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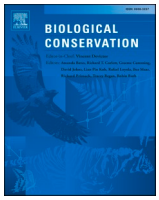

A climate-vulnerable species uses cooler forest microclimates during heat waves

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ABSTRACT

While climate change will have significant impacts on terrestrial organisms, microclimates offer potential refugia for vulnerable species when regional conditions become unsuitable and temperatures exceed physiological limits. The efficacy of microclimates as buffers to extreme events is determined not only by their availability, but also by the behavioral flexibility of individuals to access these unique environments during stressful periods. We characterized (i) how forest structure and topography shaped microclimates at roost sites used by California spotted owls (*Strix occidentalis occidentalis*), a climate-vulnerable species, and (ii) how owls outfitted with temperature sensors used microclimates during warm temperature events. Higher elevations, taller canopies, and greater canopy cover promoted cooler maximum temperatures in stands used for roosting. Within those stands, individuals roosted in cooler sites, especially when roosts were in forest stands on warmer slopes. Tall canopies created relatively cooler microclimates when temperatures were hot, and individuals actively used roost sites that minimized increases in operative temperature, suggesting spotted owls have an adaptive capacity to use cooler microclimates. However, roosts at low elevations consistently exceeded physiological thresholds when temperatures were warm, potentially explaining vacancies in low elevation territories with more open forest. For spotted owls to persist in warming environments, conserving tall, closed-canopy forests that promote cooler microclimates for roosting is critical. While a future climate promises heat events that approach and exceed thermal extremes for a suite of canopy-dwelling species, cooler microclimates provided by forest structure and topography could constitute important refugia in a rapidly changing system.

1. Introduction

Species have evolved to occur within a specific array of abiotic conditions, or climate space, and exposure to conditions that exceed or fall below their physiological tolerance can lead to stress and decreased fitness (Deutsch et al., 2008; Huey et al., 2009). Stress avoidance is a mechanism by which climate constrains the ability of organisms to occupy space, and organisms respond to deviations from suitable conditions through dispersal, physiological and behavioral plasticity, or adaptation (Huey et al., 2012). Warming temperatures are projected to have significant impacts on the space occupied by terrestrial organisms (Chen et al., 2011) and thus the distribution of many species has, and is expected, to shift over time as the climate warms (Beever et al., 2017; Parmesan, 2006; Freeman and Class Freeman, 2014). While regional conditions may become unsuitable for climate-sensitive species (i.e., temperatures exceeding upper thermal tolerance limits), smaller areas of habitat within a landscape may retain suitable conditions where individuals can seek refuge (Keppel et al., 2012; Morelli et al., 2016).

Microclimates can be decoupled from macroclimates and emerge due to local variability in elevation, topography, and land cover (Latimer and Zuckerberg, 2017; Riddell et al., 2019; Maclean, 2020). Elevation and topography are some of the strongest drivers of microclimate variation (Frey et al., 2016b), yet vegetation composition and structural complexity also play a large role in determining local climatology (Dobrowski, 2011; Zellweger et al., 2019). In forested ecosystems, canopy cover provides refuge for organisms from extreme thermal events; understory air temperature extremes can be considerably less variable than macro-temperatures, especially on cooler north-facing

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slopes (Frey et al., 2016b; Suggitt et al., 2011). Microclimates within forest stands are largely driven by the amount of solar radiation that breaches the canopy, which is influenced by canopy cover and the height of the dominant trees (Chen et al., 1993; Latimer and Zuckerberg, 2017). While microclimates offer potential refugia where individuals can "wait-out" weather extremes, individuals must be able to access such sites to fully benefit from a buffering effect.

Behavioral flexibility in response to unsuitable climate conditions can be vital for climate-vulnerable species to persist. Habitat preferences change as environmental conditions like temperature and precipitation affect an individual's energetic requirements or alter the perceived value of habitat types (Johnson, 1980). One species that capitalizes on cool microclimates is the American pika (*Ochotona princeps),* a mammal sensitive to even moderate temperature increases. Pikas exhibit stronger selection for cool interstitial microclimates (e.g., rock piles, talus) when ambient temperatures exceed 20 °C, allowing populations to persist even when macro-scale temperatures are outside the range of tolerance for the species (Varner and Dearing, 2014). Avian species also show preference for less extreme microclimates, and individuals actively seek out sites that are effectively buffered from inclement environmental conditions (Veľký et al., 2009; Anthony et al., 2021; Shipley et al., 2020). With rising temperatures and more variable precipitation, a species' response to changing climatic conditions will be determined by both the availability of stable microclimates and the ability of individuals to seek them out.

