

RESEARCH ARTICLE

Cool shade and not-so-cool shade: How habitat loss may accelerate thermal stress under current and future climate

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Abstract

Worldwide habitat loss, land-use changes, and climate change threaten biodiversity, and we urgently need models that predict the combined impacts of these threats on organisms. Current models, however, overlook microhabitat diversity within landscapes and so do not accurately inform conservation efforts, particularly for ectotherms. Here, we built and field-parameterized a model to examine the effects of habitat loss and climate change on activity and microhabitat selection by a diurnal desert lizard. Our model predicted that lizards in rock-free areas would reduce summer activity levels (e.g. foraging, basking) and that future warming will gradually decrease summer activity in rocky areas, as even large rocks become thermally stressful. Warmer winters will enable more activity but will require bushes and small rocks as shade retreats. Hence, microhabitats that may seem unimportant today will become important under climate change. Modelling frameworks should consider the microhabitat requirements of organisms to improve conservation outcomes.

KEYWORDS

biophysical modelling, climate change, land use, management, refuge, rocks, thermoregulation, vegetation

1 | INTRODUCTION

The lives of organisms are fundamentally dictated by daily and seasonal fluctuations in solar radiation, temperature, and other abiotic and biotic factors (Wieser, 1973). These fluctuations, along with heterogeneity within habitats (i.e. microhabitats), provide opportunities for organisms to coexist (Hutchinson, 1978) and make use of natural shifts in environmental conditions to optimize fitness (Besson & Cree, 2010; Hertz, 1992; Magnuson et al., 1979; Scheers & Van Damme, 2002). Yet, current models of climate effects simplify habitat parameters, overlooking the importance of temporal and spatial heterogeneity. In our modern era of accelerating habitat loss and climate change, we urgently need field data on microhabitat

quality and use by organisms over daily and seasonal scales, as well as process-based theoretical frameworks to understand how diverse microhabitats promote ecological systems (Hantson et al., 2021; Williams et al., 2022; Williams & Newbold, 2020, 2021). With these capabilities, we will be able to accurately predict the impacts of habitat degradation or restoration on populations and form appropriate management plans (Webb & Shine, 1998).

Currently, most ecological models are parameterized with simplified microhabitat characteristics that do not capture the diversity of microhabitats in natural landscapes and are therefore too coarse to provide useful predictions. Habitats with myriad object types and sizes supply animals with a greater range of thermal opportunities, from which they can select as they search for food,

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mating partners, or defend territories (Ayers & Shine, 1997; Garcia & Clusella-Trullas, 2019; Kerr & Bull, 2004; Lagos et al., 1995; Levy et al., 2012; Robertson & Weatherhead, 1992). Increasingly, models of the possible impacts of climate change account for thermoregulatory behaviours by enabling simulated animals to shuttle between open and shaded microhabitats (Buckley, 2008; Carlo et al., 2018; Kearney, 2013; Levy et al., 2015; Levy, Buckley, et al., 2016a; Maino et al., 2016; Pincebourde et al., 2016; Sears et al., 2011). However, most of these models assume that shade, which is critical for dry-skinned ectotherms under warming climates (e.g. Kearney, 2013; Sears et al., 2011; Sunday et al., 2014), is supplied only by vegetation cover during activity (e.g. Kearney et al., 2009; Levy et al., 2015; Levy, Buckley, et al., 2016a), and therefore unnaturally reduce microclimatic diversity. By incorporating different types and sizes of microhabitats in our models, we can more accurately predict the use of microhabitats by species of concern, understand how habitat loss can affect microclimate diversity, and identify the microhabitat features that will be most important for species under future climate scenarios.

Microhabitat diversity is likely to be particularly important for ectotherms, which depend on external temperatures to maintain preferred body temperatures, as each supplies a different microclimate and thus opportunity for thermoregulation (Huey et al., 2012). Diurnal lizards, for example, shuttle among shaded and open spaces over the day to optimize body temperature (Huey & Slatkin, 1976). Here, we built a novel modelling framework based on diverse, realistic microhabitats, and show how it can be applied to predict the impacts of habitat loss and climate change on desert ectotherms. We focus on vegetation and rock cover, two microhabitats that offer shade cover, as well as protection from predators and competitors. First, we incorporated habitat degradation as loss of vegetation and/or rock cover, which occurs via denuding of landscape, agriculture, mining, urbanization, camping sites, trailing, and more (Michael et al., 2008, 2021; Sasaki et al., 2015; Shine et al., 1998; reviewed by Fitzsimons & Michael, 2017; Giam, 2017; Scanes, 2018). We focused our model on thermoregulation and parameterized the model by measuring the thermal conditions in six shaded desert microhabitats within the Judean Desert that varied in the size of bushes and rocks, and by recording the field and preferred body temperatures of diurnal lizards captured from these areas. We focus on aboveground activity and therefore did not include other possible sources of shade, such as burrows.

We used our model to predict how climate warming and loss of vegetation or rocks would affect lizards' opportunities for thermoregulation, predicting that degradation of shaded microhabitats would decrease activity times and thermoregulation accuracy, even when lizards could still access shade provided by other microhabitats. We also predicted that, in response to climate warming, lizards would gradually shift activity towards novel shaded microhabitats. For simplicity, we did not incorporate shifts in precipitation regimes that can occur under climate change (Melillo et al., 1993). Overall, we found that a diversity of shaded microhabitats is fundamentally important for ectothermic thermoregulation—with some types

of microhabitats crucial currently and others potentially more important in future climate scenarios. Hence, in simplifying shade conditions, current ecological models miscalculate the thermal opportunities of organisms and thus may misdirect conservation strategies.

2 | MATERIALS AND METHODS

2.1 | Modelling microhabitat selection by active lizards

We modelled microhabitat selection by ectotherms based on a diurnal desert lizard that chooses to position itself among thermal opportunities in its natural habitat. In the model, we simulate hourly microclimates across rock- or bush-shaded microhabitats, and the lizard can select to be active in a particular microhabitat if its operative temperature there is within the range that enables activity. If activity is possible in more than one microhabitat, then the lizard chooses the microhabitat that maximizes thermal accuracy (i.e. minimizes DE, the difference between a preferred temperature and the operative temperature in the microhabitat, where values closer to zero represent better accuracy, Hertz et al., 1993). We simplified the model by assuming that lizards use a sit-and-wait strategy, choosing only one microhabitat per time step (i.e. 1 h)—although in nature many animals thermoregulate by shuttling between different microhabitats. Shuttling behaviour can be easily enabled in our model by decreasing temporal scale. In cases where none of the microhabitats enable activity, the model assumes the lizard is resting in a thermally suitable burrow (see flowchart in Figure S1).

Using this model, we then investigated the possible consequences of habitat loss and/or climate change on lizard activity. To simulate habitat loss, we either removed rock or bush cover from the accessible microhabitats and reran the model to predict how and when lizards would operate in each scenario. To simulate different magnitudes of climate change, we added 0.5°–6°C to field-measured air and ground temperatures (both shaded and open microhabitats) in summer and winter. Although this simplifies the thermal profiles expected with climate change (e.g. minimal and maximal temperatures may not uniformly change, Davy et al., 2017; Dillon et al., 2010), this assumption enabled us to explore the relative effect of temperature increases on microhabitat selection. To predict how future warming may affect lizards between 2080 and 2100, we estimated climatic shifts in temperature by assuming the ssp585 emission scenario (Meinshausen et al., 2020). We used predictions from global circulation models in WorldClim 2.1 (Fick & Hijmans, 2017) for our analysis.

To run the model, we developed an hourly dataset of microclimates, and calculated the operative body temperatures of a lizard (i.e. the steady state temperature in a particular microclimate, Bakken, 1992) in each of our seven microhabitats (i.e. open/unshaded or shaded by small, medium, or large rocks or bushes) for each hour. To summarize the model's results, we calculated the percentage of time that lizards selected each microhabitat, as well as the

mean thermal accuracy for each microhabitat when it was selected. We used the difference between the operative temperature and the preferred temperature (DE, Hertz et al., 1993) as a thermoregulation criterion. Negative and positive values represent operative temperatures below or above the preferred body temperature, respectively. This criterion allowed us to differentiate between activity at the warmer part of the thermal performance curve, where performance decreases rapidly with increasing temperatures. We repeated analyses under conditions for habitat loss and climate warming severity, as described above.

2.2 | Model parameterization

We parameterized the model using the small-spotted lizard *M. bahaeldini* as a model ectotherm (see below); we measured lizards' preferred body temperatures in the field and laboratory and the microclimate conditions (ground temperatures and meteorological data) in a natural area where the lizard is found. We then used a biophysical model of heat transfer, as described in Fei et al. (2012), to calculate operative temperatures for each hour of the dataset. A detailed description of the biophysical model, list of parameter values, and validation results are shown in Table S1.

2.3 | Model area

To parameterize the model, we collected field data in the Judean Desert in Israel (31°28'N, 35°10'E), which is bounded to the east by the Dead Sea, ~400m below sea level. Flora is predominantly perennial shrubs and annual grasses, which vary in density (Moncaz et al., 2012). Our collection and measurements efforts focused on two main sites in the region: Parking Tse'elim River (31°21'04.8"N 35°21'11"E) and Nahal Mishmar (31°22'51.1"N 35°22'52.9"E). Parking Tse'elim River is rocky, with very sparse vegetation, while Nahal Mishmar has much denser vegetative cover (i.e. mostly bushes and a few *Acacia raddiana* trees).

Temperatures in the Judean Desert vary substantially between summer and winter, and microclimates play a major role in the ecology and physiology of animals. During summer, mean ground temperatures in the open range from 30°C in the early morning to 44°C at noon; cover offers substantial thermal shelter—maximal ground temperatures reach only 37°C under rocks (Levy, Dayan, et al., 2016). Winter temperatures are cooler, with ground temperatures reaching 27°C in the open and 25°C in the shade (Levy, Dayan, et al., 2016).

2.4 | Microclimate measurements

To measure the ground temperatures that lizards would experience across microclimates, we placed 24 miniature iButton temperature loggers (DS1923; accuracy: $\pm 0.5^\circ\text{C}$, resolution: 0.5°C ; Maxim Integrated) under 12 rocks and 12 bushes (2 sites \times 2 microhabitats

(rock and bush) \times 3 sizes (large, medium and small) \times 2 replications = 24 loggers). The sizes of individual thermoregulatory shelters (i.e. rocks or bushes; length \times width \times height) were defined as small ($<40\text{cm}^3$), medium ($40\text{--}100\text{cm}^3$), and large ($>100\text{--}500\text{cm}^3$). See Supplementary Information S1 for examples of shelters in the Judean Desert (Figure S2). iButtons were placed in the eastern part of each microhabitat to avoid biased recording of temperatures from different angles (Franzmeier et al., 1969; Schwarz et al., 2022) and were constantly in the shade. We recorded the ground temperature under each shelter every hour during the summer of 2020 (July–September 2020) and the winter of 2022 (January–February 2022). Summer and winter are the most thermally challenging seasons in the Judean Desert.

