

Topographic variation shapes organismal responses across mountain landscapes

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Topography is expected to mediate species' responses to climate change by providing terrain-driven microclimates that buffer animals from warming, yet how topographic shading drives animal responses to climate change remains poorly understood. Using bioenergetic simulations that incorporate topographic shading to predict the ecological and physiological consequences of climate warming, we show that topographic variation can reduce energy expenditure by as much as 20.8% and increase the buffering benefits of shifting elevation by 82.1% for diurnal ectotherms. In contrast, topographic shading provided little buffering for nocturnal ectotherms. Warming also increased energetic costs most at low elevations, widening elevational differences in energetic costs. Across North America, 48.9% of mountain ranges are depleted in topographic features that buffer the effects of warming, with tectonic history shaping present-day terrain-driven microclimates. Together, our results highlight topographic variation as a critical variable shaping organismal experiences of climate change at both landscape and continental scales.

Nearly half of assessed species are exhibiting range shifts in response to climate change¹. Although many species and populations are shifting to higher latitudes and elevations to avoid warming^{2–4}, these responses can be complex and difficult to predict^{5–8}. Topographic variation (for example, elevation, slope and aspect), in particular, may complicate predictions of species' responses to climate change by creating terrain-driven microclimates, altering rates of local warming, and modifying animal heat budgets through direct effects on incident solar radiation and indirect effects on near-surface temperature, moisture and heat exchange with the environment^{9–11}. Due to the potential for topographic variation to buffer species from warming by creating these microclimates, accurate forecasts of future range dynamics and extinction risk¹² likely depend on incorporating topography. Models grounded in thermodynamics have begun to explore the thermal consequences of topographic variation¹³ and its consequences for activity in heliothermic ectotherms¹¹, but their implications for buffering energetic and activity costs across real montane landscapes, for ectotherms with alternative activity patterns, and for the buffering potential of both elevation and aspect remain unclear. Although correlative models suggest that suitable habitat for ectotherms may shift across both elevation and aspect¹⁴, these approaches have yet to

resolve the mechanistic effects of terrain-driven solar radiation on activity and energy expenditure, or the extent to which shifts in aspect and elevation can buffer organisms from warming.

Bioenergetic models predict organismal performance across time and space, making them a powerful tool for predicting responses to climate change^{15–17}. These models use first principles to calculate energy and mass exchange between an organism and fine-scale microclimates, which allows for predictions of fitness-related metrics like activity and energy expenditure¹⁸. By linking microclimate variation to organismal performance, biophysical models play a key role in connecting climate change to population- and species-level responses by identifying the physiological and behavioural mechanisms that shape vulnerability^{19,20}. Accurate simulations rely on detailed information about the morphology, physiology and behaviour of focal organisms²¹, along with an understanding of the physical principles shaping relevant microclimates across complex topographic landscapes^{22,23}. In temperate regions, equatorial-facing slopes receive more solar radiation than poleward-facing slopes²⁴, leading to increased air and soil temperature and lower relative humidity on equatorial-facing slopes²⁵. Differences in abiotic and vegetative communities between slopes also drive variation in the distribution and abundance of mammals^{26–28}, birds²⁹, reptiles^{30,31}

and invertebrates^{32–34}. Despite the cascading effects that topography can have on ecosystems, the influence of topographic variation has been oversimplified in many bioenergetic models by assuming solar radiation on a horizontal surface. Although work has incorporated topographic effects on solar radiation into microclimate models^{10,13,35}, we still lack a clear understanding of how these effects vary across taxa with different activity patterns and how they alter predictions of elevational shifts to climate change.

We examined how topographic variation influences calculations of direct solar radiation across North America and the subsequent impacts on the ecological and physiological responses to climate change. For these simulations, we employed a case study approach with two ectotherm species, the western fence lizard (*Sceloporus occidentalis*) and the southern grey-cheeked salamander (*Plethodon metcalfi*), to demonstrate how activity and energetic cost predictions can be altered by topographic variation under current and future climates. These two species were chosen because their relationships to direct solar radiation differ dramatically: *S. occidentalis* is heliothermic and occupies arid, sparsely vegetated terrain, whereas *P. metcalfi* is nocturnal and occupies cool, forested environments. Together, they represent a broad range of possible ecological responses to topographic variation, helping identify when topographic shading meaningfully alters model predictions and when it can reasonably be ignored. We then used current and future predictions of energy expenditure for *S. occidentalis* to evaluate whether individuals could buffer the energetic costs of warming through three potential responses: shifting aspect, shifting elevation and shifting both aspect and elevation. Finally, we quantified the distributions of aspects among North American mountain ranges to determine how often landscapes are depleted in aspects that could help buffer terrestrial organisms from warming. This study demonstrates that topographic variation can markedly increase the buffering capacity of upslope movement in response to climate warming, but differences in aspect diversity across mountain ranges may constrain these benefits.

Solar radiation simulations across North America

Incorporating terrain-driven shading from topographic variation, or topographic shading, increased variability in solar radiation estimates across North America (Fig. 1a), with finer-scale effects illustrated in the focal lizard and salamander landscapes (Fig. 1b,c). We evaluated how a topographic shading treatment and terrain features influenced solar radiation predictions using effect sizes (ω^2) derived from a mixed-effects model. The topographic shading treatment compared simulations with solar radiation calculated on a horizontal plane with terrain-corrected solar radiation, and terrain features included elevation, slope and aspect. The topographic shading treatment ($\omega^2 = 0.17$), elevation ($\omega^2 = 0.16$), topographic shading treatment $\times$ northness ($\omega^2 = 0.76$), topographic shading treatment $\times$ slope ($\omega^2 = 0.23$) and topographic shading treatment $\times$ northness $\times$ slope ($\omega^2 = 0.65$) had the largest effects on solar radiation (Supplementary Fig. 1). All other predictors had very small effect sizes ($\omega^2 < 0.01$; Supplementary Table 1). Solar radiation decreased $6.3 \pm 3.3\%$ (mean $\pm$ s.d.) on northern slopes and increased $4.2 \pm 4.3\%$ on southern slopes when topographic shading was included (Fig. 1b,c). The slope of the terrain also interacted with aspect, where topographic shading had greater effects on steeper slopes (Supplementary Fig. 1e). For example, considering the steepest 10% of slopes across the landscape, there was an $18.0 \pm 7.6\%$ decrease in solar radiation on northern slopes and a $10.0 \pm 6.2\%$ increase on southern slopes after including topographic shading (mean $\pm$ s.d.). We then incorporated topographic shading into bioenergetic models for lizards and salamanders to understand the downstream effects on duration of activity and energy expenditure.

Lizard activity and energetics

For lizards, topographic shading altered activity (h yr⁻¹) and energy expenditure (kJ yr⁻¹) across the simulated landscapes, which we

illustrated using polar plots that included several interactions (Fig. 2). Changes in yearly activity and energy expenditure ranged from 19.5% to -27.8% and from 10.7% to -20.8%, respectively (Fig. 2a,d). Both yearly activity and metabolic energy expenditure for lizards were strongly affected by climate period (current or future), elevation and the interaction between the topographic shading treatment and northness (Supplementary Figs. 2 and 3). Lizards were more active and expended more energy in the future climate period ($\omega^2 = 0.63$ for activity; $\omega^2 = 0.98$ for energy expenditure) and at lower elevations ($\omega^2 = 0.81$ for activity; $\omega^2 = 0.94$ for energy expenditure). The topographic shading treatment alone had small effects on lizard activity and energy expenditure ($\omega^2 \leq 0.01$ for both; Supplementary Table 1), but the interaction between topographic shading and northness had a large effect on activity ($\omega^2 = 0.23$) and energy expenditure ($\omega^2 = 0.54$). Northness also had a large independent effect on lizard activity ($\omega^2 = 0.14$). The polar plots illustrate that activity and energy expenditure increased on southern slopes and decreased on northern slopes when solar radiation was corrected for terrain (Fig. 2a,d). Based on these plots, changes appeared to be especially pronounced during the current climate period for northern slopes (Fig. 2b,e) and at higher elevations for both northern and southern slopes (Fig. 2c,f). These shifts in activity and energy expenditure may reflect lower initial values at high elevations and during the current period, making changes due to topographic shading proportionally larger. Additionally, there was a strong interaction between climate period and elevation for lizard metabolism and activity ('Warming steepens physiological gradients along mountains').

Including topographic shading led to temporal shifts in lizard activity and energy expenditure that were mediated by aspect and slope (Extended Data Fig. 1). Lizards on northern slopes experienced contractions in activity at the beginning and end of the active season, while the length of the active season increased for lizards on southern slopes (Extended Data Fig. 1a). On eastern and western slopes, topographic shading altered diel patterns of activity rather than season length, with lizards on eastern slopes emerging and retreating earlier in the day and lizards on western slopes emerging and retreating later in the day. Shifts in energy expenditure mirrored those of activity across all aspects but were more modest (Extended Data Fig. 1b). The magnitude of shifts in activity and energy expenditure also increased with slope steepness (Supplementary Fig. 4), with lizards on steeper slopes experiencing greater effects of topography. Overall, topographic shading produced heterogeneity in seasonal and diel timing of lizard activity and metabolism, with aspect shaping the type of shift and slope determining its strength.

Salamander activity and energetics

Being nocturnal, topographic shading had a much smaller effect on salamanders. Metabolic energy expenditure experienced small shifts across all locations (ranging from 0.15% to -0.19%), while topographic shading increased or decreased salamander activity for only 0.09% of locations across the simulated landscape. Like lizards, salamander energy expenditure increased under the future climate scenario ($\omega^2 = 1.00$) and decreased with elevation ($\omega^2 = 0.72$; Supplementary Fig. 5), while their activity slightly decreased in the future period ($\omega^2 = 0.08$) and increased at higher elevations ($\omega^2 = 0.88$; Supplementary Fig. 6). We also detected important interactions between climate period and elevation for salamander metabolism and activity ('Warming steepens physiological gradients along mountains'). All other predictors of salamander activity and energetics had small effect sizes ($\omega^2 \leq 0.02$; Supplementary Table 1).

