3 | Effect of interspecific competition between desert and mesic species

Broadscale patterns of distribution indicate a high extent of both range and environmental niche overlap among species identified as potential competitors. Range overlap was particularly high among the desert-obligate *H. ariel/bodenheimeri* and the desert-subtropical bat, *P. rueppellii*, and the two species have a similar environmental niche. Indeed the distribution of both species is closely associated with the warmer Arava desert, and both have reduced activity in the Central Negev Highlands for part of the year (Korine & Pinshow, 2004), hence the strong effect of high temperature on their modelled habitat suitability. Similarly, in a semiarid region of Spain, sympatric *Pipistrellus* species, including *P. kuhlii*, were shown to have high degree of range overlap and similar habitat preferences (Lisón & Calvo, 2013). However, in arid environments, we found that *P. kuhlii* has a significantly different environmental niche from sympatric *Pipistrellus* species, likely because this mesic species is less adapted to the harsher arid environments than its desert specialist competitors (Muñoz-Garcia et al., 2016). Similarly, Santos et al. (2014) show that cryptic bat species pairs with similar biogeographical affinities tend to have higher extents of niche overlap than those with different biogeographical associations.

Despite similar broadscale distributions, at the fine scale, within their potential suitable range, *H. ariel/bodenheimeri* and *P. rueppellii* partition their use of water resources, being separated along the pond characteristics axis. The activity of *P. rueppellii* increases with pond length, indicating it preferentially uses larger ponds, and is higher over artificial ponds, while the activity of *H. ariel/bodenheimeri* is more strongly associated with the presence of water in general and lower elevations. Similarly, differential patterns of fine-scale habitat selection were suggested as potential mechanisms of resource partitioning among sympatric temperate *Pipistrellus* species, whereby *P. pygmaeus* is associated with aquatic habitats, while *P. pipistrellus* with woodland edge and tree lines (Nicholls & Racey, 2006). Differential use of foraging microhabitats was also shown to act as a mechanism of coexistence among sympatric desert rodents that shift their patterns of habitat use following the removal of competitors (Price, 1978).

5 | CONCLUSIONS

We identified factors limiting the distribution, diversity and patterns of habitat use by bats in arid environments at multiple spatial scales. The importance of temperature across spatial scales reflects the higher diversity and activity of desert-adapted species in warmer

and more arid deserts. The effect of water availability on both fine and broadscale patterns of diversity and distribution of bats and other mammals (Vale et al., 2016) in arid environments highlight the importance of water resources and year-round water availability for desert wildlife. We show that coexistence in arid environments among potentially competing species that have high extents of range and niche overlap at the broadscale may be facilitated through spatial partitioning of water resources at the fine scale. Adaptations to drier and warmer environmental conditions and differences in their ecological niches allow desert-obligate species to prevail in more arid environments despite the expansion of nondesert species. However, this competitive advantage may disappear as anthropogenic activities encroach further into desert habitats.

The strong associations of desert wildlife with water resources is worrying given the forecasted decrease in availability of free water in arid environments under future climate change scenarios (IPCC, 2014), and the predicted consequent changes in species interactions (McCluney et al., 2012). Reduced water availability in arid environments can affect the survival and reproductive success of not only bats (Adams & Hayes, 2008), but also other desert mammals (Christian, 1979; Vale & Brito, 2015), birds (Coe & Rotenberry, 2003; McKechnie & Wolf, 2010), and more immediately, aquatic fauna. Moreover, intra- and interspecific competition for drinking and foraging space above remaining water bodies are likely to increase (Hall, Lambert, Larsen, Knight, & McMillan, 2016), further affecting both aquatic and terrestrial desert animals that rely on scarce water resources. Our study shows that of particular concern is the potential competitive advantage of nondesert, mesic species that expanded their distributions to arid environments following human settlements and irrigated agriculture, because they are more likely to benefit from increased artificial water availability in anthropogenic habitats. Therefore, only through understanding species ecological requirements and interactions among species in arid environments across spatial scales will we be able to develop appropriate adaptive conservation management strategies in face of global environmental changes.

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DATA ARCHIVING

Maxent species distribution modelling outputs and R scripts for running the GLMMs available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.f8c0c8h.

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BIOSKETCH

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SUPPORTING INFORMATION

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

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