During the same period, we placed a mobile meteorological station (MaxiMet GMX501 Compact Weather Station, GILL) in the Tse'elim River study site to record the weather conditions in the open (e.g. solar radiation, air temperature, ground temperature, wind speed, wind direction, and relative humidity) at 10-min intervals. Although the station was periodically offline due to battery issues in the summer field season, we were still able to record 55 full days of meteorological data.

2.5 | Model animal

We chose the small-spotted lizard, *Mesalina bahaeldini*, as a model species for our simulation because its activity is limited by warm and cold temperatures in both summer and winter and it depends on rocks and bushes for thermoregulation (Stark et al., 2022). During inactivity hours, lizards can be found resting below rocks or inside burrows (Orr et al., 1979). The species belongs to the family Lacertidae, with adult body sizes (snout vent length, SVL) of males and females ranging between 36–51 and 40–53 mm, respectively (Goldberg, 2012), and with a body mass of 0.6–3.2 g when SVL $>31\text{mm}$ (Orr et al., 1979). These lizards are diurnal and terrestrial, and forage for insects (mainly ants and termites) on the ground near vegetation and rocks (Orr et al., 1979). This oviparous species lays eggs during the months of May and June, and the neonates hatch in July (Orr et al., 1979). The species can be found across most desert habitats in the region, including the southern Sinai Mountains, the Israeli Negev and Judean Deserts, the West Bank, Jordan, and northern Saudi Arabia (Sindaco et al., 2018). The species is preyed upon by scorpions (e.g. *Buthus (Leiurus) quinquestratus*), centipedes (*Scolopendra* sp.), reptiles (e.g. *Coluber rogersi*), and birds (e.g. *Lanius excubitor*) (Orr et al., 1979).

2.6 | Animal field body temperature and preferred body temperature

We conducted measurements of field and preferred body temperatures in both summer and winter, to capture seasonal variations in these parameters (Angilletta, 2009) due to differences in climate,

life history, body condition, and hydration levels (Orr et al., 1979). During winter (December 2019–February 2020) and summer (June–September 2019), we hand-captured 57 *M. bahaeldini* from our two study sites, Nahal Mishmar (summer: $n=11$, winter: $n=15$) and Parking Tse'elim River (summer: $n=16$, winter: $n=15$). Upon capture, we immediately measured each lizard's field body temperature by inserting a contact thermometer (Hibok 18, precision: 0.1°C , accuracy: $\pm 0.2\%$), fitted with a k-type thermocouple probe, a few millimetres into the cloaca of the animal. We then brought the lizards to the Zoological Research Garden at Tel Aviv University to experimentally record preferred body temperatures during daytime, using a thermal gradient between approximately 20 and 60°C . To validate that free-ranging lizards in our experiment were thermoregulating near their preferred body temperatures, we compared the preferred temperatures to field body temperatures. See Supplementary Information S1 for a detailed description of the experiment and comparison between field and laboratory body temperatures.

3 | RESULTS

3.1 | Preferred body temperatures

We examined the preferred body temperatures of 56 individual lizards in both field and laboratory settings (note: one lizard died at the start of the experiment). In winter, lizards' preferred body temperatures (T_{pref}) ranged from 28.7 to 35.3°C (80% CI), with an average of $31.7 \pm 2.6^{\circ}\text{C}$ (mean \pm SD); in the summer, T_{pref} ranged from 32.4 to 37.8°C (80% CI) with an average of $35.3 \pm 2.3^{\circ}\text{C}$ (Figure 1). Overall, T_{pref} was $3.6 \pm 0.5^{\circ}\text{C}$ (mean \pm SD) lower in winter compared with summer ($t=-7.1$, $p<.0001$) and was $1.3 \pm 0.5^{\circ}\text{C}$ higher than field body temperatures ($t=2.8$, $p=.008$) during both seasons (location (laboratory) \times season (winter) interaction: $-0.07 \pm 1.03^{\circ}\text{C}$, $t=-0.07$, $p=.9$; Figure S3).

3.2 | Microclimate diversity

We found that empirical ground temperature varied daily and seasonally across types and sizes of microhabitats (Table S2). Not surprisingly, in all seasons and microhabitats, ground temperatures were lowest in the mornings and evenings, while the highest temperatures were observed at noon and late afternoon in the open and shaded microhabitats, respectively (Figure 1). Minimal and maximal ground temperatures were most extreme in the open habitat (Table S2)—for example, in the summer, maximal temperatures in the open were 7.5°C higher than in the second warmest microhabitat (small bushes). Among the shaded microhabitats, rock shade offered cooler ground temperatures than vegetation shade (Table S2) at noon and was more thermally stable (i.e. Max–Min temperatures, Table S2). This was particularly the case for medium and large rocks, where maximum summer temperatures were 3.1 , and 5.8°C lower, respectively, compared to bushes of the same size.

3.3 | Compatibility between lizard thermal preference and microhabitats

The compatibility of T_{pref} to the measured temperatures at each microhabitat varied across seasons, and among types and sizes of microhabitats. During winter, the T_{pref} of lizards was much higher than the temperature under bushes or rocks of all sizes, especially in the morning and under rock cover (Figure 1). In the summer, temperatures in the open, under bushes of all sizes, and under small rocks were all well above lizards' average T_{pref} , except during the early morning hours (Figure 1). During summer, medium to large rocks were the only microhabitats offering suitable temperatures for lizards during the warmest hours (14:00–16:00, Figure 1a,b).

3.4 | Microhabitat choice

Using our biophysical (i.e. heat transfer) and microhabitat selection models, we found that the relative importance of different microhabitats varied daily and seasonally. Ultimately, our model predicted that lizards should thermoregulate across all types of microhabitats over the year (Figure 2). During winter, simulated lizards were only active 11% of the time, exclusively in the open (Figure 2b) and during midday (Figure 3g); the remainder of the time (89%), they were inactive in their burrows. In contrast, during summer, simulated lizards were active 65% of the time—using all microhabitats, but primarily shaded areas under medium (17%) or large (30%) rocks (Figure 2a). Our predictions suggest that medium or large rocks were especially favourable during the warmest hours of the day, while the open and bushed microhabitats would be mostly selected during the morning hours (Figure 3a).

3.5 | The impacts of habitat loss

Our simulations of habitat loss of either rocks or bushes revealed the importance of each shelter type and size for the thermal opportunities and thermal accuracy of lizards. In particular, when simulated lizards lost access to rocks due to habitat degradation (e.g. roads, camping sites, mining), their opportunities for activity during daytime decreased by $1.88\times$ from 66% to 35% during summer (Figure 2). Without rocks, simulated lizards shifted activity to other microhabitats, especially under medium bushes (Figure 2); however, given temperatures in these habitats, they could only be active during the morning hours (Figure 3). Since lizards were predicted to shift activity to sub-optimal microhabitats due to habitat loss, thermal accuracy during activity was also predicted to decrease (i.e. increasing DE, the difference between the operative temperature and the preferred temperature), both below and above T_{pref} when habitat degradation was characterized by a loss of bushes, and only below T_{pref} when habitat degradation was characterized by a loss of rocks (Figure 4; Table 1). During winter, loss of rocks or bushes cover did not affect the predicted thermal opportunity and accuracy, as

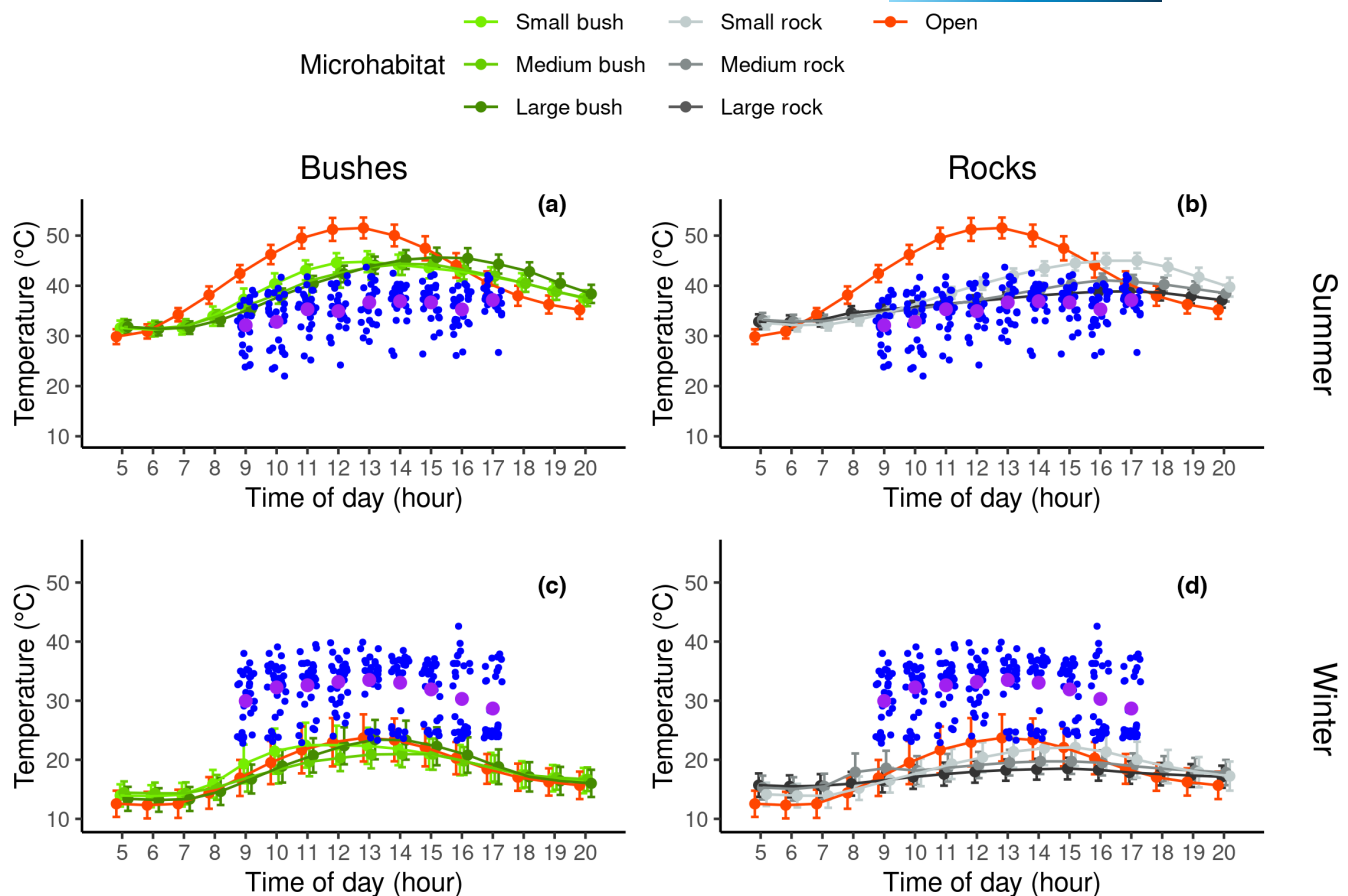


FIGURE 1 Comparison between the preferred body temperature of lizards under a thermal gradient (blue points—individual values, purple—mean values) and the ground temperature at the different microhabitats during the day (red—open; green—bushes; grey—rocks) during summer (top row; a and b) and winter (lower row; c and d). The size of bushes and rocks is represented by the darkness of their colour, with dark colours representing larger objects. Light green to dark green for bushes, and light grey to dark grey for rocks. Within each season, each panel depicts the same temperatures of the open microhabitat.

simulated lizards were active only in open habitats at that time of year (Figure 4; Table 1).