Warming steepens physiological gradients along mountains

To test whether the consequences of topographic shading depended on climate scenarios, we tested for interactions among topographic

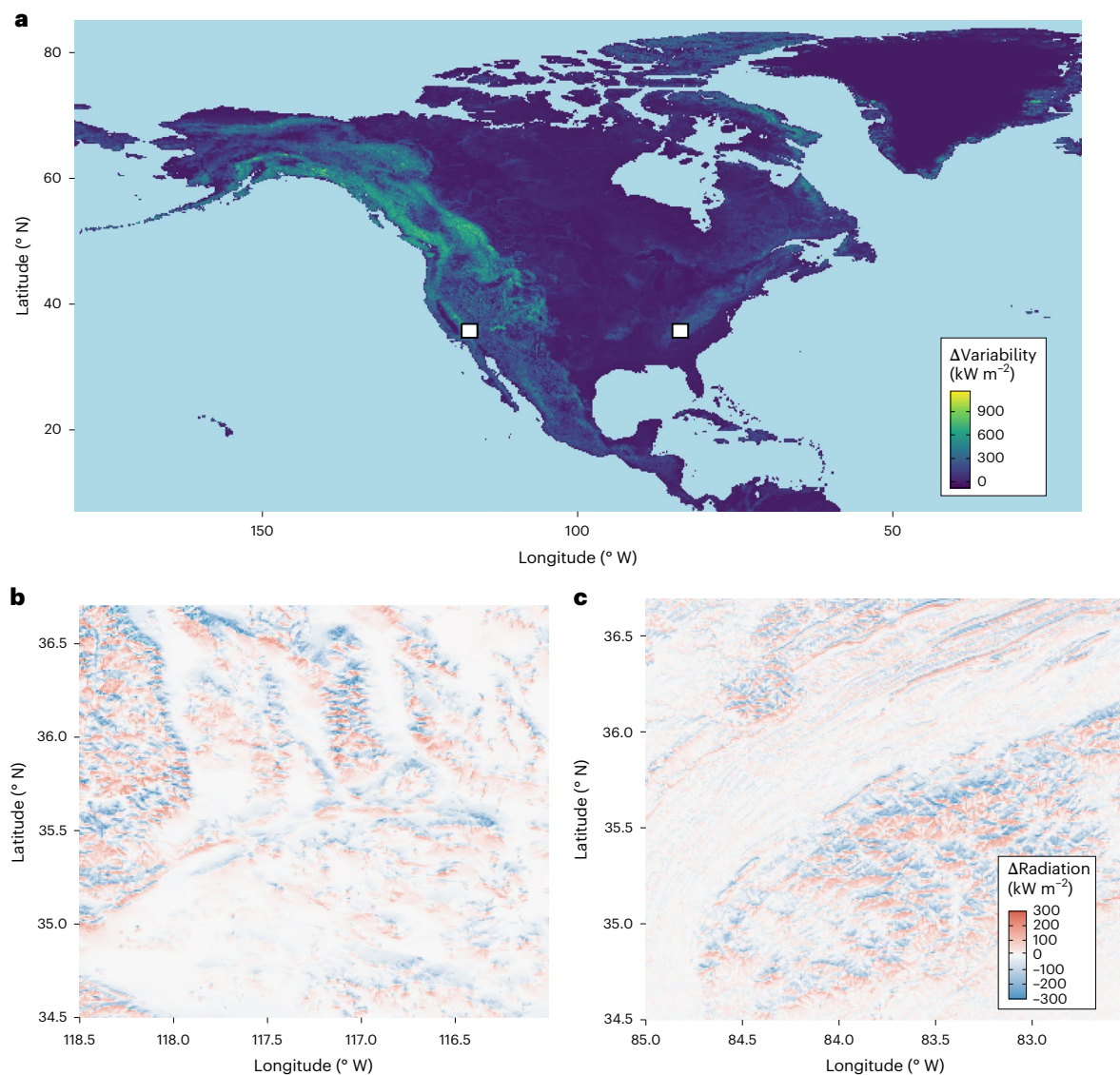


Fig. 1 | Topographic shading influences on annual solar radiation predictions across North America. a, Change in variability of solar radiation calculated by coarsening rasters of solar radiation by a factor of 25 (to $\sim 0.21^\circ$ resolution) and computing the range of solar radiation within each block ($\Delta\text{Variability} = \text{range}_{\text{shade}} - \text{range}_{\text{no shade}}$). White boxes indicate approximate biophysical modelling regions for

S. occidentalis in southern California (**b**) and *P. metcalfi* in the southern Appalachians (**c**). **b, c,** Changes in solar radiation with topographic shading (WGS84; $\sim 0.0083^\circ$ resolution). Red areas indicate increases in solar radiation when topographic effects were included, while blue areas indicate decreases in solar radiation (underlying elevation and slope data from refs. 59,60).

shading, elevation and climate scenario. The effects of topographic shading did not vary between current and future climate scenarios; however, lizard and salamander energy expenditure showed a large interaction with climate period and elevation ($\omega^2 = 0.85$ for lizards, $\omega^2 = 0.80$ for salamanders). Energy expenditure was consistently higher under future warming and decreased with elevation in both climate scenarios. However, the increase in energy expenditure under future climate conditions was greatest at lower elevations and diminished with elevation, resulting in larger differences between periods at lower elevations (Extended Data Fig. 2a,b). The interaction between climate period and elevation also influenced lizard and salamander activity ($\omega^2 = 0.38$ for lizards, $\omega^2 = 0.18$ for salamanders). For lizards, activity generally increased in the future, except at lower elevations where high temperatures restricted activity (Extended Data Fig. 2c). For salamanders, activity strongly increased at high elevations but not lower elevations (Extended Data Fig. 2d). The interaction between climate scenario and elevation likely results from the non-linearity of metabolic rate for ectotherms, in which metabolic rates increase at a faster rate at

warmer temperatures³⁶. From this energetic perspective, elevational gradients are energetically steeper under future warming scenarios than current scenarios.

Elevation and aspect shifts buffer future energetic costs

We then used dispersal simulations to understand how diurnal ectotherms, like *S. occidentalis*, might use elevation and aspect, both in isolation and collectively, to minimize the activity and energetic costs associated with climate warming. These simulations revealed that shifting to cooler aspects can substantially increase the buffering capacity of movement. We modelled the energetic buffering capacity, defined as the capacity of an individual to reduce the impact of future warming on energy expenditure by dispersing to environments with the same energetic costs as their original location under current climate conditions. By shifting only in aspect or only elevation, energetic buffering capacity was $1.5 \pm 5.4\%$ and $16.8 \pm 20.9\%$, respectively (median $\pm$ s.d.; Fig. 3a). However, by allowing both dispersal

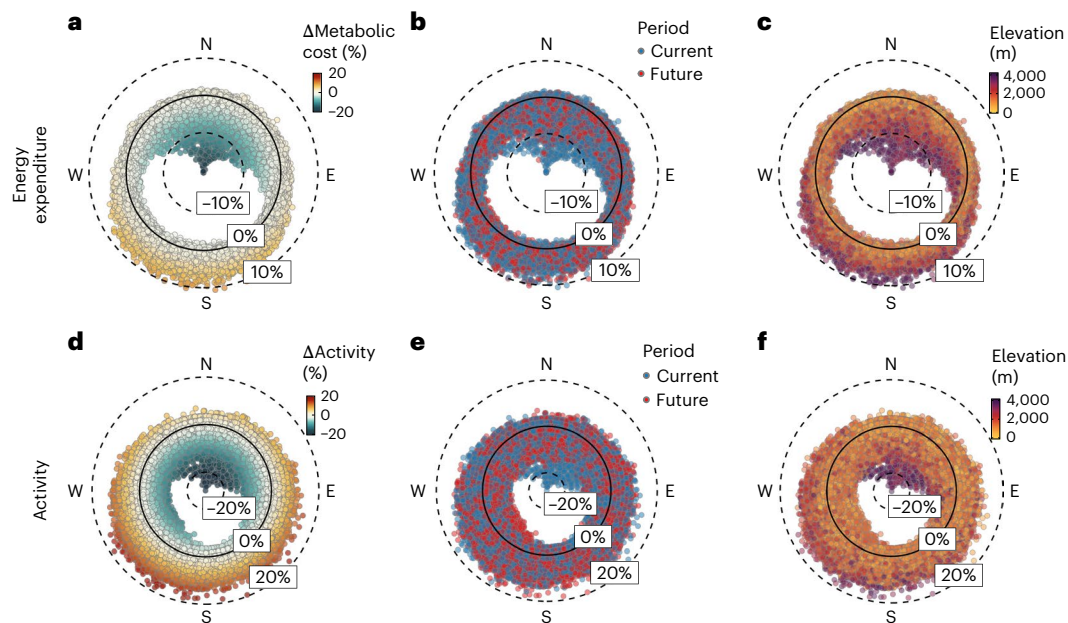


Fig. 2 | Variable impact of topographic shading on lizard energy expenditure and activity across aspects. **a–f**, Polar plots showing the percentage change in lizard metabolic energy expenditure (**a–c**) and activity (**d–f**) across slope aspect when topographic shading is incorporated. Points represent unique locations

and are coloured by percentage change (**a,d**), climate period (**b,e**) and elevation (**c,f**). Solid black rings indicate no change, and black dashed rings indicate $\pm 10\%$ change (**a–c**) or $\pm 30\%$ change (**d–f**). Percentage changes were calculated relative to predictions assuming horizontal radiation.

across aspect and elevation, median buffering capacity increased to $30.6 \pm 21.9\%$ (Fig. 3a). Moreover, the number of individuals decreased on south-facing slopes and increased on north-facing slopes in the future warming scenario (Fig. 3b), indicating that availability of cool, northern slopes will be critical for organisms to buffer themselves against warming. When topographic shading was not included, fewer individuals shifted to northern slopes and experienced the full energetic buffering potential of shifting aspects (Fig. 3a,b). Specifically, the number of individuals occupying northern slopes increased by 119.0% when topographic shading was included, compared to only 10.0% without shading. For diurnal species, the ability of species to shift aspect along with elevation may be critical for mitigating the negative effects of climate change.

Aspect diversity across North American mountains

Because slope aspect influences solar exposure and the thermal environments available to organisms, we quantified aspect diversity across North American mountain ranges. Across all North American mountain ranges, east- and west-facing slopes were slightly overrepresented, accounting for 28.1% and 27.7% of montane surface area, respectively (Fig. 4a). The more shaded, north-facing slopes were the most underrepresented, accounting for 21.9% of surface area (Fig. 4a). However, individual mountain ranges displayed diverse aspect profiles, varying in the degree and direction of aspect skew (Fig. 4b–f and Supplementary Table 2). Many mountain ranges were skewed towards eastern and/or western slopes (44.4%), but others were skewed along different axes (southwest–northeast: 15.6%; southeast–northwest: 4.4%; north–south: 4.4%) or not biased at all (31.1%; Fig. 4g). Aspect availability also differed across elevation (Supplementary Fig. 7). For example, the Greater Yellowstone Rockies, which overall exhibits a uniform distribution of aspects, has a greater availability of east- and north-facing slopes at lower elevations. Variation in aspect distributions along elevational gradients and among North American mountain ranges likely reflects geological history and could shape species' responses to climate change by influencing the availability of terrain-driven microclimates.