3.6 | The impacts of climate change

Under climate change, the temperatures in the Judean Desert are predicted to increase by +6.5°C during summer and +4.9°C during winter by 2080–2100 (assuming a ssp585 emission scenario, see Supplementary Information for description of calculations). As we simulated climate warming, the relative importance of each microhabitat also shifted. During winter, warming increased the thermal opportunity of simulated lizards, increasing activity time by 5% for every +1°C (Figure 5b). In addition, beginning with climatic shifts of +1, +2.5, and +6°C, simulated lizards in winter increasingly needed to seek shade under small, large, and medium bushes, respectively (Figures 3 and 6). In response to intermediate climatic increases of +3°C and +4.5°C, lizards increasingly relied on the shade of small and medium rocks, respectively (Figures 3 and 6). By the winters of 2100, simulated lizards became active over the early midday period and in the evening, using bushes mostly at noon and rocks in the

evenings (Figure 3j). During summer, warming gradually decreased thermal opportunity for activity (Figures 5a and 6), especially in rocky microhabitats, which increasingly became too warm for activity. Simulated lizards gradually ceased activity in the late midday period and, by 2100, their activity became restricted to early mornings (Figure 3d).

Our simulation of climate warming indicates that as temperatures gradually increase, there will be shifts in thermal opportunity and the temperatures experienced during activity, resulting in changes in thermal accuracy. Specifically, our analysis suggests that by 2100, the frequency of operative temperatures above T_{pref} (positive DE values) will increase during both seasons, while the frequency of operative temperatures below T_{pref} (negative DE values) will also decrease, but only during summer (Figure 4). Warming will also lead to an improvement in thermal accuracy, with mean negative DE values becoming closer to zero, particularly during summer (Figure 5e,f). However, during summer, warming will not increase the mean positive DE until an increase of +6°C (Figure 5c), possibly because operative temperatures are already high under the current climate, and every increase in temperature causes a decrease in activity (Figure 6a). During

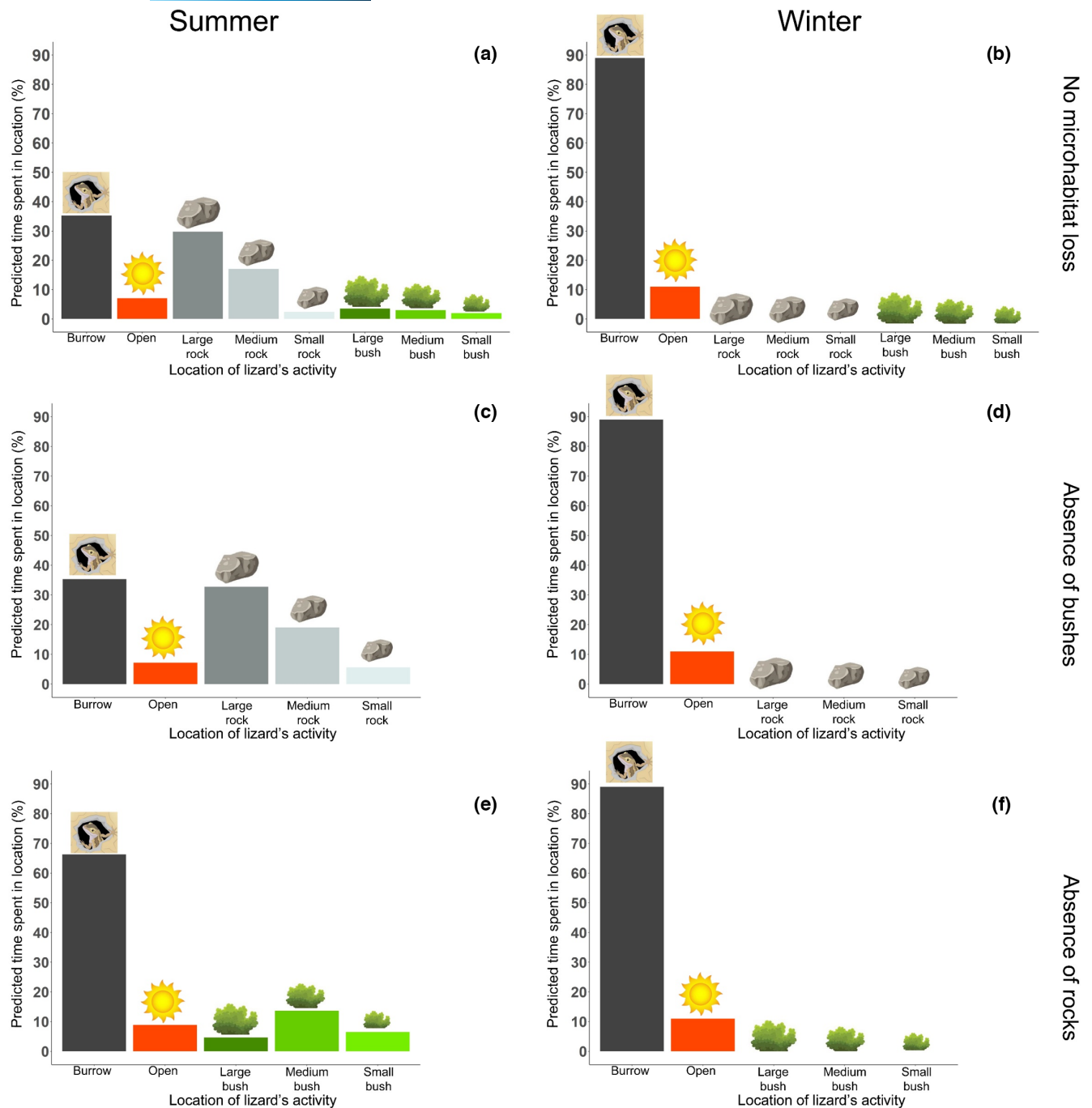


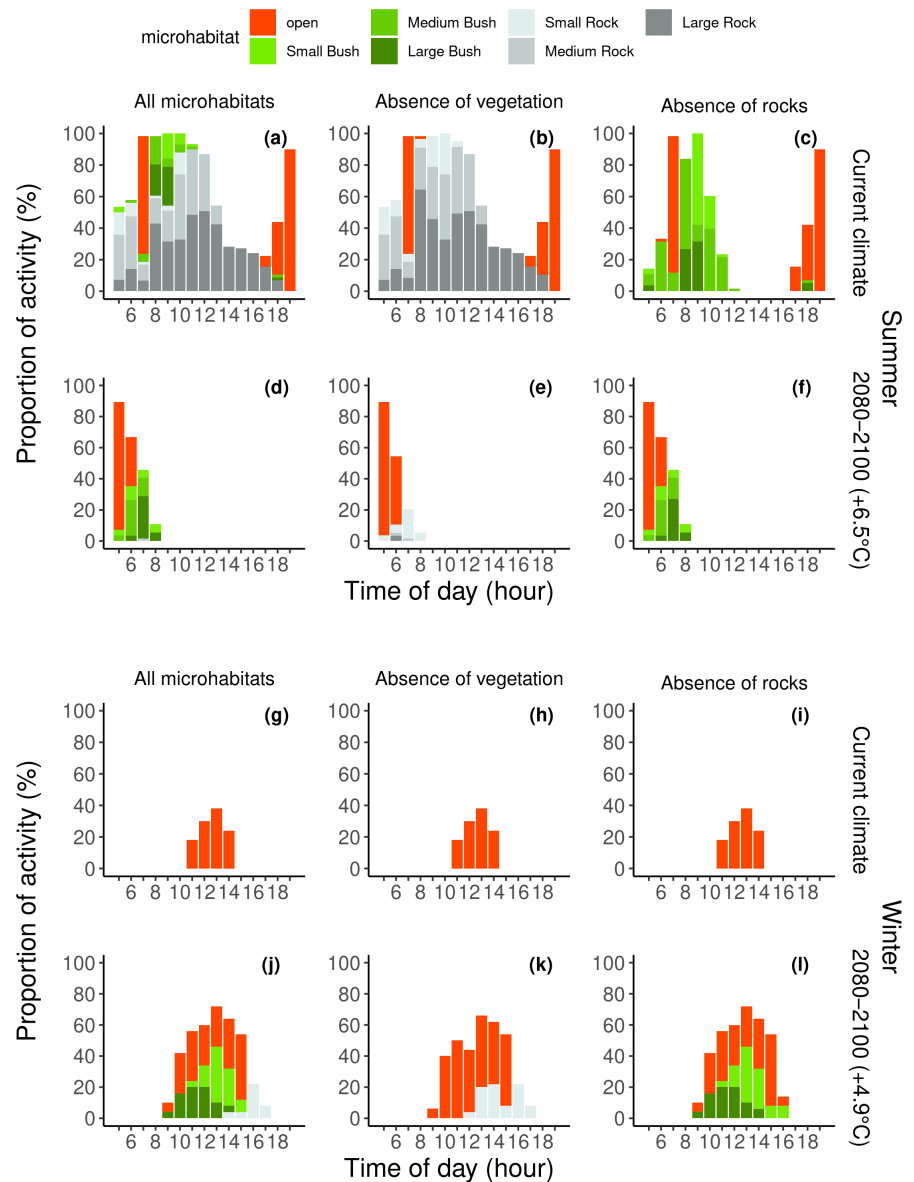
FIGURE 2 Predicted microhabitat selection varies across microhabitat type and size, and habitat loss is predicted to reduce lizards' activity or shift it to other microhabitats. We show the proportion of the amount of time spent (out of the daytime hours—summer: 5–19 h, winter: 6–18 h) in each microhabitat under different scenarios: no microhabitat loss in the summer (a) and winter (b), absence of bushes in the summer (c) and winter (d) or absence of rock in the summer (e) and winter (f). Lizards can either be inactive in the burrow (black) or active in the open (red) or one of the shaded microhabitats (rocks—grey, bushes—green). The size of bushes and rocks is represented by the darkness of their colour, with darker colours representing larger objects: light green to dark green for bushes, and light grey to dark grey for rocks.

winter, the warming will increase the mean positive DE until a warming of +2.5°C is reached, but it will decrease in warmer scenarios (Figure 5d). This may be due to an increase in the use of shaded microhabitats, which were previously too cold for activity (Figure 6b).

3.7 | Interacting effects of climate change and habitat loss

In future summers characterized by habitat loss and climate warming, lizards are predicted to keep losing opportunities for activity—they

FIGURE 3 Predicted activity times and microhabitat choices vary daily and seasonally (summer: a–i; winter: j–r) and across climate change scenarios (current, +3°C, +6°C) and available microhabitats (left: all, centre: loss of bushes, right: loss of rocks). In each hour, the bar represents the percentage of times when activity was possible. The colours of bars in each hour represent the chosen microhabitats (red—open; green—bushes; grey—rocks). The size of bushes and rocks is represented by the darkness of their colour, with darker colours representing larger objects: light green to dark green for bushes, and light grey to black for rocks. The length of each bar represents the percentage of times the microhabitat was selected for activity in our simulation. Hours with no bars represent hours of inactivity.



will lose these opportunities more rapidly when either bushes or no habitat is lost compared to when rocks are lost (Figure 5a). This is probably because a loss of rocks even now, under contemporary climates, would cause substantial declines in the lizards' activity. However, at a climatic increase of +4°C, we predict that rocks will become too warm for activity and the declines in opportunity for activity will be the same under all habitat loss scenarios. In winter, on the other hand, thermal opportunity will continue to increase at the same rate regardless of habitat loss (Figure 5b).

During both seasons, as simulated lizards gain or lose thermal opportunities, their thermal accuracy will vary with changes in habitat structure (Figures 4b,d and 5c–f; Table 1). If lizards lose access to bushes, they will maintain activity but their thermal accuracy will decrease, as operative temperatures will be more often below T_{pref} during summer and above T_{pref} during winter compared to other habitat loss scenarios (Figure 4b,d). Moreover, the mean distance from T_{pref} will increase, below T_{pref} during both winter and summer and above T_{pref} only during winter (Table 1, Figure 5). Losing access to

rocks, on the other hand, causes greater loss of thermal opportunity than thermal accuracy.

4 | DISCUSSION

4.1 | The importance of microhabitat diversity in the face of climate change

Microhabitats are ecological resources that promote species' coexistence and provide individual animals with diverse thermoregulatory opportunities (Garcia & Clusella-Trullas, 2019; Jorgensen, 2004; Li et al., 2017; Magnuson et al., 1979; Pascoe et al., 2019; Scheffers et al., 2014). In this study, we modelled the relative importance of one open and six shaded microhabitats to a small desert lizard. We found that—under current climatic conditions—medium and large rocks enable lizards to maintain their activity throughout hot summers, and that

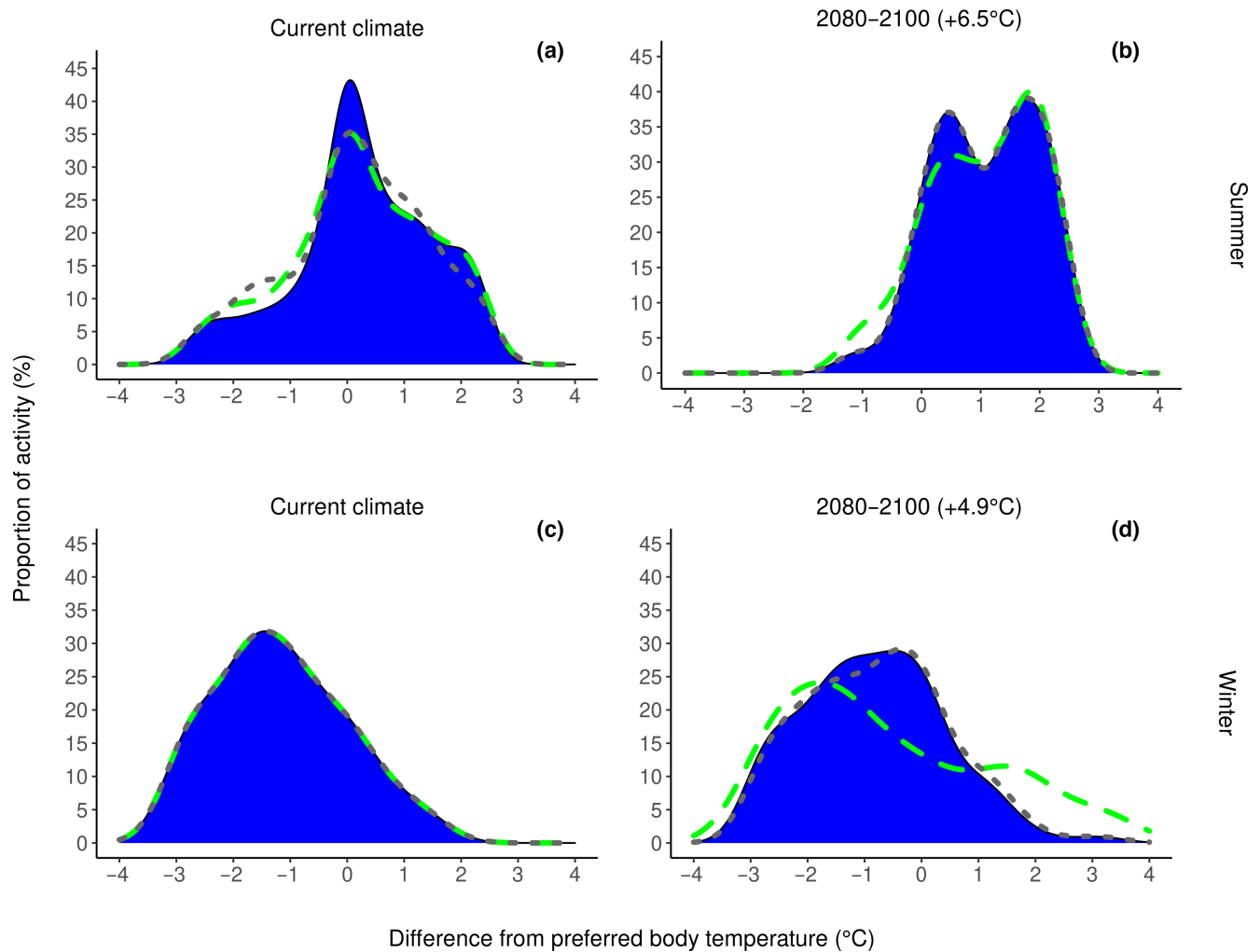


FIGURE 4 Habitat loss is predicted to decrease the amounts of activity at preferred body temperature during current and warmer climates. We show the predicted frequency distribution of the difference of simulated operative temperatures during activity from the preferred body temperature when all microhabitats are available (blue histogram) and in the absence of bushes (green dashed line) or rocks (grey dotted line). Under current climate, the simulated absence of either bushes or rocks decreases the percentage of activity at preferred temperature during summer (a) but not during winter (b). By 2080–2100, only bush loss will decrease the percentage of activity at preferred temperature, with more time below preferred body temperature during summer (c) and above preferred body temperature during winter (d).

TABLE 1 Habitat loss is predicted to shift lizards' activity to suboptimal microhabitats.

	Current climate		2080–2100 warming	
	Below T_{pref}	Above T_{pref}	Below T_{pref}	Above T_{pref}
Winter				
All microhabitats	-1.52 ± 0.85	0.66 ± 0.50	-1.36 ± 0.86	0.79 ± 0.73
Absence of bushes	-1.52 ± 0.85 (0.0%)	0.66 ± 0.50 (0.0%)	-1.66 ± 0.83 (22.1%)	1.60 ± 1.01 (103%)
Absence of rocks	-1.52 ± 0.85 (0.0%)	0.66 ± 0.50 (0.0%)	-1.34 ± 0.86 (−1.5%)	0.81 ± 0.73 (2.5%)
Summer				
All microhabitats	-0.88 ± 0.84	1.02 ± 0.75	-0.41 ± 0.41	1.27 ± 0.74
Absence of bushes	-0.96 ± 0.82 (9.1%)	1.07 ± 0.75 (4.9%)	-0.52 ± 0.43 (26.8%)	1.31 ± 0.72 (3.1%)
Absence of rocks	-0.96 ± 0.83 (9.1%)	1.02 ± 0.71 (0.0%)	-0.41 ± 0.41 (0.0%)	1.27 ± 0.74 (0.0%)

Note: We show the mean and standard deviation of thermal accuracy (DE, the difference of the operative temperature during activity from the preferred body temperature, T_{pref}). Since the direction of DE (above or below T_{pref}) can differently affect performance, we report the mean DE (\pm SD) of positive and negative values. Percentage in parenthesis represents the relative change due to habitat loss compared to the scenario where all microhabitats are available.