Discussion

Our simulations reveal the potential for topographic variation, beyond simply elevation, to provide terrain-driven microclimates that buffer organisms from climate change. Our models demonstrated that topographic shading redistributed direct solar radiation across slopes and aspects, increasing microclimate heterogeneity (Fig. 1). Microclimate differences translated to changes in energy expenditure and activity, with southern slopes experiencing increases and northern slopes experiencing decreases (Fig. 2a,d), especially at high elevations (Fig. 2c,f) under current climatic conditions (Fig. 2b,e). As a result of these differences in energy expenditure, dispersal simulations revealed that shifting aspects along with elevation substantially reduced the energetic costs of future warming. Indeed, the energetic benefits of shifting elevation increased by 82.1% when organisms also shifted from southern slopes to more northerly slopes, which occurred more often when topographic shading was incorporated (Fig. 3). Feldmeier et al.¹⁴ similarly highlighted that aspect shifts may complement elevational shifts in montane ectotherms, but their correlative framework did not explicitly model topographic shading, its effects on the thermal environment or the body temperatures experienced by organisms, which are central to our approach. Our results demonstrate that the interplay between topographic complexity, local microclimates and organismal ecophysiology will have important consequences for species movement and persistence under climate change. Models that predict the ecological consequences of climate change but ignore the full breadth of topographic variation may overestimate extinction risk.

We also assessed the potential for terrain-driven buffering by examining the availability of cool slopes across North America. North American mountain ranges vary substantially in their aspect distributions (Fig. 4), and much of this variation appears to reflect the diverse geological histories of mountain ranges. For example, many volcanic mountain ranges (for example, Oregon Coast Range, Aleutian Range and Trans-Mexican Volcanic Belt) have uniform aspect distributions, reflecting the process of magma erupting and cooling to form cone-like structures³⁷. Other mountain ranges like the Appalachian and Ouachita Mountains (Fig. 4) are fold mountains and have bimodal aspect biases orthogonal to their range orientation (for example, mountain ranges

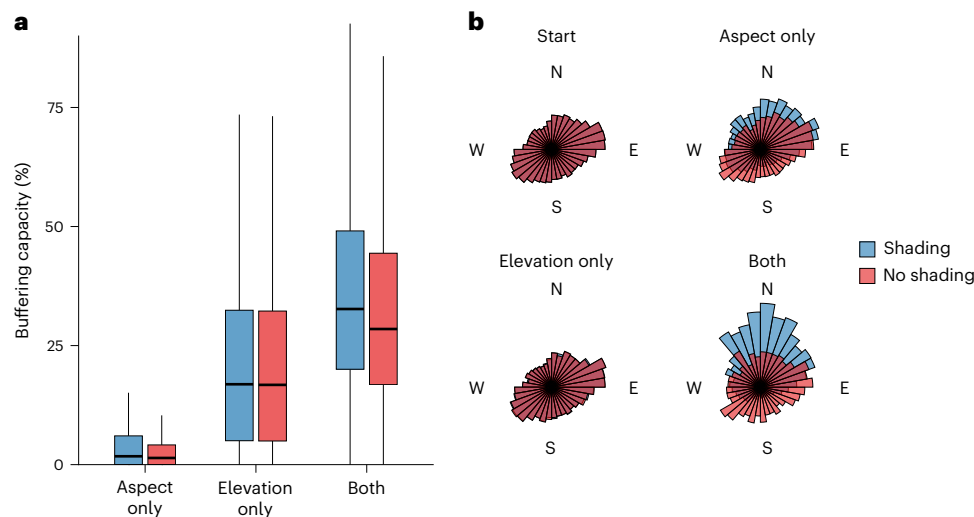


Fig. 3 | Differences in predicted buffering capacity and aspect shifts across climate change responses. a, Metabolic buffering capacity of climate response strategies where individuals can shift aspect, elevation or both aspect and elevation. Buffering capacity quantifies how well individuals could maintain their current metabolic costs by changing locations, relative to remaining in the same location ($n = 42,332$ unique starting locations). Data are presented as boxplots where the lower and upper hinges represent the 25th and 75th percentiles, respectively, and the middle line represents the median. Lower and

upper whiskers represent the minimum and maximum values within 1.5 times the interquartile range of the lower and upper hinges, respectively. Outliers are not plotted to improve visual clarity. **b**, Starting and ending aspect distributions for lizards in the three climate response simulations. Colours in **a** and **b** indicate whether metabolic energy expenditure values were produced for simulations that included topographic shading (shading, blue) or assumed horizontal direct solar radiation (no shading, red).

which run north–south predominantly have east- and west-facing slopes). Fold mountains are generally formed through the compression and folding of the Earth's crust along convergent plate boundaries, creating long, linear mountain ranges³⁷. Fault-block mountain ranges including the Sierra Nevada and Southwest Basins and Ranges have more unimodal aspect biases. These ranges occur when part of the Earth's surface is displaced, often resulting in tilted blocks that are steep on one side (low surface area and aspect bias) and gently sloping on the other (high surface area and aspect bias)³⁷. The unique geological history of each mountain range, influenced by interactions of tectonic plates, drives current patterns in aspect-driven microclimate availability, with potential consequences for species distributions now and in the future.

The specific aspect distribution of a mountain range may affect how organisms both experience and respond to climate change. If north-facing slopes warm slower¹⁰, they may limit species exposure to climate change. When these cool aspects are abundant, species can more easily buffer the effects of climate change by shifting aspects. However, our analysis revealed that nearly half of all mountain ranges in North America have limited availability of cool, northern or north-eastern slopes (48.9%; Fig. 4). These ranges, which primarily run north–south or northeast–southwest, may restrict opportunities for aspect shifts. Instead, species in these areas may benefit from latitudinal movement corridors associated with north–south-oriented mountain chains³⁸. Elevation-dependent aspect distributions may also limit or facilitate shifts to higher, cooler slopes, depending on a species' current altitudinal distribution (Supplementary Fig. 7). Physical constraints on aspect availability will lay the foundation for species-specific responses to climate change in montane landscapes.

Species differ in their physiological sensitivities^{39–41} and behavioural strategies, making aspect-associated climate buffering inherently species-specific. We detected divergent effects of aspect and topographic shading based on species' life history and local environment. In our bioenergetic models, behavioural and physiological predictions for diurnal, desert-dwelling ectotherms responded strongly to aspect and topographic shading, shifting the total amount and timing of energy expenditure (Fig. 2 and Extended Data Fig. 1). In contrast, the

behaviour and physiology of nocturnal ectotherms in a forested environment were largely insensitive to topographic shading and aspect (Supplementary Fig. 6). Nocturnal activity periods combined with canopy shading in forested environments largely decoupled nocturnal ectotherm body temperatures from direct solar radiation, minimizing the potential effects of topographic shading on activity and energetics. These results indicate that diurnal ectotherms in environments with sparse vegetation may benefit more from microrefugia associated with aspect and topographic shading compared to nocturnal ectotherms inhabiting forested environments^{42,43}. Species-specific differences may be further complicated by indirect effects of aspect beyond direct solar radiation.

Topographic shading across aspects has cascading effects on the abiotic and biotic features of ecosystems^{24,25}. Our model incorporated the effects of topographic shading as changes in direct solar radiation and its effects on soil temperature, but indirect effects of topographic shading on soil moisture⁴⁴ and vegetative communities³⁸ were not considered. Recent work has shown that vegetation restructures the strength and direction of climate velocities, with dense areas of tropical forest providing microclimate refugia⁴⁵. In temperate forests, aspect often has strong effects on vegetative communities^{46,47}. Therefore, organisms in temperate mountains may still display preferences for aspects driven by the indirect effects of topographic shading, despite not being affected by variation in direct solar radiation (for example, nocturnal ectotherms). This is supported by the frequent observation that the abundance and species richness of nocturnal ectotherms is often higher on northern slopes^{32,48–51}. The direct and indirect effects of topographic shading likely influence individual behaviour and physiology, and shape ecological responses to climate change.

The effects of climate change on ectotherm populations are expected to be mediated by energetic constraints⁵². Ectotherm metabolism scales exponentially with temperature, meaning the same degree of warming will have a disproportionate effect on metabolic demand for populations starting at warmer baseline temperatures, like those at lower elevations⁵³. Our results are consistent with this principle, predicting that future increases in metabolic costs for ectotherms will be greatest at lower elevations (Extended Data Fig. 2a,b). In other words, with warming temperatures, mountains will become 'energetically

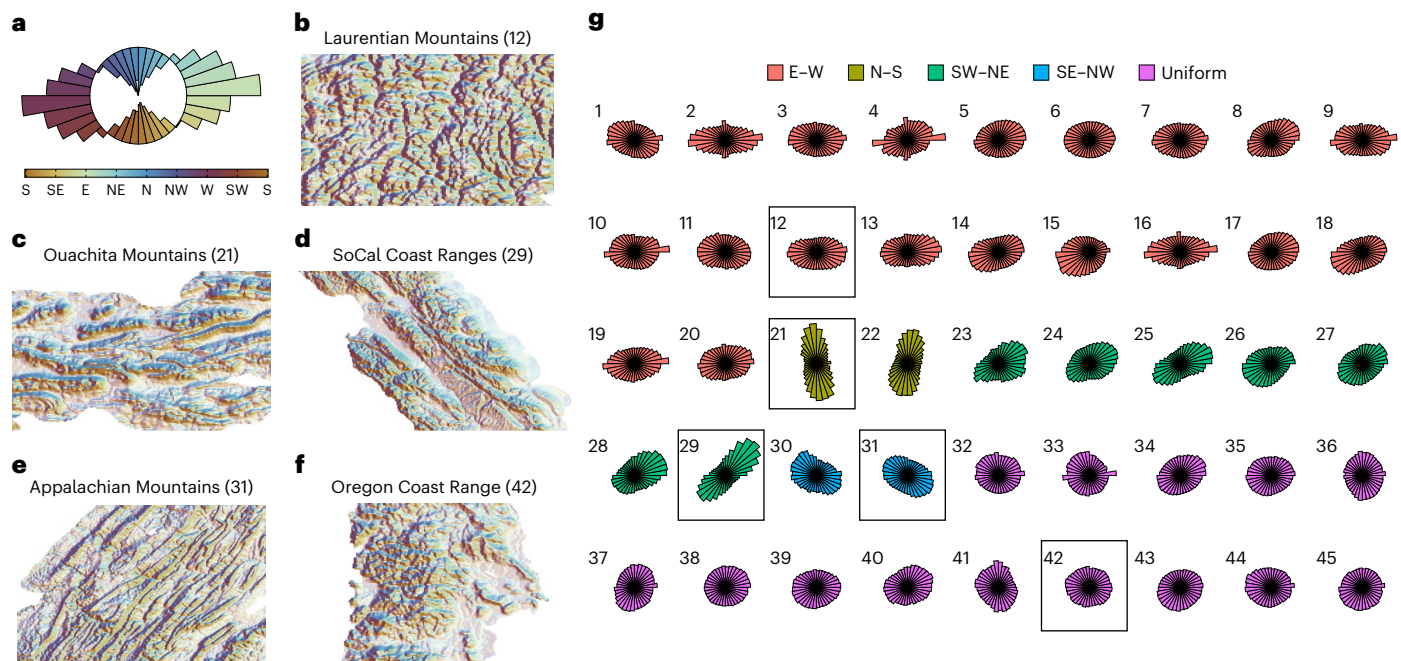


Fig. 4 | Aspect distributions of North American mountain ranges. **a**, The relative representation of aspects across all North American mountain ranges, where bars extending outwards are overrepresented aspects, while bars extending inwards are underrepresented aspects. **b–f**, Slope-aspect maps of mountain ranges representing the five aspect distribution categories: east–west (**b**), north–south (**c**), southwest–northeast (**d**), southeast–northwest (**e**) and uniform (**f**). The colour of each cell corresponds to aspect, and areas with steeper