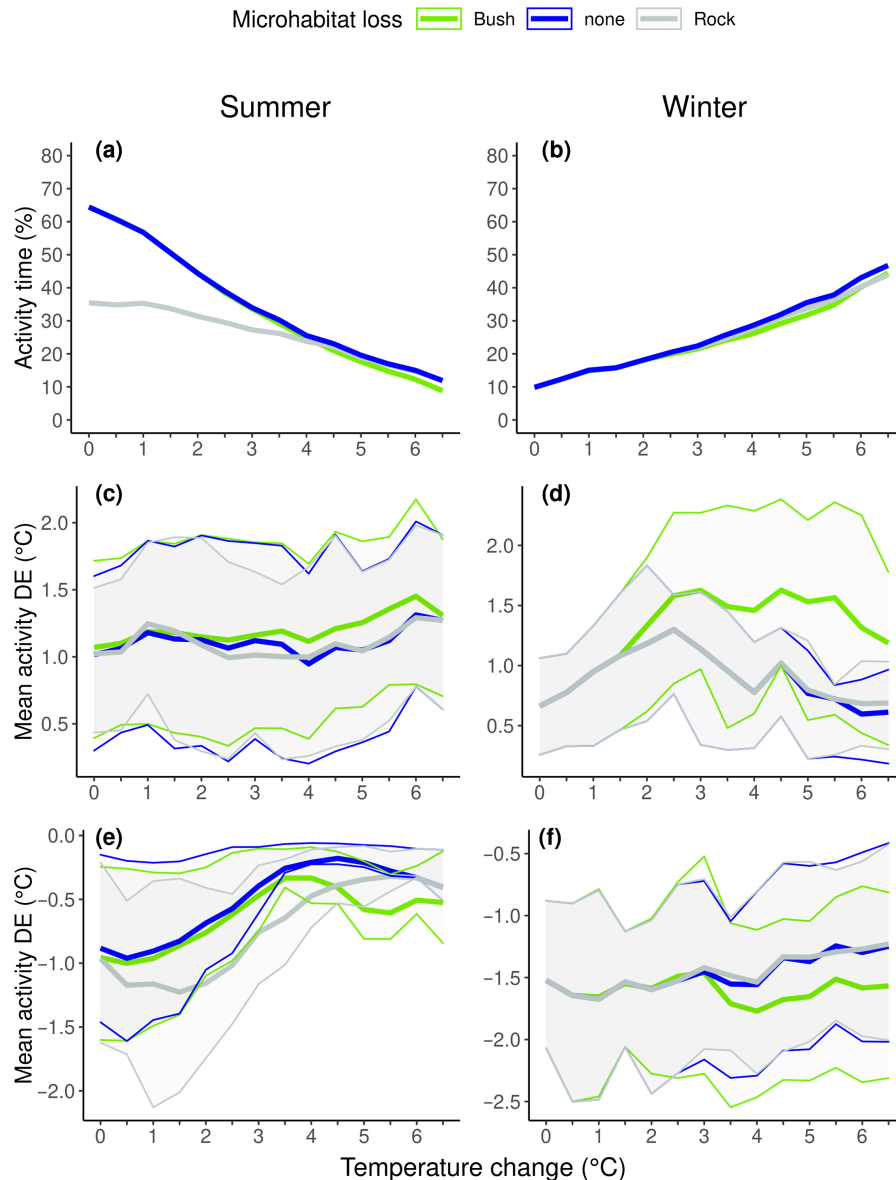


FIGURE 5 Predicted changes in thermal opportunities vary with seasons, warming climate, and habitat loss scenarios (a—summer; b—winter). Thermal accuracy decreases with habitat loss, especially under loss of bush cover (Above T_{pref} : c—summer, d—winter. Below T_{pref} : e—summer; f—winter). Thermal accuracy is calculated as DE (i.e. the difference between the predicted operative temperature and preferred body temperature), where values closer to zero represent better accuracy. Line colours represent the habitat loss scenarios (green—loss of bushes; grey—loss of rocks; blue—no habitat loss). In panels c–f, middle bold line and top/bottom lines represent the mean and 25%/75% CI of the predicted DE.

rock removal would pose a threat to these animals, leading to a large decline in thermal opportunity, even if vegetation cover remained intact. We also modelled climate change and found that, as temperatures increased, lizards could no longer be active in the summer; winter emerged as a new active season. In situations where climate and habitat change, we found that some shaded microhabitats that appear unimportant today may become important as new thermoregulatory challenges evolve.

Our simulation also suggests that the loss of habitats may lead to a decrease in thermal accuracy, even when thermal

opportunity remains the same (Figures 4 and 5). For desert species already at the edge of their thermal maximal tolerance (Vale & Brito, 2015), decreases in thermal accuracy can lead to a rapid decline in performance. Many performance traits (e.g. running speed and digestion) decline very rapidly in temperatures above optimum (Martin & Huey, 2008; such as running speed, digestion and more, Angilletta, 2009). Such loss of performance is likely to have considerable impacts on lizard populations, by limiting their foraging efficiency, energy assimilation, and reproduction rates (Angilletta, 2009; Deutsch et al., 2008; Kingsolver et al., 2013; Martin & Huey, 2008; Sinervo et al., 2010).

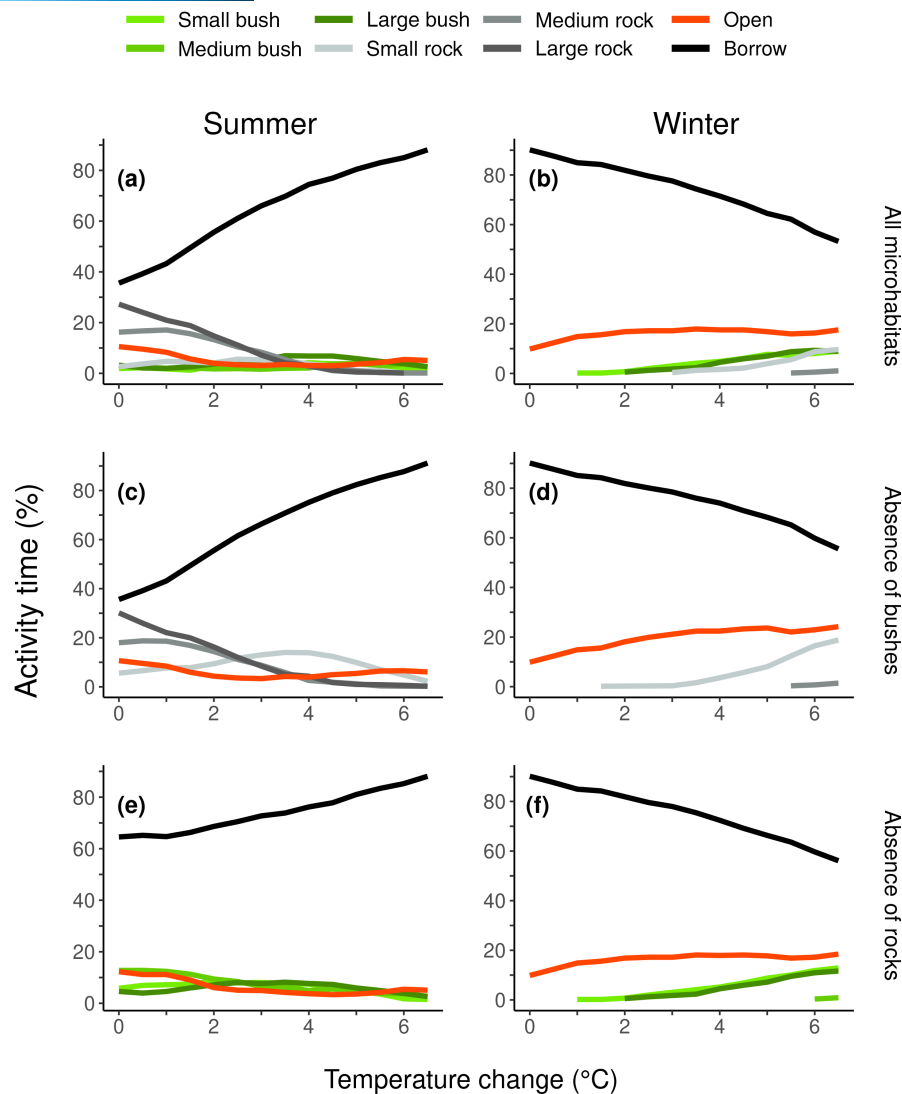


FIGURE 6 Climate warming is predicted to shift lizards' microhabitat choices, depending on the degree of warming and habitat loss scenarios. We show the effect of microhabitat loss on the activity of lizards, and the amount of time spent in the remaining microhabitats: Scenario 1—no habitat loss (a—winter; b—summer), Scenario 2—vegetation available (c—winter; d—summer). Scenario 3—no rocks available (e—winter; f—summer).

4.2 | Microhabitat diversity increases thermal heterogeneity and resilient to climate change

Our field data from the Judean Desert show that temperatures vary substantially among shaded areas depending on shade type (i.e. under rocks or bushes) and size. Our model indicates that animals can maximize activity times, thermal accuracy, and both, by selecting among all available microhabitats. Climate change models must therefore account for the thermal heterogeneity of microhabitats (e.g. bushes and rocks of different sizes) to effectively predict the temporal and spatial patterns of habitat use by animals and, ultimately, to empower targeted, effective management plans (Scheffers et al., 2014). Furthermore, as habitat destruction accelerates worldwide (Shine et al., 1998; e.g. removal of rocks, Pike et al., 2010), alongside changes in precipitation, extreme events, and fire regimes (e.g. decreasing vegetation cover, Halofsky et al., 2020;

Nolan et al., 2021), we must better understand the resulting thermal constraints on activity in animals (Kearney et al., 2021). Information on the buffering effects of microhabitats and the importance of microhabitat diversity is important to developing a theoretical framework of animals' responses to climate change (Kearney et al., 2009). Moving forward, identifying and protecting microhabitats with conservation value will give populations a better chance of persistence.

In the current study, the most thermally important shelters for our simulated ground-dwelling lizards were rocks rather than vegetation. Our field observations show that diurnal temperatures increase more slowly under larger rocks than under vegetation, therefore supplying adequate thermal conditions to lizards even in the warmest part of the day. Rocks are also important thermal buffers for other species, including Garter snakes, *Thamnophis elegans* (Huey et al., 1989) and flat rock spiders *Morebilus plagusius* (van den Berg et al., 2015). As rocks are abundant in the Judean Desert, it is

possible that natural selection or thermal acclimation (or both) have shaped the thermal preferences of lizards to match the temperatures under such retreats and thus maximize activity times (but see Gilbert & Miles, 2017; Huey & Bennett, 1987; Pafilis et al., 2019). However, due to the rapid environmental change caused by habitat loss and climate change, only thermal acclimation may help lizards shift their thermal performance curves to track the common temperatures of the novel environment (Gunderson et al., 2009; Logan et al., 2014).

4.3 | The abiotic importance of microhabitat size for thermoregulation

Lizards in our simulation preferred medium and large-sized shelters, indicating that the physical characteristics of refuges play an important role for thermoregulation, as was found in previous studies (Chukwuka et al., 2021; Huey et al., 1989; Kearney, 2002; Webb & Shine, 1998). Shelters vary widely in thermal characteristics (Chukwuka et al., 2021; Kearney & Predavec, 2000). For example, the size of a rock determines its heat flux; rocks have slower heat transfer from the top to the bottom during the day so that larger rocks remain cooler on hot days and maintain more heat at night than smaller rocks (Huey et al., 1989). Moreover, larger shelters may offer a greater amount of space under them, which animals can exploit (e.g. by moving to the edges to get warm, and then retreating to the centre to get cool; Chukwuka et al., 2020).

Our model suggests that bushes and small rocks—which are less important for thermoregulation in the current climate—will become more important as winter and summer temperatures rise (Figures 3 and 6). On the other hand, medium and large rocks will lose their benefits to lizards, becoming too hot in summer and remaining too cold in winter for use. Though future lizards can still shuttle between the open and large rocks, they will have to do so more often, increasing energy consumption and predation risk. Large rocks may also provide warm retreats during night-time, promoting efficient digestion and increase net energy available (i.e. the difference between digested energy and the energy lost from metabolism, Waldschmidt et al., 1987) and eventually in energy storage (Amo et al., 2007; Huey et al., 1989; Melville & Schulte II, 2001; Monasterio et al., 2010). Our study increases the resolution on the microclimatic decisions ectotherms make when deciding on retreat sites, highlighting the complex trade-offs between physiological and ecological requirements that organisms must navigate in heterogeneous habitats.