slopes are more opaque. All maps have the same spatial resolution ($\approx 0.0083^\circ$) but vary in spatial extent to facilitate visualization. Parenthetical numbers correspond to the numbers in **g** (range outlines in **b–f** from refs. 61,62). **g**, Individual aspect distributions for each North American mountain range shown as circular histograms. Colours indicate the aspect distribution category, and numbers correspond to mountain range names in Supplementary Table 2. Black boxes indicate mountain ranges shown in **b–f**.

steeper', such that the energetic difference between low and high elevations will be greater in the future than it is today. Janzen⁵⁴ famously argued that dispersal barriers in montane ecosystems are shaped by the steepness of altitudinal thermal gradients relative to species' physiological tolerances, leading him to propose that tropical mountains are 'higher' than temperate mountains because even modest changes in elevation can move tropical organisms outside the narrow range of temperatures to which they are adapted⁵⁴. We expect that temperate mountains will become similarly 'higher' in the future for ectotherms from an energetic perspective, which will limit dispersal among mountains and increase the need for ectotherms to exploit higher elevations and cooler slopes. Rapidly increasing energetic costs may also compromise fitness⁵⁵, potentially leading to population extirpation at low elevation and explaining why altitudinal range shifts are more common in ectotherms than endotherms⁵⁶.

Our simulations were designed to isolate the potential for elevation and aspect shifts to buffer metabolic costs for ectotherms rather than assess the complete feasibility of movement. Realized movement will also depend on other traits and processes, including critical thermal limits, hydration state, life stage, predation risk, prey availability, habitat structure, dispersal motivation and species-specific movement behaviour. Additionally, we assumed phenotypic traits do not change across space. Thus, our approach does not capture population-specific variation in morphology, physiology, behaviour or life history that may occur across elevational gradients^{57,58}. Future work investigating animal responses to warming should consider other ecological factors affecting dispersal and incorporate geographic variation in phenotypic traits. Mechanistic bioenergetic models, like those used here, provide a flexible framework which could accommodate more complex models of dispersal and trait variation.

The fate of montane biodiversity in the context of global warming will depend on species' ability to adapt to new conditions or track favourable climates. The direction of favourable environments has

often been simplified to higher latitudes and elevations; however, empirical evidence suggests that responses to warming are more variable⁶. We show that a narrow focus on elevation inhibits a comprehensive understanding of topographic influences on organismal resilience to climate change. Instead, predictions should incorporate other axes of topography (for example, aspect and slope) and their downstream effects on abiotic conditions and biotic communities to identify micro-refugia under global warming.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41558-026-02773-z>.

References

1. IPCC *Climate Change 2023: Synthesis Report* (eds Core Writing Team, Lee, H. & Romero, J.) AR6 Synthesis Report: Climate Change 2023 <https://www.ipcc.ch/report/ar6/syr/> (IPCC, 2023).
2. Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B. & Thomas, C. D. Rapid range shifts of species associated with high levels of climate warming. *Science* **333**, 1024–1026 (2011).
3. Lenoir, J. et al. A significant upward shift in plant species optimum elevation during the 20th century. *Science* **320**, 1768–1771 (2008).
4. Parmesan, C. & Yohe, G. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42 (2003).
5. La Sorte, F. A. & Jetz, W. Tracking of climatic niche boundaries under recent climate change. *J. Anim. Ecol.* **81**, 914–925 (2012).
6. Rubenstein, M. A. et al. Climate change and the global redistribution of biodiversity: substantial variation in empirical support for expected range shifts. *Environ. Evid.* **12**, 7 (2023).

7. Chen, Y.-H., Lenoir, J. & Chen, I.-C. Limited evidence for range shift-driven extinction in mountain biota. *Science* **388**, 741–747 (2025).
8. Lawlor, J. A. et al. Mechanisms, detection and impacts of species redistributions under climate change. *Nat. Rev. Earth Environ.* **5**, 351–368 (2024).
9. Ashcroft, M. B., Chisholm, L. A. & French, K. O. Climate change at the landscape scale: predicting fine-grained spatial heterogeneity in warming and potential refugia for vegetation. *Glob. Change Biol.* **15**, 656–667 (2009).
10. Maclean, I. M. D., Suggitt, A. J., Wilson, R. J., Duffy, J. P. & Bennie, J. J. Fine-scale climate change: modelling spatial variation in biologically meaningful rates of warming. *Glob. Change Biol.* **23**, 256–268 (2017).
11. Sears, M. W., Raskin, E. & Angilletta, M. J. Jr The world is not flat: defining relevant thermal landscapes in the context of climate change. *Integr. Comp. Biol.* **51**, 666–675 (2011).
12. Suggitt, A. J. et al. Extinction risk from climate change is reduced by microclimatic buffering. *Nat. Clim. Change* **8**, 713–717 (2018).
13. Bennie, J., Huntley, B., Wiltshire, A., Hill, M. O. & Baxter, R. Slope, aspect and climate: spatially explicit and implicit models of topographic microclimate in chalk grassland. *Ecol. Model.* **216**, 47–59 (2008).
14. Feldmeier, S. et al. Shifting aspect or elevation? The climate change response of ectotherms in a complex mountain topography. *Divers. Distrib.* **26**, 1483–1495 (2020).
15. Briscoe, N. J. et al. Mechanistic forecasts of species responses to climate change: the promise of biophysical ecology. *Glob. Change Biol.* **29**, 1451–1470 (2023).
16. Buckley, L. B. et al. Can mechanism inform species' distribution models? *Ecol. Lett.* **13**, 1041–1054 (2010).
17. Kearney, M. & Porter, W. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecol. Lett.* **12**, 334–350 (2009).
18. Kearney, M. R. & Porter, W. P. NicheMapR – an R package for biophysical modelling: the ectotherm and Dynamic Energy Budget models. *Ecography* **43**, 85–96 (2020).
19. Wild, K. H. et al. Climate change and the cost-of-living squeeze in desert lizards. *Science* **387**, 303–309 (2025).
20. Buckley, L. B. Linking traits to energetics and population dynamics to predict lizard ranges in changing environments. *Am. Nat.* **171**, E1–E19 (2008).
21. Riddell, E. A. et al. Parameterizing mechanistic niche models in biophysical ecology: a review of empirical approaches. *J. Exp. Biol.* **226**, jeb245543 (2023).
22. Maclean, I. M. D. & Klings, D. H. Microclimc: a mechanistic model of above, below and within-canopy microclimate. *Ecol. Model.* **451**, 109567 (2021).
23. Meyer, A. V., Sakairi, Y., Kearney, M. R. & Buckley, L. B. A guide and tools for selecting and accessing microclimate data for mechanistic niche modeling. *Ecosphere* **14**, e4506 (2023).
24. Maclean, I. M. D., Hopkins, J. J., Bennie, J., Lawson, C. R. & Wilson, R. J. Microclimates buffer the responses of plant communities to climate change. *Glob. Ecol. Biogeogr.* **24**, 1340–1350 (2015).
25. Desta, F., Colbert, J. J., Rentch, J. S. & Gottschalk, K. W. Aspect Induced differences in vegetation, soil, and microclimatic characteristics of an Appalachian watershed. *Castanea* **69**, 92–108 (2004).
26. Hall, L. E., Chalfoun, A. D., Beever, E. A. & Loosen, A. E. Microrefuges and the occurrence of thermal specialists: implications for wildlife persistence amidst changing temperatures. *Clim. Chang. Responses* **3**, 8 (2016).
27. Kilgore, M. J. & Fairbanks, W. S. Winter habitat selection by reintroduced pronghorn on Antelope Island, Great Salt Lake, Utah. *Gt Basin Nat.* **57**, 149–154 (1997).
28. Shuai, L.-Y., Ren, C.-L., Yan, W.-B., Song, Y.-L. & Zeng, Z.-G. Different elevational patterns of rodent species richness between the southern and northern slopes of a mountain. *Sci. Rep.* **7**, 8743 (2017).
29. Shields, W. M. & Grubb, T. C. Winter bird densities on north and south slopes. *Wilson Bull.* **86**, 125–130 (1974).
30. Michael, D. R., Ikin, K., Crane, M., Okada, S. & Lindenmayer, D. B. Scale-dependent occupancy patterns in reptiles across topographically different landscapes. *Ecography* **40**, 415–424 (2017).
31. Schwarz, R., Stark, G. & Meiri, S. A shift in reptile diversity and abundance over the last 25 years. *Isr. J. Ecol. Evol.* **65**, 10–20 (2019).
32. Finkel, M. et al. Arachnid assemblage composition diverge between south- and north-facing slopes in a Levantine microgeographic site. *Diversity* **16**, 540 (2024).
33. Gilgado, J. D. et al. Six groups of ground-dwelling arthropods show different diversity responses along elevational gradients in the Swiss Alps. *PLoS ONE* **17**, e0271831 (2022).
34. Tolbert, W. W. The effects of slope exposure on arthropod distribution patterns. *Am. Midl. Nat.* **94**, 38–53 (1975).
35. Maclean, I. M. D. Microclimf: Fast modelling of microclimate across real landscapes in R. *Methods Ecol. Evol.* **17**, 1112–1123 <https://doi.org/10.1111/2041-210x.70253> (2026).
36. Angilletta, M. J. *Thermal Adaptation: A Theoretical and Empirical Synthesis* <https://doi.org/10.1093/acprof:oso/9780198570875.001.1> (Oxford Univ. Press, 2009).
37. Price, M. F. *Mountain Geography: Physical and Human Dimensions* (Univ. of California Press, 2013).
38. Ackerly, D. D. et al. Topoclimates, refugia, and biotic responses to climate change. *Front. Ecol. Environ.* **18**, 288–297 (2020).
39. Buckley, L. B., Hurlbert, A. H. & Jetz, W. Broad-scale ecological implications of ectothermy and endothermy in changing environments. *Glob. Ecol. Biogeogr.* **21**, 873–885 (2012).
40. Buckley, L. B., Khaliq, I., Swanson, D. L. & Hof, C. Does metabolism constrain bird and mammal ranges and predict shifts in response to climate change? *Ecol. Evol.* **8**, 12375–12385 (2018).
41. Khaliq, I. et al. Global variation in thermal physiology of birds and mammals: evidence for phylogenetic niche conservatism only in the tropics. *J. Biogeogr.* **42**, 2187–2196 (2015).
42. Gaudenti, N., Nix, E., Maier, P., Westphal, M. F. & Taylor, E. N. Habitat heterogeneity affects the thermal ecology of an endangered lizard. *Ecol. Evol.* **11**, 14843–14856 (2021).
43. De Frenne, P. et al. Global buffering of temperatures under forest canopies. *Nat. Ecol. Evol.* **3**, 744–749 (2019).
44. Stark, J. R. & Fridley, J. D. Topographic drivers of soil moisture across a large sensor network in the Southern Appalachian Mountains (USA). *Water Resour. Res.* **59**, e2022WR034315 (2023).
45. Soifer, L. G., Ball, J., Asmath, H., Maclean, I. M. D. & Coomes, D. Microclimates slow and alter the direction of climate velocities in tropical forests. *Nat. Clim. Change* **16**, 95–101 (2025).
46. Yang, J., El-Kassaby, Y. A. & Guan, W. The effect of slope aspect on vegetation attributes in a mountainous dry valley, Southwest China. *Sci. Rep.* **10**, 16465 (2020).
47. Singh, S. Understanding the role of slope aspect in shaping the vegetation attributes and soil properties in Montane ecosystems. *Trop. Ecol.* **59**, 417–430 (2018).
48. O'Donnell, K. M., Thompson, F. R. & Semlitsch, R. D. Partitioning detectability components in populations subject to within-season temporary emigration using binomial mixture models. *PLoS ONE* **10**, e0117216 (2015).
49. Harper, C. A. & Guynn, D. C. Factors affecting salamander density and distribution within four forest types in the Southern Appalachian Mountains. *For. Ecol. Manag.* **114**, 245–252 (1999).

50. Khatiwada, J. R. & Haugaasen, T. Anuran species richness and abundance along an elevational gradient in Chitwan, Nepal. *Zool. Ecol.* **25**, 110–119 (2015).
51. Tatarian, P. J. Movement patterns of California red-legged frogs (*Rana draytonii*) in an inland California environment. *Herpetol. Conserv. Biol.* **3**, 155–169 (2008).
52. Dillon, M. E., Wang, G. & Huey, R. B. Global metabolic impacts of recent climate warming. *Nature* **467**, 704–706 (2010).
53. Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M. & Charnov, E. L. Effects of size and temperature on metabolic rate. *Science* **293**, 2248–2251 (2001).
54. Janzen, D. H. Why mountain passes are higher in the tropics. *Am. Nat.* **101**, 233–249 (1967).
55. Huey, R. B. & Kingsolver, J. G. Climate warming, resource availability, and the metabolic meltdown of ectotherms. *Am. Nat.* **194**, E140–E150 (2019).
56. Ramalho, Q. et al. Evidence of stronger range shift response to ongoing climate change by ectotherms and high-latitude species. *Biol. Conserv.* **279**, 109911 (2023).
57. Powers, S. D., McTernan, M. R., Powers, D. R. & Anderson, R. A. Energetic consequences for a northern, range-edge lizard population. *Copeia* **106**, 468–476 (2018).
58. Sears, M. W. & Angilletta, M. J. Jr Body size clines in *Sceloporus* lizards: proximate mechanisms and demographic constraints. *Integr. Comp. Biol.* **44**, 433–442 (2004).
59. Amatulli, G. et al. A suite of global, cross-scale topographic variables for environmental and biodiversity modeling. *Sci. Data* **5**, 180040 (2018).
60. Fick, S. E. & Hijmans, R. J. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* **37**, 4302–4315 (2017).
61. Snethlage, M. A. et al. A hierarchical inventory of the world's mountains for global comparative mountain science. *Sci. Data* **9**, 149 (2022).
62. Snethlage, M. A. et al. GMBA Mountain Inventory v2. *GMBA-EarthEnv* <https://doi.org/10.48601/earthenv-t9k2-1407> (2022).

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Methods

General approach

We first developed a topographic shading algorithm ('General topographic shading algorithm') to understand how topographic variation influences solar radiation across North America ('Solar radiation simulations across North America'). We then used bioenergetic models to examine the impact of topographic shading on predictions of activity and energy expenditure for two ectotherm species occupying different habitats: western fence lizards (*S. occidentalis*) in southern California (spatial extent: 116.13–118.52° W and 34.52–36.74° N) and the southern grey-cheeked salamander (*P. metcalfei*) in the southern Appalachians (spatial extent: 80.00–85.00° W and 34.00–38.00° N) ('Lizard simulations of activity and energetics' and 'Salamander simulations of activity and energetics'). These models generated hourly predictions of operative temperatures (or humid operative temperatures for salamanders), potential durations of daily activity and energy expenditure integrated across the year based on conditions from the middle day of each month, representing the monthly average. Values for a given month were multiplied by the number of days in that month and summed to obtain yearly values. We implemented models under current (1970–2000) and future climate conditions (2081–2100; Global Circulation Model (GCM): Euro-Mediterranean Center on Climate Change Earth System Model2 (CMCC-ESM2); scenario: Shared Socioeconomic Pathway 3-7.0) using WorldClim v.2.1 temperature and elevation data and EarthEnv slope data with a spatial resolution of 30 arcsec^{59,60}. Because this framework compares two climate-period averages rather than continuous annual or decadal trajectories, it does not evaluate non-linear changes in energetic costs through time or capture short-term temperature variability, including extreme events such as heatwaves. At 30-arcsec resolution, our model captures landscape-scale topographic effects, including mountains, large hillslopes, elevational gradients and major differences in slope aspect, but does not resolve fine-scale microtopography such as boulders, small ravines and other metre-scale refugia. We calculated aspect values from the 30-arcsec WorldClim elevation raster using the terra package in R⁶³. To understand the impact of terrain, we ran simulations with and without a topographic shading algorithm for each species and climate period combination. We conducted simulations in Python (v.3.10.7) using an array-based approach, which we describe in greater detail below. We then developed a dispersal model to understand how elevation and aspect influence the capacity of a lizard to buffer the energetic costs of warming ('Elevation and aspect shifts buffer future energetic costs' in the Methods). Finally, we characterized the distributions of aspect diversity across mountain ranges in North America to determine the extent to which mountain ranges lack aspects that may buffer organisms from climate warming ('Aspect diversity across North American mountains' in the Methods).

General topographic shading algorithm

An important component of modelling microclimates is calculating the amount of solar radiation received by a location. Here we define a topographic shading algorithm that accounts for terrain-driven shading from slope, aspect, self-shading and cast shadows, while recognizing that it does not resolve finer-scale shading from vegetation, shrubs, rocks, crevices or other microhabitat features below the spatial resolution of the model. We used widely adopted solar radiation equations to calculate the amount of radiation on a horizontal plane given the location, day of year and time of day^{64,65}. For simulations including terrain effects, direct solar radiation values were adjusted to account for self-shading, cast shadows and the angle of incidence. The algorithm checked each location for self-shading, which occurred when a location's slope was greater than the solar altitude angle and the solar azimuth was not within ± 90 degrees of the slope aspect⁶⁶. To incorporate shading from cast shadows for a given location, we compared the horizon angle of each cell along the azimuth angle to the solar altitude angle (with a maximum tracking distance of 50 km)⁶⁶. If any horizon angles

along the solar azimuth exceeded the solar altitude angle, the direct solar radiation component for that cell was set to zero. Steps along the azimuth angle were calculated in metres to avoid angle distortion in degrees. For locations without shading, we corrected direct solar radiation on a horizontal plane to account for sloping surfaces using the following conversion factor in ref. 67: $\frac{\cos \theta}{\cos \varphi}$, where θ is the angle of incidence and φ is the solar zenith angle. We calculated the angle of incidence as: $\cos(\theta) = \cos(\varphi) \times \cos(i) + \sin(\varphi) \times \sin(i) \times \cos(\gamma - \alpha)$, where i is slope steepness, γ is the solar azimuth and α is slope aspect. We used these calculations to define a categorical topographic shading treatment comparing two simulation conditions: horizontal radiation, in which incoming solar radiation was calculated for a horizontal plane without terrain effects, and terrain-corrected radiation, in which incoming solar radiation was adjusted for slope, aspect, self-shading and cast shadows. We also note that because WorldClim air-temperature layers are spatially interpolated across real landscapes, horizontal-plane simulations still retain some implicit aspect-associated variation in air temperature, even though direct solar radiation is not corrected for slope, aspect, self-shading or cast shadows.

Soil temperature

Following ref. 68, we calculated soil surface temperatures by adapting the surface energy balance equations in ref. 69. The energy balance model iteratively predicted soil surface temperatures by incorporating sensible heat flux, net radiative flux, ground storage of heat and, in salamander simulations, latent heat flux. For lizard simulations, latent heat flux was excluded because soils in the southwestern USA are generally arid⁷⁰. Subsurface temperatures were calculated using a one-dimensional explicit finite-difference heat diffusion simulation based on soil surface temperatures.

Soil properties varied between salamander and lizard soil temperature models. Namely, for lizard simulations, soil thermal conductivity was $0.25 \text{ W m}^{-1} \text{ K}^{-1}$ and soil-specific heat was $0.83 \text{ kJ kg}^{-1} \text{ }^{\circ}\text{C}^{-1}$ (refs. 71,72). For salamander simulations, soil thermal conductivity was $0.2 \text{ W m}^{-1} \text{ K}^{-1}$ and soil-specific heat was $1.92 \text{ kJ kg}^{-1} \text{ }^{\circ}\text{C}^{-1}$ (refs. 71,73). To incorporate spatial variation in soil properties, we used bulk density and soil water content maps obtained from SoilGrids 2.0⁷⁴. Appalachian soil temperatures rarely drop below freezing, likely due to the zero-curtain effect⁷⁵, so we set a lower limit of $0 \text{ }^{\circ}\text{C}$ for Appalachian soils. To approximate canopy shading in Appalachian forests, we reduced direct solar radiation to 10%, a conservative simplification reflecting the strong reduction in understory radiation beneath closed forest canopies⁷⁶.