4.4 | Seasonal thermal flexibility and climate change risks

We observed that the thermal preference of individual lizards varied dramatically among seasons and that, overall, lizards preferred lower body temperatures during winter (Figure 1); this suggests that plastic responses of T_{pref} are possible in this species. In fact, behavioural flexibility likely enables the lizards to adapt to the harsh,

variable desert conditions across the year (Ortega et al., 2014; Ortega & Pérez-Mellado, 2016). We found seasonal differences in microclimate conditions, the T_{pref} and activity of lizards, and model predictions—highlighting the importance of studying the thermal ecology of ectotherms across the year rather than in one season (Huey et al. 1977, 2021a, 2021b; Porter et al., 1973), particularly for desert, alpine, or temperate species that experience large seasonal fluctuations (James & Porter, 1979).

Our warming simulation suggests that temperature by 2080–2100 will severely limit the summer activity of small lizards in this region, increasing the risk of starvation and dehydration, as food and water intake may not be sufficient to sustain metabolic and water loss rates. Such a decrease in activity and food intake may also cause ‘metabolic meltdown’, in which activity is further decreased as animals prefer lower temperatures that minimize metabolic rates (Huey & Kingsolver, 2019). As winter warms, it may emerge as a new activity season (Huey et al., 2021a). Such phenological shifts may enable species to adapt to climate change, but pose risks to ecological interactions (Barnagaud et al., 2013; Beebe, 1995; Philippart et al., 2003; Walther et al., 2002) and early life stages (Levy et al., 2015; Levy, Buckley, et al., 2016a).

4.5 | Ecological importance of rocks and vegetation

In the desert, rocks and vegetation play additional ecological roles beyond that of thermal shelter. In various ecological systems, rocks increase prey abundance and diversity (Borkhataria et al., 2012; Guenat et al., 2017; Johnson, 2000), reduce competition, food-searching movement, and increase foraging efficiency (Attum & Eason, 2006; Belliure et al., 1996; Kearney et al., 2021), reduce escape distances from predators (Amo et al., 2007; Huey, 1991; Monasterio et al., 2010; Newbold & MacMahon, 2014; Pietrek et al., 2009), and reduce water loss (Rozen-Rechels et al., 2019). In desert habitats where rocks are less abundant (like sandy deserts), bushes, trees, and burrows may provide most of the shade (Cain et al., 2008) and protection from predation (Pietrek et al., 2009) and competition (Zeng et al., 2016); such habitats may be at risk due to novel warmer and drier climates (Kim et al., 2018; Levy, Buckley, et al., 2016b), invasive species (Garcia & Clusella-Trullas, 2019), and habitat loss (Estavillo et al., 2013). The loss of bushes and trees will decrease arthropod abundance and thus food availability for their predators (Blaise et al., 2022; Braun et al., 2021; Estavillo et al., 2013).

Recent work found that the body condition of *M. bahaeldini* lizards improves with proximity to rocks and vegetation (Stark et al., 2022). However, the lizards benefit from rocks only within their home range, while the benefit from bushes extends well beyond their home range—this indicates that rocks are directly beneficial, perhaps as thermal and predatory shelters, while vegetation is indirectly beneficial by supporting insects that the lizards eat (Stark et al., 2022). However, simulations in the current study suggest that lizards foraging under bushes may pay a considerable price in

performance (e.g. running speed, endurance and assimilation rates) due to low thermal accuracy (Angilletta, 2009).

4.6 | Caveats and future directions

Although our framework provides new insights on the importance of microhabitat diversity, it lacks key characteristics of real ecological systems. In particular, ecological interactions such as competition and predation risk may shift the activity patterns of animals to unfavourable microclimates even when preferred conditions are available (Abramsky et al., 1996; Hughes et al., 1994; Kotler & Brown, 1999; Rusch & Angilletta, 2017). Our model can be adapted to consider ecological interactions that prevent lizards from using a microhabitat—for example, a predator keeping lizards away from rock shade is another, more temporary form of habitat loss of rocks. Moreover, as thermal preferences and tolerances can vary with life stages, sex, female reproductive condition, and state of hydration (Angilletta, 2009), incorporating such variability in our framework may further increase its predictive power, and enable more reliable assessments of reactions to climate change, habitat loss, and new conservation opportunities.

Our model also simplifies the conditions experienced by lizards. In particular, it lacks information on the spatial distribution of microclimates and movement of animals between them, which contribute to the costs of thermoregulation and thermal accuracy (Basson et al., 2017; Sears et al., 2016). Hence, our model predictions represent a best-case-scenario with no significant costs of moving between thermal patches. Our model may also underestimate the shifts in the climatic conditions under climate change, since we only simulated a warming scenario but other factors such as decreased precipitation and increased thermal variation may also be impacted by climate change (Melillo et al., 1993). Finally, we model thermoregulation through summer and winter without considering the transitional seasons of spring and fall. Nevertheless, our focus on seasonal extremes has still revealed the important role of microclimate diversity.

The field of biophysical ecology presents a promising avenue for investigating the potential impacts of climate change (as reviewed by Briscoe et al., 2023). While our biophysical framework was designed specifically for our target species and microclimate conditions, our heat balance calculations of operative temperatures are similar to those used in the R's NicheMapR ectotherm model (Kearney & Porter, 2019). By incorporating various microhabitat types and habitat loss scenarios into NicheMapR's microclimate (Kearney & Porter, 2017) and ectotherm (Kearney & Porter, 2019) models, users can adapt biophysical ecology as a tool for managing habitat conservation and restoration.

4.7 | Summary

We demonstrate the fundamental importance of microclimate diversity to resilient ecological systems. Our framework shows that,

depending on their type and size, shaded microhabitats differ in their importance to small ectotherms, and that accounting for such differences is critical to understanding and managing the effects of future habitat degradation and climate change. Models of biophysical ecology and climate change are needed to understand how organisms will react to environmental shifts, yet most still simplify ecological interactions and microclimates. By incorporating realistic microhabitats, models like ours can improve realism in theories of ecological physiology and climate change, revealing the relevance of seemingly unimportant microhabitats for the resilience of ecological systems and better informing habitat conservation and recovery programs.

4.8 | Ethics

We received permits to conduct experiments on the focal lizard species from the Tel Aviv University ethics in animal experimentation committee (04-20-007, 04-20-008). The collections of lizards were approved by the National Parks Authority (permits no. 2020/42436).

AUTHOR CONTRIBUTIONS

GS and OL conceived and designed the study. GS collected and analysed the data and wrote the first draft of the manuscript. OL contributed mentorship, materials, and analysis tools. OL, GS, LM, ZGZ, and WGD commented on the first draft and participated in revising the manuscript.

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CONFLICT OF INTEREST STATEMENT

There are no competing interests among all authors for this manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo at: <https://doi.org/10.5281/zenodo.7955816>.

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REFERENCES

- Abramsky, Z., Strauss, E., Subach, A., Kotler, B. P., & Riechman, A. (1996). The effect of barn owls (*Tyto alba*) on the activity and microhabitat selection of *Gerrhonotus alleni* and *G. pyramidum*. *Oecologia*, 105, 313–319.
- Amo, L., López, P., & Martín, J. (2007). Refuge use: A conflict between avoiding predation and losing mass in lizards. *Physiology & Behavior*, 90, 334–343.
- Angilletta, M. J. (2009). *Thermal adaptation: A theoretical and empirical synthesis*. Oxford University Press.
- Attum, O. A., & Eason, P. K. (2006). Effects of vegetation loss on a sand dune lizard. *Journal of Wildlife Management*, 70, 27–30.
- Ayers, D. Y., & Shine, R. (1997). Thermal influences on foraging ability: Body size, posture and cooling rate of an ambush predator, the python. *Functional Ecology*, 11, 342–347.
- Bakken, G. S. (1992). Measurement and application of operative and standard operative temperatures in ecology. *American Zoologist*, 32, 194–216.
- Barnagaud, J.-Y., Barbaro, L., Hampe, A., Jiguet, F., & Archaux, F. (2013). Species' thermal preferences affect forest bird communities along landscape and local scale habitat gradients. *Ecography*, 36, 1218–1226.
- Basson, C. H., Levy, O., Angilletta, M. J., & Clusella-Trullas, S. (2017). Lizards paid a greater opportunity cost to thermoregulate in a less heterogeneous environment. *Functional Ecology*, 31, 856–865.
- Beebe, T. J. C. (1995). Amphibian breeding and climate. *Nature*, 374, 219–220.
- Belliure, J., Carrascal, L. M., & Díaz, J. A. (1996). Covariation of thermal biology and foraging mode in two mediterranean lacertid lizards. *Ecology*, 77, 1163–1173.
- Besson, A. A., & Cree, A. (2010). A cold-adapted reptile becomes a more effective thermoregulator in a thermally challenging environment. *Oecologia*, 163, 571–581.
- Blaise, C., Mazzia, C., Bischoff, A., Millon, A., Ponel, P., & Blight, O. (2022). Vegetation increases abundances of ground and canopy arthropods in Mediterranean vineyards. *Scientific Reports*, 12, 3680.
- Borkhataria, R. R., Collazo, J. A., & Groom, M. J. (2012). Species abundance and potential biological control services in shade vs. sun coffee in Puerto Rico. *Agriculture, Ecosystems and Environment*, 151, 1–5.
- Braun, J., Westphal, M., & Lortie, C. J. (2021). The shrub *Ephedra californica* facilitates arthropod communities along a regional desert climatic gradient. *Ecosphere*, 12, e03760.
- Briscoe, N. J., Morris, S. D., Mathewson, P. D., Buckley, L. B., Jusup, M., Levy, O., Maclean, I. M. D., Pincebourde, S., Riddell, E. A., Roberts, J. A., Schouten, R., Sears, M. W., & Kearney, M. R. (2023). Mechanistic forecasts of species responses to climate change: The promise of biophysical ecology. *Global Change Biology*, 29, 1451–1470.
- Buckley, L. B. (2008). Linking traits to energetics and population dynamics to predict lizard ranges in changing environments. *The American Naturalist*, 171, E1–E19.
- Cain, J. W., Jansen, B. D., Wilson, R. R., & Krausman, P. R. (2008). Potential thermoregulatory advantages of shade use by desert bighorn sheep. *Journal of Arid Environments*, 72, 1518–1525.
- Carlo, M. A., Riddell, E. A., Levy, O., & Sears, M. W. (2018). Recurrent sublethal warming reduces embryonic survival, inhibits juvenile growth, and alters species distribution projections under climate change. *Ecology Letters*, 21, 104–116.
- Chukwuka, C. O., Mello, R. S. R., Cree, A., & Monks, J. M. (2021). Thermal heterogeneity of selected retreats in cool-temperate viviparous lizards suggests a potential benefit of future climate warming. *Journal of Thermal Biology*, 97, 102869.
- Chukwuka, C. O., Monks, J. M., & Cree, A. (2020). Heat and water loss versus shelter: A dilemma in thermoregulatory decision making for a retreat-dwelling nocturnal gecko. *The Journal of Experimental Biology*, 223, jeb231241.
- Davy, R., Esau, I., Chernokulsky, A., Outten, S., & Zilitinkevich, S. (2017). Diurnal asymmetry to the observed global warming. *International Journal of Climatology*, 37, 79–93.
- Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., & Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 6668–6672.
- Dillon, M. E., Wang, G., & Huey, R. B. (2010). Global metabolic impacts of recent climate warming. *Nature*, 467, 704–706.
- Estavillo, C., Pardini, R., & da Rocha, P. L. B. (2013). Forest loss and the biodiversity threshold: An evaluation considering species habitat requirements and the use of matrix habitats. *PLoS One*, 8, e82369.
- Fei, T., Skidmore, A. K., Venus, V., Wang, T., Schlerf, M., Toxopeus, B., van Overjik, S., Bian, M., & Liu, Y. (2012). A body temperature model for lizards as estimated from the thermal environment. *Journal of Thermal Biology*, 37, 56–64.
- Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37, 4302–4315.
- Fitzsimons, J. A., & Michael, D. R. (2017). Rocky outcrops: A hard road in the conservation of critical habitats. *Biological Conservation*, 211, 36–44.
- Franzmeier, D. P., Pedersen, E. J., Longwell, T. J., Byrne, J. G., & Losche, C. K. (1969). Properties of some soils in the Cumberland plateau as related to slope aspect and position. *Soil Science Society of America Journal*, 33, 755–761.
- García, R. A., & Clusella-Trullas, S. (2019). Thermal landscape change as a driver of ectotherm responses to plant invasions. *Proceedings of the Biological Sciences*, 286, 20191020.
- Giam, X. (2017). Global biodiversity loss from tropical deforestation. *Proceedings of the National Academy of Sciences of the United States of America*, 114, 5775–5777.
- Gilbert, A. L., & Miles, D. B. (2017). Natural selection on thermal preference, critical thermal maxima and locomotor performance. *Proceedings of the Royal Society B: Biological Sciences*, 284, 20170536.
- Goldberg, S. R. (2012). Reproduction in the Desert Lacerta, *Mesalina guttulata*, from Israel. *Zoology in the Middle East*, 56, 27–30.
- Guenat, S., Kaartinen, R., & Jonsson, M. (2017). Shade trees decrease pest abundances on brassica crops in Kenya. *Agroforestry Systems*, 93, 1–12.
- Gunderson, C. A., O'Hara, K. H., Campion, C. M., Walker, A. V., & Edwards, N. T. (2009). Thermal plasticity of photosynthesis: The role of acclimation in forest responses to a warming climate. *Global Change Biology*, 16, 2272–2286.
- Halofsky, J. E., Peterson, D. L., & Harvey, B. J. (2020). Changing wildfire, changing forests: The effects of climate change on fire regimes and vegetation in the Pacific Northwest, USA. *Fire Ecology*, 16, 4.
- Hantson, S., Huxman, T. E., Kimball, S., Randerson, J. T., & Goulden, M. L. (2021). Warming as a driver of vegetation loss in the Sonoran Desert of California. *Journal of Geophysical Research: Biogeosciences*, 126, e2020JG005942.
- Hertz, P. E. (1992). Evaluating thermal resource partitioning: By sympatric lizards *Anolis cooki* and *A. cristatellus*: A field test using null hypotheses. *Oecologia*, 90, 127–136.
- Hertz, P. E., Huey, R. B., & Stevenson, R. D. (1993). Evaluating temperature regulation by field-active ectotherms: The fallacy of the inappropriate question. *The American Naturalist*, 142, 796–818.
- Huey, R. B. (1991). Physiological consequences of habitat selection. *The American Naturalist*, 137, S91–S115.