We validated soil temperature models for sandy soils in southwestern USA and soils in the southern Appalachians. Simulated soil temperatures were compared to soil temperatures recorded by the Soil Climate Analysis Network (<https://www.nrcs.usda.gov/resources/data-and-reports/soil-climate-analysis-network>, accessed 1 August 2025) at three soil depths (2 in, 4 in and 8 in) across five sites for southwestern soils and ten sites for southern Appalachian soils (Supplementary Table 3). Validation sites were primarily located on relatively flat terrain (Supplementary Table 3). Model performance was evaluated using linear regressions between simulated and observed soil temperatures. There was high congruence for both Appalachian (Supplementary Fig. 8; $R^2 = 0.91$ – 0.95 , slope = 0.98 – 1.08 , root mean square error = 1.89 – $2.27 \text{ }^{\circ}\text{C}$, bias = 0.29 – $0.66 \text{ }^{\circ}\text{C}$ across depths) and southwestern soils (Supplementary Fig. 9; $R^2 = 0.88$ – 0.93 , slope = 1.02 – 1.19 , root mean square error = 2.69 – $3.52 \text{ }^{\circ}\text{C}$, bias = 0.26 – $0.83 \text{ }^{\circ}\text{C}$ across depths).

Solar radiation simulations across North America

To investigate the broad-scale impact of our shading simulation, we incorporated the terrain algorithm into calculations of monthly and yearly solar radiation received across North America (20 – 180° W and 7 – 85° N). We applied the algorithm to WorldClim elevation and EarthEnv slope data at a resolution of 30 arcsec (refs. 59,60). We modelled

solar radiation for the middle day of each month and extrapolated to monthly and yearly values. We quantified how the shading algorithm affected variability in solar radiation by coarsening rasters of solar radiation by a factor of 25 (chosen to facilitate visualization in Fig. 1a) and calculating the range of values within each block.

We validated our solar radiation model by comparing our non-shaded predictions to ground horizontal irradiance values produced by the National Solar Radiation Database using linear regression⁷⁷. We cropped the solar radiation rasters from our predictions and the National Solar Radiation Database to their overlapping extents and resampled both rasters to 2.5 arcmin resolution using bilinear interpolation. We took a random sample of 100,000 locations to conduct our regression analysis and found broad agreement between datasets (Supplementary Fig. 10; $R^2 = 0.88$, slope = 1.03), although residuals were larger at high predicted irradiance values, where our model tended to overpredict relative to the National Solar Radiation Database.

Lizard simulations of activity and energetics

In the lizard simulations, individuals were active during the daytime (that is, when solar altitude angles were greater than zero) whenever surface operative temperatures were within suitable thermal conditions, which ranged from 26.4 °C to 37.8 °C based on reported field active body temperatures for *S. occidentalis*⁷⁸. Whenever surface operative temperatures in full sun exceeded 37.8 °C, lizards retreated to shaded surface microclimates where we assumed 80% shade. We assumed that lizards maintained the preferred body temperature of *S. occidentalis* (35 °C)⁷⁹ if open microhabitats were above their preferred temperature and shaded microhabitats were below their preferred temperature. Lizards were inactive in a burrow whenever operative temperatures in both open and shaded microclimates exceeded 37.8 °C. Operative temperatures represent the steady-state body temperature of an animal by incorporating aspects of thermal exchange (that is, convection and radiation) with the environment⁸⁰. For lizards, evaporative heat exchange generally has modest effects on body temperature (except for panting at high ambient temperatures⁸¹), and operative temperatures are a common and accurate way to quantify their thermal environments^{17,82}. Operative temperatures were calculated using the following equation in ref. 64:

$$T_e = T_a + \frac{R_{\text{abs}} - \varepsilon_s \sigma T_a^4}{c_p(g_r + g_{\text{Ha}})}$$

where T_e is the operative temperature, T_a is the ambient temperature (here we used air temperatures 1 cm above the surface), R_{abs} is absorbed radiant energy, ε_s is the organism's emissivity (0.965)⁸³, σ is the Stefan–Boltzmann constant, c_p is the specific heat of air, g_r is boundary conductance and g_{Ha} is radiative conductance. We calculated absorbed R_{abs} assuming a shortwave absorptance of 0.9 and a longwave absorptance of 0.965 (refs. 83,84). During periods of inactivity, lizards maintained body temperatures equivalent to soil temperature at 10 cm below the surface, a depth consistent with shallow subsurface retreat depths used in prior lizard thermal ecology studies on *S. occidentalis*⁸⁵. Energy expenditure (kJ h^{-1}) for *S. occidentalis* was calculated each hour based on lizard mass, body temperature (T_b) and activity status ($20.2 \times 10^{0.038 \times T_b - 1.771} \times \text{mass}^{0.82} \times \text{activity scope} \times 0.001$ (refs. 86,87). Lizard mass was held constant at 9 g (ref. 88). The activity multiplier was set to 1 for inactive hours and 1.5 for active hours, reflecting the assumed increase in metabolic rate during activity for iguanids⁸⁹. By assuming phenotypic traits do not change across space, our approach does not capture population-specific variation in morphology, physiology, behaviour or life history that may occur across elevational gradients, but allows the direct comparison of energetic consequences across topographic scenarios while holding organismal traits constant. To evaluate the potential impacts of morphological and behavioural variation on lizard energetics predictions, we

conducted sensitivity analyses across a range of body sizes (2.6 g, 4.8 g, 7.3 g, 12.4 g and 38.0 g)⁹⁰, shortwave solar absorptances (0.6, 0.7, 0.8, 0.9 and 0.985) and voluntary thermal limits (± 2 °C; Supplementary Figs. 11–13). We varied each parameter independently and found no qualitative changes to primary results across the range of tested values.

Salamander simulations of activity and energetics

For salamander simulations, individuals were active at night under permissive thermal and hydric conditions. Salamander body mass was held constant at 3 g, approximating the mass of a typical adult *P. metcalfei*⁹¹. Humid operative temperatures required for activity ranged between 5 and 25 °C (refs. 92,93). Humid operative temperatures are similar to operative temperature, but also incorporate evaporative cooling from water loss. They were calculated using the following equation from ref. 64:

$$T_{\text{eh}} = T_a + \frac{\gamma^*}{s + \gamma^*} \left(\frac{R_{\text{abs}} - \varepsilon_s \sigma T_a^4}{c_p g_{\text{Hr}}} - \frac{D}{\gamma^* p_a} \right)$$

T_{eh} is the humid operative temperature, T_a is the ambient temperature (here we used soil surface temperature), γ^* is the apparent psychrometer constant, s is the slope of saturation mole fraction function, R_{abs} is absorbed radiant energy, ε_s is the organism's emissivity (0.96), σ is the Stefan–Boltzmann constant, c_p is the specific heat of air, g_{Hr} is the combined boundary layer and radiative conductance, D is the vapour pressure deficit of the air and p_a is the atmospheric air pressure.

Hydric conditions influence salamander activity by influencing rates of evaporative water loss⁹⁴. We calculated water loss (g h^{-1}) following ref. 95. Though salamanders exhibit plasticity in their skin resistance to water loss^{92,96}, we simplified resistance and held it constant at 5 s cm^{-1} . Salamanders ceased activity whenever 7% of their body mass was lost to dehydration during a given night⁹⁴. During periods of inactivity, salamanders retreated to 20 cm below the soil surface⁹⁷ and body temperatures were equivalent to soil temperature. Energy expenditure was calculated based on the thermal sensitivity of $\dot{V}\text{O}_2$, with the following equation from ref. 92:

$$\log \dot{V}\text{O}_2 = (0.041 \times \text{body temperature}) + (0.59 \times \log(\text{mass})) + 1.05$$

Statistical analyses

To evaluate the effects of topographic shading treatment and terrain features (that is, elevation, slope and aspect) on yearly predictions of North American solar radiation and bioenergetic predictions (activity and metabolic energy expenditure) for salamanders and lizards, we fit linear mixed-effects models with the lme4 package⁹⁸ in R (v.4.1.2). We limited our analyses to parts of the landscape with slopes greater than 2.5%, which represented 28.0% of North America, 57.4% of the southern California region ($n = 43,212$ locations for *S. occidentalis*) and 54.9% of the southern Appalachian region ($n = 157,339$ locations for *P. metcalfei*). All numeric predictor variables were standardized. Model assumptions for normality and homoscedasticity of residuals were evaluated using diagnostic plots, and multicollinearity was assessed using variance inflation factors. All statistical inferences were conducted at the level of unique spatial locations, with repeated simulations between climate periods and topographic shading treatments modelled as non-independent observations using random effects.

For the solar radiation simulations across North America, we randomly sampled 100,000 locations and fitted a mixed-effects model with topographic shading treatment, environmental variables as fixed effects and location as a random effect:

$$\begin{aligned} \text{Annual solar radiation} \sim & (\text{shading treatment} \times \text{northness} \times \text{slope}) \\ & + \text{eastness} + \text{elevation} + (1|\text{location}) \end{aligned}$$

Models for annual activity and metabolic energy expenditure for lizards had the general structure:

$$\begin{aligned} \text{Response} \sim & (\text{shading treatment} \times \text{climate period}) \\ & \times (\text{northness} + \text{eastness} + \text{slope} + \text{poly}(\text{elevation}, 2)) \\ & + (1|\text{location}) + (1|\text{location}:\text{climate period}) \end{aligned}$$

For salamander activity and energy expenditure models, we retained shading treatment, climate period, elevation and climate period $\times$ poly(elevation, 2) due to model non-convergence and instability when incorporating other predictors and interactions. Therefore, salamander models took the following structure:

$$\begin{aligned} \text{Response} \sim & \text{shading treatment} + (\text{climate period} \times \text{poly}(\text{elevation}, 2)) \\ & + (1|\text{location}) + (1|\text{location}:\text{climate period}) \end{aligned}$$

We included a quadratic term for elevation to allow for a non-linear relationship with activity and metabolism. The interactive random effect, (1|location:climate period), created random intercepts for each location $\times$ climate period combination. Slope aspect, a circular variable, was broken down into two orthogonal components: eastness and northness. Eastness was calculated as the sine of aspect (west-facing slopes = -1; east-facing slopes = +1) and northness was calculated as the cosine of aspect (north-facing slopes = -1; south-facing slopes = +1). Analysing ecological simulation models with frequentist tests of statistical significance can be misleading due to large sample sizes⁹⁹. Instead, we calculated effect sizes for each parameter using omega-squared values (ω^2) with the function 'omega_squared' from the effectsize package¹⁰⁰. We interpreted ω^2 values following ref. 101, where $\omega^2 \geq 0.14$ is a large effect, $0.06 \leq \omega^2 \leq 0.14$ is a medium effect and $\omega^2 \leq 0.06$ is a small effect.