- Huey, R. B., & Bennett, A. F. (1987). Phylogenetic studies of coadaptation: Preferred temperatures versus optimal performance temperatures of lizards. *Evolution*, 41, 1098.
- Huey, R. B., Kearney, M. R., Krockenberger, A., Holtum, J. A. M., Jess, M., & Williams, S. E. (2012). Predicting organismal vulnerability to climate warming: Roles of behaviour, physiology and adaptation. *Philosophical Transactions of the Royal Society of London. Series B, Biological sciences*, 367, 1665–1679.
- Huey, R. B., & Kingsolver, J. G. (2019). Climate warming, resource availability, and the metabolic meltdown of ectotherms. *The American Naturalist*, 194, E140–E150.
- Huey, R. B., Ma, L., Levy, O., & Kearney, M. R. (2021). Three questions about the eco-physiology of overwintering underground. *Ecology Letters*, 24, 170–185.
- Huey, R. B., Miles, D. B., & Pianka, E. R. (2021). Seasonality in Kgalagadi lizards: Inferences from legacy data. *The American Naturalist*, 198, 759–771.
- Huey, R. B., Peterson, C. R., Arnold, S. J., & Porter, W. P. (1989). Hot rocks and not-so-hot rocks: Retreat-site selection by garter snakes and its thermal consequences. *Ecology*, 70, 931–944.
- Huey, R. B., Pianka, E. R., & Hoffman, J. A. (1977). Seasonal variation in thermoregulatory behavior and body temperature of diurnal Kalahari lizards. *Ecology*, 58, 1066–1075.
- Huey, R. B., & Slatkin, M. (1976). Cost and benefits of lizard thermoregulation. *The Quarterly Review of Biology*, 51, 363–384.
- Hughes, J. J., Ward, D., & Perrin, M. R. (1994). Predation risk and competition affect habitat selection and activity of Namib Desert gerbils. *Ecology*, 75, 1397–1405.
- Hutchinson, G. E. (1978). *Introduction to population ecology*. Yale University Press.
- James, F. C., & Porter, W. P. (1979). Behavior-microclimate relationships in the African rainbow lizard, *Agama agama*. *Copeia*, 1979, 585.
- Johnson, M. D. (2000). Effects of shade-tree species and crop structure on the winter arthropod and bird communities in a Jamaican shade coffee plantation. *Biotropica*, 32, 133–145.
- Jorgensen, E. E. (2004). Small mammal use of microhabitat reviewed. *Journal of Mammalogy*, 85, 531–539.
- Kearney, M. (2002). Hot rocks and much-too-hot rocks: Seasonal patterns of retreat-site selection by a nocturnal ectotherm. *Journal of Thermal Biology*, 27, 205–218.
- Kearney, M. (2013). Activity restriction and the mechanistic basis for extinctions under climate warming. *Ecology Letters*, 16, 1470–1479.
- Kearney, M., & Predavec, M. (2000). Do nocturnal ectotherms thermoregulate? A study of the temperate gecko *Christinus marmoratus*. *Ecology*, 81, 2984–2996.
- Kearney, M., Shine, R., & Porter, W. P. (2009). The potential for behavioral thermoregulation to buffer “cold-blooded” animals against climate warming. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 3835–3840.
- Kearney, M. R., & Porter, W. P. (2017). NicheMapR—An R package for biophysical modelling: The microclimate model. *Ecography*, 40, 664–674.
- Kearney, M. R., & Porter, W. P. (2019). NicheMapR—An R package for biophysical modelling: The ectotherm and dynamic energy budget models. *Ecography*, 43, 85–96.
- Kearney, M. R., Porter, W. P., & Huey, R. B. (2021). Modeling the joint effects of body size and microclimate on heat budgets and foraging opportunities of ectotherms. *Methods in Ecology and Evolution*, 12, 458–467.
- Kerr, G. D., & Bull, C. M. (2004). Microhabitat use by the scincid lizard. *Journal of Herpetology*, 38, 536–545.
- Kim, J. B., Kerns, B. K., Drapek, R. J., Pitts, G. S., & Halofsky, J. E. (2018). Simulating vegetation response to climate change in the Blue Mountains with MC2 dynamic global vegetation model. *Climate Services*, 10, 20–32.
- Kingsolver, J. G., Diamond, S. E., & Buckley, L. B. (2013). Heat stress and the fitness consequences of climate change for terrestrial ectotherms. *Functional Ecology*, 27, 1415–1423.
- Kotler, B. P., & Brown, J. S. (1999). Mechanisms of coexistence of optimal foragers as determinants of local abundances and distributions of desert granivores. *Journal of Mammalogy*, 80, 361–374.
- Lagos, V. O., Bozinovic, F., & Contreras, L. C. (1995). Microhabitat use by a small diurnal rodent (*Octodon degus*) in a semiarid environment—Thermoregulatory constraints or predation risk. *Journal of Mammalogy*, 76, 900–905.
- Levy, O., Buckley, L. B., Keitt, T. H., & Angilletta, M. J. (2016a). Ontogeny constrains phenology: Opportunities for activity and reproduction interact to dictate potential phenologies in a changing climate. *Ecology Letters*, 19, 620–628.
- Levy, O., Buckley, L. B., Keitt, T. H., & Angilletta, M. J. (2016b). Dynamically downscaled projections of past and future climates. *Ecology*, 97, 1888.
- Levy, O., Buckley, L. B., Keitt, T. H., Smith, C. D., Boateng, K. O., Kumar, D. S., & Angilletta, M. J., Jr. (2015). Resolving the life cycle alters expected impacts of climate change. *Proceedings of the Biological Sciences*, 282, 20150837.
- Levy, O., Dayan, T., Porter, W. P., & Kronfeld-Schor, N. (2016). Foraging activity pattern is shaped by water loss rates in a diurnal desert rodent. *The American Naturalist*, 188, 205–218.
- Levy, O., Dayan, T., Rotics, S., & Kronfeld-Schor, N. (2012). Foraging sequence, energy intake and torpor: An individual-based field study of energy balancing in desert golden spiny mice. *Ecology Letters*, 15, 1240–1248.
- Li, S. R., Wang, Y., Ma, L., Zeng, Z. G., Bi, J. H., & Du, W. G. (2017). Thermal ecology of three coexistent desert lizards: Implications for habitat divergence and thermal vulnerability. *Journal of Comparative Physiology. B*, 187, 1009–1018.
- Logan, M. L., Cox, R. M., & Calsbeek, R. (2014). Natural selection on thermal performance in a novel thermal environment. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 14165–14169.
- Magnuson, J. J., Crowder, L. B., & Medvick, P. A. (1979). Temperature as an ecological resource. *American Zoologist*, 19, 331–343.
- Maino, J. L., Kong, J. D., Hoffmann, A. A., Barton, M. G., & Kearney, M. R. (2016). Mechanistic models for predicting insect responses to climate change. *Current Research in Insect Science*, 17, 81–86.
- Martin, T. L., & Huey, R. B. (2008). Why “suboptimal” is optimal: Jensen's inequality and ectotherm thermal preferences. *The American Naturalist*, 171, E102–E118.
- Meinshausen, M., Nicholls, Z. R. J., Lewis, J., Gidden, M. J., Vogel, E., Freund, M., Beyerle, U., Gessner, C., Nauels, A., Bauer, N., Canadell, J. G., Daniel, J. S., John, A., Krummel, P. B., Luderer, G., Meinshausen, N., Montzka, S. A., Rayner, P. J., Reimann, S., ... Wang, R. H. J. (2020). The shared socio-economic pathway (SSP) greenhouse gas concentrations and their extensions to 2500. *Geoscientific Model Development*, 13, 3571–3605.
- Melillo, J. M., McGuire, A. D., Kicklighter, D. W., Moore, B., Vorosmarty, C. J., & Schloss, A. L. (1993). Global climate change and terrestrial net primary production. *Nature*, 363, 234–240.
- Melville, J., & Schulte, J. A., II. (2001). Correlates of active body temperatures and microhabitat occupation in nine species of central Australian agamid lizards. *Austral Ecology*, 26, 660–669.
- Michael, D. R., Cunningham, R. B., & Lindenmayer, D. B. (2008). A forgotten habitat? Granite inselbergs conserve reptile diversity in fragmented agricultural landscapes. *Journal of Applied Ecology*, 45, 1742–1752.
- Michael, D. R., Moore, H., Wassens, S., Craig, M. D., Tingley, R., Chapple, D. G., O'Sullivan, J., Hobbs, R. J., & Nimmo, D. G. (2021). Rock removal associated with agricultural intensification will exacerbate the loss of reptile diversity. *Journal of Applied Ecology*, 58, 1557–1565.
- Monasterio, C., Salvador, A., & Díaz, J. A. (2010). Altitude and rock cover explain the distribution and abundance of a mediterranean alpine lizard. *Journal of Herpetology*, 44, 158–163.

- Moncaz, A., Faiman, R., Kirstein, O., & Warburg, A. (2012). Breeding sites of *Phlebotomus sergenti*, the sand fly vector of cutaneous leishmaniasis in the Judean Desert. *PLoS Neglected Tropical Diseases*, 6, e1725.
- Newbold, T. A. S., & MacMahon, J. A. (2014). Determinants of habitat selection by desert horned lizards (*Phrynosoma platyrhinos*): The importance of abiotic factors associated with vegetation structure. *Journal of Herpetology*, 48, 306–316.
- Nolan, R. H., Collins, L., Leigh, A., Ooi, M. K. J., Curran, T. J., Fairman, T. A., Resco de Dios, V., & Bradstock, R. (2021). Limits to post-fire vegetation recovery under climate change. *Plant, Cell & Environment*, 44, 3471–3489.
- Orr, Y., Shachak, M., & Steinberger, Y. (1979). Ecology of the small spotted lizard (*Eremias guttulata guttulata*) in the Negev desert (Israel). *Journal of Arid Environments*, 2, 151–161.
- Ortega, Z., & Pérez-Mellado, V. (2016). Seasonal patterns of body temperature and microhabitat selection in a lacertid lizard. *Acta Oecologica*, 77, 201–206.
- Ortega, Z., Pérez-Mellado, V., Garrido, M., Guerra, C., Villa-García, A., & Alonso-Fernández, T. (2014). Seasonal changes in thermal biology of *Podarcis lilfordi* (Squamata, Lacertidae) consistently depend on habitat traits. *Journal of Thermal Biology*, 39, 32–39.
- Pafilis, P., Herrel, A., Kapsalas, G., Vasilopoulou-Kampitsi, M., Fabre, A.-C., Foufopoulos, J., & Donihue, C. M. (2019). Habitat shapes the thermoregulation of Mediterranean lizards introduced to replicate experimental islets. *Journal of Thermal Biology*, 84, 368–374.
- Pascoe, E. L., Pareeth, S., Rocchini, D., & Marcantonio, M. (2019). A lack of “environmental earth data” at the microhabitat scale impacts efforts to control invasive arthropods that vector pathogens. *Data (Basel)*, 4, 133.
- Philippart, C. J. M., van Aken, H. M., Beukema, J. J., Bos, O. G., Cadée, G. C., & Dekker, R. (2003). Climate-related changes in recruitment of the bivalve *Macoma balthica*. *Limnology and Oceanography*, 48, 2171–2185.
- Pietrek, A. G., Walker, R. S., & Novaro, A. J. (2009). Susceptibility of lizards to predation under two levels of vegetative cover. *Journal of Arid Environments*, 73, 574–577.
- Pike, D. A., Croak, B. M., Webb, J. K., & Shine, R. (2010). Subtle—but easily reversible—anthropogenic disturbance seriously degrades habitat quality for rock-dwelling reptiles. *Animal Conservation*, 13, 411–418.
- Pincebourde, S., Murdock, C. C., Vickers, M., & Sears, M. W. (2016). Fine-scale microclimatic variation can shape the responses of organisms to global change in both natural and urban environments. *Integrative and Comparative Biology*, 56, 45–61.
- Porter, W. P., Mitchell, J. W., Beckman, W. A., & Dewitt, C. B. (1973). Behavioral implications of mechanistic ecology: Thermal and behavioral modeling of desert ectotherms and their microenvironment. *Oecologia*, 13, 1–54.
- Robertson, I. C., & Weatherhead, P. J. (1992). The role of temperature in microhabitat selection by northern water snakes (*Nerodia sipedon*). *Canadian Journal of Zoology*, 70, 417–422.
- Rozen-Rechels, D., Dupoué, A., Lourda, O., Chamaillé-Jammes, S., Meylan, S., Clobert, J., & Le Galliard, J. F. (2019). When water interacts with temperature: Ecological and evolutionary implications of thermo-hydroregulation in terrestrial ectotherms. *Ecology and evolution*, 9, 10029–10043.
- Rusch, T. W., & Angilletta, M. J. (2017). Competition during thermoregulation altered the body temperatures and hormone levels of lizards. *Functional Ecology*, 31, 1519–1528.
- Sasaki, K., Lesbarrères, D., Watson, G., & Litzgus, J. (2015). Mining-caused changes to habitat structure affect amphibian and reptile population ecology more than metal pollution. *Ecological Applications*, 25, 2240–2254.
- Scanes, C. G. (2018). Human activity and habitat loss: Destruction, fragmentation, and degradation. In *Animals and human society* (pp. 451–482). Elsevier.
- Scheers, H., & Van Damme, R. (2002). Micro-scale differences in thermal habitat quality and a possible case of evolutionary flexibility in the thermal physiology of lacertid lizards. *Oecologia*, 132, 323–331.
- Scheffers, B. R., Edwards, D. P., Diesmos, A., Williams, S. E., & Evans, T. A. (2014). Microhabitats reduce animal's exposure to climate extremes. *Global Change Biology*, 20, 495–503.
- Schwarz, R., Dror, L., Stark, G., Gefen, E., Kronfeld-Schor, N., Chapple, D. G., & Meiri, S. (2022). Conserved ecophysiology despite disparate microclimatic conditions in a gecko. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology*, 337, 316–328.
- Sears, M. W., Angilletta Jr, M. J., Schuler, M. S., Borchert, J., Dilliplane, K. F., Stegman, M., Rusch, T. W., & Mitchell, W. A. (2016). Configuration of the thermal landscape determines thermoregulatory performance of ectotherms. *Proceedings of the National Academy of Sciences of the United States of America*, 113, 10595–10600.
- Sears, M. W., Raskin, E., & Angilletta, M. J. (2011). The world is not flat: Defining relevant thermal landscapes in the context of climate change. *Integrative and Comparative Biology*, 51, 666–675.
- Shine, R., Webb, J. K., Fitzgerald, M., & Sumner, J. (1998). The impact of bush-rock removal on an endangered snake species, *Hoplocephalus bungaroides* (Serpentes: Elapidae). *Wildlife Research*, 25, 285.
- Sindaco, R., Simó-Riudalbas, M., Sacchi, R., & Carranza, S. (2018). Systematics of the *Mesalina guttulata* species complex (Squamata: Lacertidae) from Arabia with the description of two new species. *Zootaxa*, 4429, 513–547.
- Sinervo, B., Méndez-de-la-Cruz, F., Miles, D. B., Heulin, B., Bastiaans, E., Villagrán-Santa Cruz, M., Lara-Resendiz, R., Martínez-Méndez, N., Calderón-Espinosa, M. L., Meza-Lázaro, R. N., Gadsden, H., Avila, L. J., Morando, M., de la Riva, I. J., Sepulveda, P. V., Rocha, C. F. D., Ibarguengoytia, N., Puntriano, C. A., Massot, M., ... Sites, J. W., Jr. (2010). Erosion of lizard diversity by climate change and altered thermal niches. *Science*, 328, 894–899.
- Stark, G., Ma, L., Zeng, Z.-G., Du, W.-G., & Levy, O. (2022). Rocks and vegetation cover improve body condition of desert lizards during both summer and winter. *Integrative and Comparative Biology*, 62, 1031–1041.
- Sunday, J. M., Bates, A. E., Kearney, M. R., Colwell, R. K., Dulvy, N. K., Longino, J. T., & Huey, R. B. (2014). Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proceedings of the National Academy of Sciences*, 111, 5610–5615.
- Vale, C. G., & Brito, J. C. (2015). Desert-adapted species are vulnerable to climate change: Insights from the warmest region on earth. *Global Ecology and Conservation*, 4, 369–379.
- van den Berg, F. T., Thompson, M. B., & Hochuli, D. F. (2015). When hot rocks get hotter: Behavior and acclimatization mitigate exposure to extreme temperatures in a spider. *Ecosphere*, 6, art88.
- Waldschmidt, S. R., Jones, S. M., & Porter, W. P. (1987). Reptilia. In T. J. Pandian & F. J. Vernberg (Eds.), *Animal energetics* (pp. 553–619). Academic Press.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J. M., Hoegh-Guldberg, O., & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, 416, 389–395.
- Webb, J. K., & Shine, R. (1998). Using thermal ecology to predict retreat-site selection by an endangered snake species. *Biological Conservation*, 86, 233–242.
- Wieser, W. (1973). Temperature relations of ectotherms: A speculative review. In W. Wieser (Ed.), *Effects of temperature on ectothermic organisms* (pp. 1–23). Springer.
- Williams, J. J., Freeman, R., Spooner, F., & Newbold, T. (2022). Vertebrate population trends are influenced by interactions between land use, climatic position, habitat loss and climate change. *Global Change Biology*, 28, 797–815.

- Williams, J. J., & Newbold, T. (2020). Local climatic changes affect biodiversity responses to land use: A review. *Diversity and Distributions*, 26, 76–92.
- Williams, J. J., & Newbold, T. (2021). Vertebrate responses to human land use are influenced by their proximity to climatic tolerance limits. *Diversity and Distributions*, 27, 1308–1323.
- Zeng, Z.-G., Bi, J.-H., Li, S.-R., Wang, Y., Robbins, T. R., Chen, S.-Y., & du, W. G. (2016). Habitat alteration influences a desert steppe lizard community: Implications of species-specific preferences and performance. *Herpetological Monographs*, 30, 34–48.

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