We used polar plots to visualize the effects of topographic shading on activity and metabolic costs across slope aspects. Each point represented a location on the landscape and was colour-coded to descriptively demonstrate the effects of climate period and elevation. Slope aspect was presented on the angular axis with 0° denoting south and increasing counterclockwise, and the change in activity or metabolism was indicated by the radial axis. To highlight relative changes in activity and metabolic costs, we expressed changes as the percentage change that occurred when topographic shading was incorporated.

Elevation and aspect shifts buffer future energetic costs

We used maps of metabolic energy expenditure for lizards in the current and future climate periods to examine the individual and combined buffering capacity of shifting elevation and aspect. We conducted three simulations with varying responses to climate change: (1) individuals could shift in aspect but only ± 10 m in elevation, (2) individuals could shift in elevation but only $\pm 10^\circ$ in aspect and (3) individuals could shift in both elevation and aspect. These simulations represent cumulative dispersal across generations, in which individuals disperse by tracking environments that maintain energetic costs similar to those experienced at their starting locations under current climate conditions. Under those constraints, lizards dispersed to cells in the future that most closely matched their current metabolic energy expenditure. We also ran simulations with less restrictive elevation and aspect constraints to examine the sensitivity of our results (± 100 m in elevation for aspect-only treatment; $\pm 25^\circ$ in aspect for elevation-only treatments; Supplementary Fig. 14). Starting locations for lizards were limited to parts of the landscape with $>2.5\%$ slope and within 0–3,300 m elevation, the known elevational range of *S. occidentalis* ($n = 42,332$ locations)¹⁰². We constrained lizard movement to a maximum distance of 3,380 m, based on 50 dispersal events with individual dispersal events being 67.6 m. The number of dispersal events was calculated assuming age of maturity of 2 years and a 100-year time period (2000–2100), and the dispersal distance was determined based on a mean natal dispersal of

45.6 m¹⁰³ plus a female home range radius of 22 m¹⁰⁴. We assessed the buffering capacity of each strategy as the percentage reduction in the projected increase in metabolic costs achieved by moving, relative to remaining in the same location in the future. To evaluate movement along aspects, we displayed circular histograms of starting and ending aspects for each response strategy (Fig. 3). This approach assumes that lizards preferentially settle in thermal environments that preserve current energetic conditions, reflecting the tendency of many ectotherms to behaviourally avoid microclimates that increase physiological costs. These simulations were designed to isolate the potential for elevation and aspect shifts to buffer metabolic costs, but we acknowledge that realized movement across landscapes will also depend on other traits and processes, including critical thermal limits, hydration state, predation risk, habitat structure, dispersal motivation and species-specific movement behaviour.

Aspect diversity across North American mountains

To understand the potential for aspect-mediated topographic shading across North America, we characterized the elevational and aspect diversity across 45 mountain ranges. We calculated aspect values from the 30-arcsec WorldClim elevation raster using the terra package in R⁶³. The surface area of each cell was calculated by dividing the planar area of each cell by the cosine of the terrain slope. We extracted aspect, elevation and surface area values for major North American mountain ranges delineated using the 300 selection of the Global Mountain Biodiversity Assessment Mountain Inventory v.2^{61,62}. We categorized mountain ranges into five categories: east–west biased, north–south biased, southwest–northeast biased, southeast–northwest biased and uniform. To calculate directional bias, we created summed surface area ratios of aspects grouped into cardinal and ordinal directions. For each ratio, we summed surface area values along a directional axis (for example, eastern and western slopes) and divided by the sum of surface areas along the corresponding orthogonal axis (for example, northern and southern slopes). We defined a mountain range as having a uniform aspect distribution if no cardinal or ordinal direction was biased by more than 20%. Cardinal and ordinal bias ratios were compared to determine if a mountain range was primarily skewed along cardinal or ordinal axes. We visualized overall aspect diversity for each mountain range using circular histograms showing the relative frequencies of terrain aspects (Fig. 4). We used hypsographic curves separated by northern, southern, eastern and western slopes to show the surface area availability of aspects across elevation (Supplementary Fig. 7).

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Climate and elevation data were retrieved from WorldClim v.2.1 (<https://worldclim.org/>)⁶⁰. Slope data were retrieved from EarthEnv (<https://www.earthenv.org/topography>)⁵⁹. Mountain range delineations were obtained from the Global Mountain Biodiversity Assessment Mountain Inventory v.2 (<https://www.earthenv.org/mountains>)^{61,62}. Spatial soil properties were obtained from SoilGrids 2.0 (<https://soilgrids.org/>)⁷⁴. Empirical soil temperature data were retrieved from the Soil Climate Analysis Network (<https://www.nrcs.usda.gov/resources/data-and-reports/soil-climate-analysis-network>)¹⁰⁵. Data and code that support the findings of this study are available via Zenodo at <https://doi.org/10.5281/zenodo.20798329> (ref. 106). Note that some intermediate data files were too large to be shared through Zenodo but are available from the corresponding author upon reasonable request.

Code availability

The scripts used to run and analyse simulations are available via Zenodo at <https://doi.org/10.5281/zenodo.20798329> (ref. 106).

References

63. Hijmans, R. J. Terra: Spatial data analysis. R version 1.8-93 <https://doi.org/10.32614/CRAN.package.terra> (2025).
64. Campbell, G. S. & Norman, J. M. *An Introduction to Environmental Biophysics* <https://doi.org/10.1007/978-1-4612-1626-1> (Springer, 1998).
65. Walraven, R. Calculating the position of the sun. *Sol. Energy* **20**, 393–397 (1978).
66. Wang, R. et al. Influence of topographic shading on the mass balance of the high mountain Asia glaciers. *Remote Sens.* **14**, 1576 (2022).
67. Ramtvedt, E. N. & Næsset, E. A simple slope correction of horizontally measured albedo in sloping terrain. *Agric. For. Meteorol.* **339**, 109547 (2023).
68. Porter, C. K., Romero, F. G., Adams, D. C., Bowie, R. C. K. & Riddell, E. A. Adaptive and non-adaptive convergent evolution in feather reflectance of California Channel Islands songbirds. *Proc. R. Soc. B* **290**, 20231914 (2023).
69. Leaf, J. S. & Erell, E. A model of the ground surface temperature for micrometeorological analysis. *Theor. Appl. Climatol.* **133**, 697–710 (2018).
70. Sheppard, P., Comrie, A., Packin, G., Angersbach, K. & Hughes, M. The climate of the US Southwest. *Clim. Res.* **21**, 219–238 (2002).
71. Alnefaie, K. A. & Abu-Hamdeh, N. H. Specific heat and volumetric heat capacity of some Saudian soils as affected by moisture and density. *Int. J. Mater.* <https://doi.org/10.46300/91018.2020.7.8> (2020).
72. Chen, S. X. Thermal conductivity of sands. *Heat Mass Transf.* **44**, 1241–1246 (2008).
73. Blanco-Canqui, H., Lal, R., Owens, L. B., Post, W. M. & Izaurrealde, R. C. Strength properties and organic carbon of soils in the north Appalachian region. *Soil Sci. Soc. Am. J.* **69**, 663–673 (2005).
74. Poggio, L. et al. SoilGrids 2.0: producing soil information for the globe with quantified spatial uncertainty. *SOIL* **7**, 217–240 (2021).
75. Outcalt, S. I., Nelson, F. E. & Hinkel, K. M. The zero-curtain effect: heat and mass transfer across an isothermal region in freezing soil. *Water Resour. Res.* **26**, 1509–1516 (1990).
76. Augspurger, C. K. & Salk, C. F. Understory plants evade shading in a temperate deciduous forest amid climate variability by shifting phenology in synchrony with canopy trees. *PLoS ONE* **19**, e0306023 (2024).
77. Sengupta, M. et al. The National Solar Radiation Data Base (NSRDB). *Renew. Sustain. Energy Rev.* **89**, 51–60 (2018).
78. Brattstrom, B. H. Body temperatures of reptiles. *Am. Midl. Nat.* **73**, 376–422 (1965).
79. McGinnis, S. M. *Sceloporus occidentalis*: preferred body temperature of the western fence lizard. *Science* **152**, 1090–1091 (1966).
80. Bakken, G. S. Measurement and application of operative and standard operative temperatures in ecology. *Am. Zool.* **32**, 194–216 (1992).
81. Loughran, C. L. & Wolf, B. O. The functional significance of panting as a mechanism of thermoregulation and its relationship to the critical thermal maxima in lizards. *J. Exp. Biol.* **223**, jeb224139 (2020).
82. Alujević, K. et al. 3D printed models are an accurate, cost-effective, and reproducible tool for quantifying terrestrial thermal environments. *J. Therm. Biol.* **119**, 103762 (2024).
83. Barlett, P. N. & Gates, D. M. The energy budget of a lizard on a tree trunk. *Ecology* **48**, 315–322 (1967).
84. Gates, D. M. *Biophysical Ecology* (Springer-Verlag, 1980).
85. Sabo, J. L. Hot rocks or no hot rocks: overnight retreat availability and selection by a diurnal lizard. *Oecologia* **136**, 329–335 (2003).
86. Bennett, A. F. & Dawson, W. R. Metabolism. In *Biology of the Reptilia Volume 5: Physiology A* (eds Gans, C. & Dawson, W. R.) 127–223 (Academic Press, 1976).
87. Grant, B. W. & Porter, W. P. Modeling global macroclimatic constraints on ectotherm energy budgets. *Am. Zool.* **32**, 154–178 (1992).
88. Jameson, E. W., Heusner, A. A. & Lem, D. Seasonal, sexual and altitudinal variations in stomach content and ingested fat in *Sceloporus occidentalis*. *J. Herpet.* **14**, 255–261 (1980).
89. Congdon, J. D. Proximate and evolutionary constraints on energy relations of reptiles. *Physiol. Zool.* **62**, 356–373 (1989).
90. Myhrvold, N. P. et al. An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. *Ecology* **96**, 3109–3109 (2015).
91. Riddell, E. A. & Sears, M. W. Geographic variation of resistance to water loss within two species of lungless salamanders: implications for activity. *Ecosphere* **6**, 1–16 (2015).
92. Riddell, E. A., Odom, J. P., Damm, J. D. & Sears, M. W. Plasticity reveals hidden resistance to extinction under climate change in the global hotspot of salamander diversity. *Sci. Adv.* **4**, eaar5471 (2018).
93. Spotila, J. R. Role of temperature and water in the ecology of lungless salamanders. *Ecol. Monogr.* **42**, 95–125 (1972).
94. Feder, M. E. & Londos, P. L. Hydric constraints upon foraging in a terrestrial salamander, *Desmognathus ochrophaeus* (Amphibia: Plethodontidae). *Oecologia* **64**, 413–418 (1984).
95. Riddell, E. A., Apanovitch, E. K., Odom, J. P. & Sears, M. W. Physical calculations of resistance to water loss improve predictions of species range models. *Ecol. Monogr.* **87**, 21–33 (2017).
96. Riddell, E. A., Roback, E. Y., Wells, C. E., Zamudio, K. R. & Sears, M. W. Thermal cues drive plasticity of desiccation resistance in montane salamanders with implications for climate change. *Nat. Commun.* **10**, 4091 (2019).
97. Taub, F. B. The distribution of the red-backed salamander, *Plethodon C. cinereus*, within the soil. *Ecology* **42**, 681–698 (1961).
98. Bates, D., Mächler, M., Bolker, B. & Walker, S. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48 (2015).
99. White, J. W., Rassweiler, A., Samhoury, J. F., Stier, A. C. & White, C. Ecologists should not use statistical significance tests to interpret simulation model results. *Oikos* **123**, 385–388 (2014).
100. Ben-Shachar, M., Lüdtke, D. & Makowski, D. effectsizr: estimation of effect size indices and standardized parameters. *J. Open Source Softw.* **5**, 2815 (2020).
101. Field, A. *Discovering Statistics Using IBM SPSS Statistics: And Sex and Drugs and Rock 'n' Roll* (Sage, 2013).
102. Bell, E. L. & Price, A. H. *Sceloporus occidentalis* (Society for the Study of Amphibians and Reptiles, 1996).
103. Massot, M., Huey, R. B., Tsuji, J. & van Berkum, F. H. Genetic, prenatal, and postnatal correlates of dispersal in hatchling fence lizards (*Sceloporus occidentalis*). *Behav. Ecol.* **14**, 650–655 (2003).
104. Tanner, W. W. & Hopkin, J. M. Ecology of *Sceloporus occidentalis longipes* Baird and *Uta stansburiana stansburiana* Baird and Girard on Rainier Mesa, Nevada test site, Nye County, Nevada. *Brigham Young Univ. Sci. Bull. Biol. Ser.* **15**, 1 (1972).
105. Schaefer, G. L., Cosh, M. H. & Jackson, T. J. The USDA Natural Resources Conservation Service Soil Climate Analysis Network (SCAN). *J. Atmos. Oceanic Technol.* **24**, 2073–2077 <https://doi.org/10.1175/2007JTECHA930.1> (2007).
106. Adams, D. R. Data and code for: Topographic variation shapes organismal responses across mountain landscapes. *Zenodo* <https://doi.org/10.5281/zenodo.20798329> (2026).

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Author contributions

E.A.R. conceived the idea for the study and secured funding. D.R.A. ran the simulations, conducted the analyses, prepared all figures and wrote the original paper. Both authors edited and revised the paper.

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Competing interests

The authors declare no competing interests.

Additional information

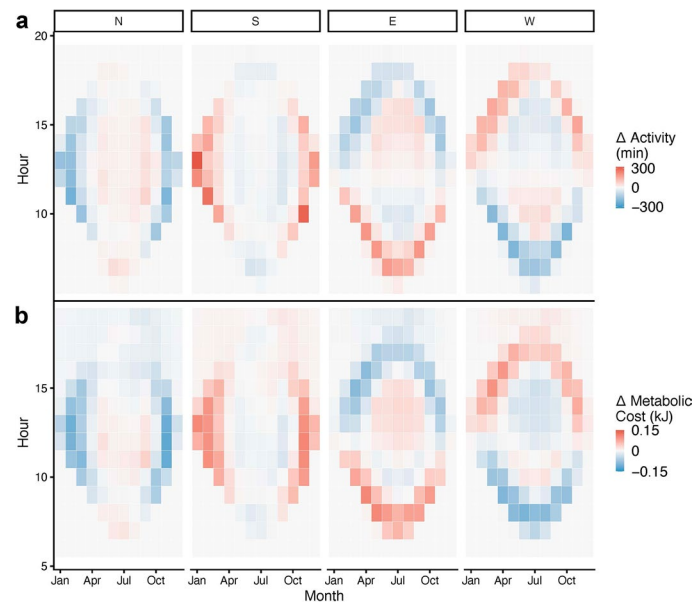
Extended data is available for this paper at <https://doi.org/10.1038/s41558-026-02773-z>.

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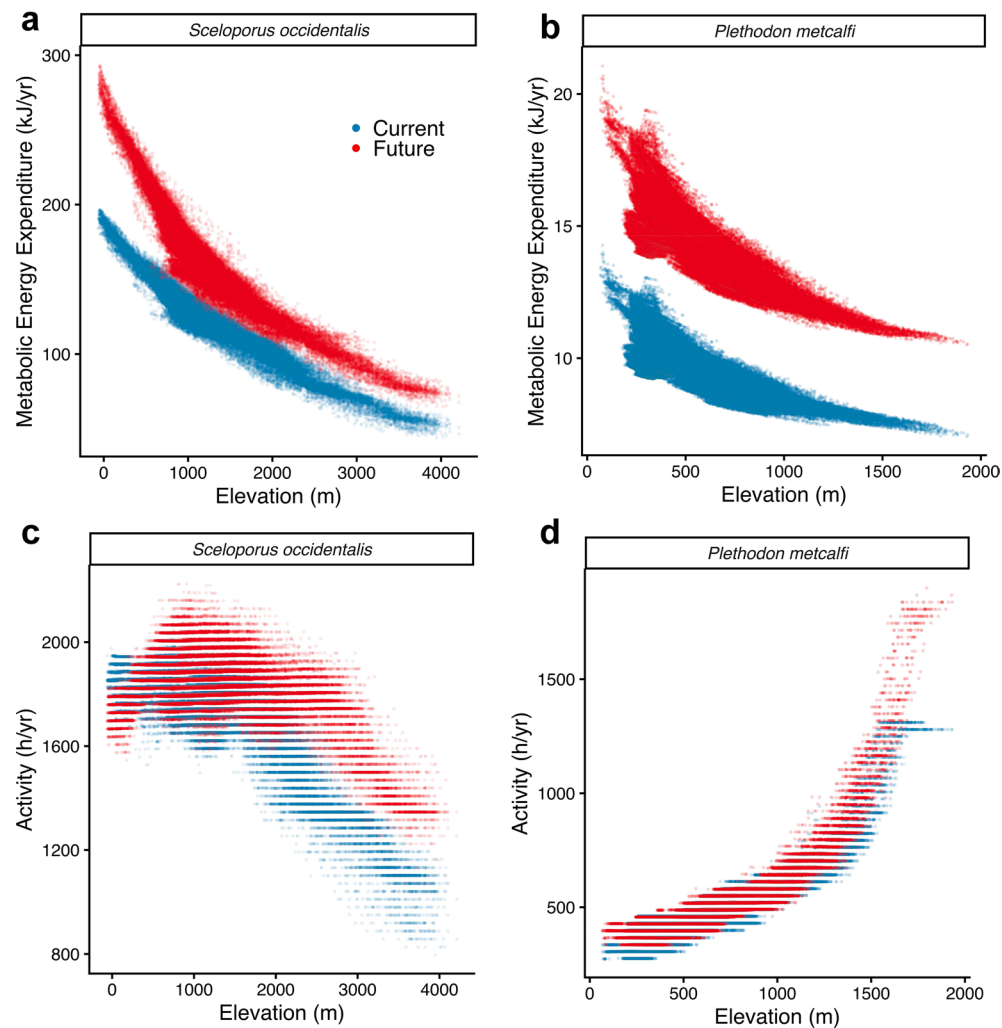
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Extended Data Fig. 1 | Temporal shifts in lizard activity and metabolic costs due to topographic shading. Topographic shading led to aspect-specific temporal shifts in **(a)** activity and **(b)** metabolic costs for lizards. Each cell

represents monthly values for each hour of a given month for the future climate period. Cells are colored by the average change in activity or metabolism across the landscape when topographic shading was included.



Extended Data Fig. 2 | Elevation and climate period interactions on metabolic energy expenditure and activity. Metabolic energy expenditure (kJ/year) declines with elevation in both time periods for *Sceloporus occidentalis* (a) and *Plethodon metcalfi* (b) and does so more rapidly under future conditions.

Activity decreases with elevation for *S. occidentalis* (c) but increases for *P. metcalfi* (d), with both species showing activity shifts with climate period. Points represent grid-cell level predictions from the bioenergetic models, colored by climate period.

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Study description

This study used a simulation-based framework to quantify how topographic shading and terrain features influence predicted solar radiation, activity, and metabolic energy expenditure across landscapes. Simulations were hierarchical, with hourly microclimate and organismal predictions generated for independent spatial locations across multiple climate periods (current and future) and shading treatments. Linear mixed-effects models were used to evaluate effects while accounting for non-independence of repeated predictions within locations.

Research sample

We conducted bioenergetic simulations of the western fence lizard (*Sceloporus occidentalis*) and the southern gray-cheeked salamander (*Plethodon metcalfei*), over areas relevant to their distributions. We used information about body size, solar reflectance, voluntary activity temperatures, metabolic physiology, etc. from existing literature (e.g., Riddell et al. 2018 Sci. Adv.; Barlett & Gates 1967 Ecology)

Sampling strategy

Spatial locations were selected based on terrain slope (>2.5%) to focus analyses on topographically complex landscapes where shading effects are biologically relevant. Sample sizes were determined by the number of qualifying landscape locations rather than by a priori power calculations.

Data collection

These data were simulated using biophysical models.

Timing and spatial scale

Simulations were conducted for contemporary conditions and a future climate period (2081–2100) using downscaled climate projections. Spatial extent ranged from regional (southern California and the southern Appalachians) to continental (North America), with simulations performed at 30-arcsecond resolution and aggregated temporally from hourly predictions to annual values.

Data exclusions

Data were not excluded from analyses.

Reproducibility	All simulations and analyses are fully reproducible. Model code and input datasets are archived in a public repository
Randomization	Randomization was not applicable because this study did not involve experimental assignment of organisms, samples, or treatments. All simulations were applied uniformly across spatial locations.
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