Older forests in western North America have demonstrated a capacity to support cool microclimates that buffer some avian populations from climatic extremes (Kim et al., 2022; Frey et al., 2016a; Frey et al., 2016b; Betts et al., 2018). While microclimates can dampen population declines (Kim et al., 2022), the potential mechanisms for this relationship remain unknown. Understanding individual behavior is vital for conserving climate-sensitive species (Jirinec et al., 2021; De Frenne et al., 2021; Frey et al., 2016a), but few studies have tested the ability of organisms to access microclimates during extreme thermal events, especially in forests. The California spotted owl (*Strix occidentalis,* ssp. *occidentalis*), henceforth spotted owl, is a putatively climate-vulnerable species that occurs across a large elevational gradient and temperatures and extreme heat events are projected to increase across their range (Franklin et al., 2000; Glenn et al., 2010; Peery et al., 2012; Jones et al., 2016). With plumage as thick as boreal-zone species, like northern hawk owls (*Surnia ulula*) and boreal owls (*Aegolius funereus*), spotted owls have a limited ability to dissipate heat (Barrows, 1981), thus prolonged exposure to conditions that approach or exceed their upper critical temperature compromises their ability to maintain thermoneutrality and likely explains the species' use of cool microclimates for roosting during their summer breeding season (Barrows, 1981; Weathers et al., 2001). Roosting is an essential behavior where owls rest in trees during the day, and roost selection is likely a behavioral adaptation to compensate for their cold-adapted physiology (Barrows, 1981). The distribution and availability of roosting habitats, and an individual's ability to access such habitat, may reduce exposure to unsuitable temperatures. Many forests in western North America are managed for timber production and increasingly exposed to wildfires (Steel et al., 2023) and drought-related tree mortality (Park Williams et al., 2013), and managing the landscape to conserve older forest could be an important, if not necessary, climate adaptation tool.

The southern range boundary of California spotted owls has recently experienced historic maximum temperatures during the breeding season (Hulley et al., 2020), offering an opportunity to measure individual responses to novel thermal conditions. Here, we sought to examine individual access to buffering microclimates and test whether individuals with variable access to such habitat across the landscape can seek out cooler locations in a complex forest. We hypothesized that spotted owls have access to and seek out cooler microclimates during heat waves. Specifically, we predicted that: 1) known roost sites are relatively cooler than available sites within forest stands, 2) these differences in roost temperatures are greatest under warmer conditions and facilitated by taller, denser forest canopies, and 3) owls selectively seek out cooler microclimates in roost stands during hotter days. The capacity of spotted owls to actively seek out cooler roosts could indicate a behavioral flexibility to respond to novel environmental conditions that could ameliorate the negative consequences of anthropogenic climate change – and suggestive of similar capacity in other older-forest species like martens (*Martes americana*) and Pacific fishers (*Martes pennanti*) and canopy-dwelling species like northern goshawks (*Accipiter gentilis*), northern flying squirrels (*Glaucomys sabrinus*), and pileated woodpeckers (*Dryocopus pileatus*).

2. Methods

2.1. Study area

In the summers of 2020 and 2021, we took advantage of record high temperatures in the southern Sierra Nevada (Sierra National Forest, SNF) and the San Bernardino Mountains (San Bernardino National Forest, SBNF) in California (USA) to study the factors underlying roosting microclimates and organismal responses to hot temperatures (Fig. 1). The SBNF represents part of the warmest and southernmost portion of the subspecies' range (Tempel et al., 2022). We tracked individual spotted owls between June–August during the warmest time of year, where regional temperatures exceeded estimated thermal tolerance limits for the species (30–35.6 °C; Weathers et al., 2001). Both the SNF and SBNF have substantial elevational gradients, where spotted owls occur in territories between ~800–3000 m and use a variety of forested habitats, leading to high variation in potential roosting microclimates. In both study areas, spotted owls occur in dense forest of mixed conifer stands and occupy hardwood forests at lower elevations, where suitable roosting habitat is generally restricted to drainages and smaller forest patches (Steger et al., 2002; Smith et al., 1999). The ecology of the SBNF is similar to the ecology of the SNF but with more rugged terrain that drives a large variety of forest structures that potentially support cool microclimates.

2.2. Capture and tracker attachment

We targeted our search for owls near locations where individuals had been identified within the past five years. We located individuals by making vocalizations, tracking vocal responses and visually confirming detections. For our study, we targeted breeding pairs because they were more reliable to recapture and more sensitive to stressful conditions as they were already under energetic constraints from rearing young. Individuals were captured using a hand-grab technique that minimizes stress to further ensure recaptures and decrease confounding factors that affect behavior (Zulla et al., 2022; Wilkinson et al., 2022). GPS trackers with VHF radio transmission (~6.2 g, ~1 % BW, Pinpoint-120, Lotek Wireless, Ontario, Canada) were attached to the two middle rectrices with non-toxic adhesive and secured with two small zip ties. Using the Pinpoint Host (v2.14.0.3), GPS trackers were programmed to record locations every hour during daytime roosting activity (6:00–20:00) (Lotek Wireless). Each fix recorded by GPS trackers additionally recorded operative temperature (T_O), which corresponds to a combination of radiant and ambient air temperatures and more accurately reflects the thermal conditions organisms experience (Helmuth et al., 2010). Preliminary testing showed that the pinpoints attached via tail-mount to rehabilitation barred owls (Dane County Humane Society) did not record temperatures that were significantly different than iButtons placed in enclosures (paired *t*-test, $t = 1.55$, df = 28, $p = 0.16$). More information of the precision of temperature measurements from GPS trackers is in Supplemental Table 4. We did not shield GPS units from solar radiation because we wanted to limit the weight of tail-mount attachments and, thus, potential damage to rectrices. The canopies of conifers and other large trees in spotted owl roosts partially filtered some solar

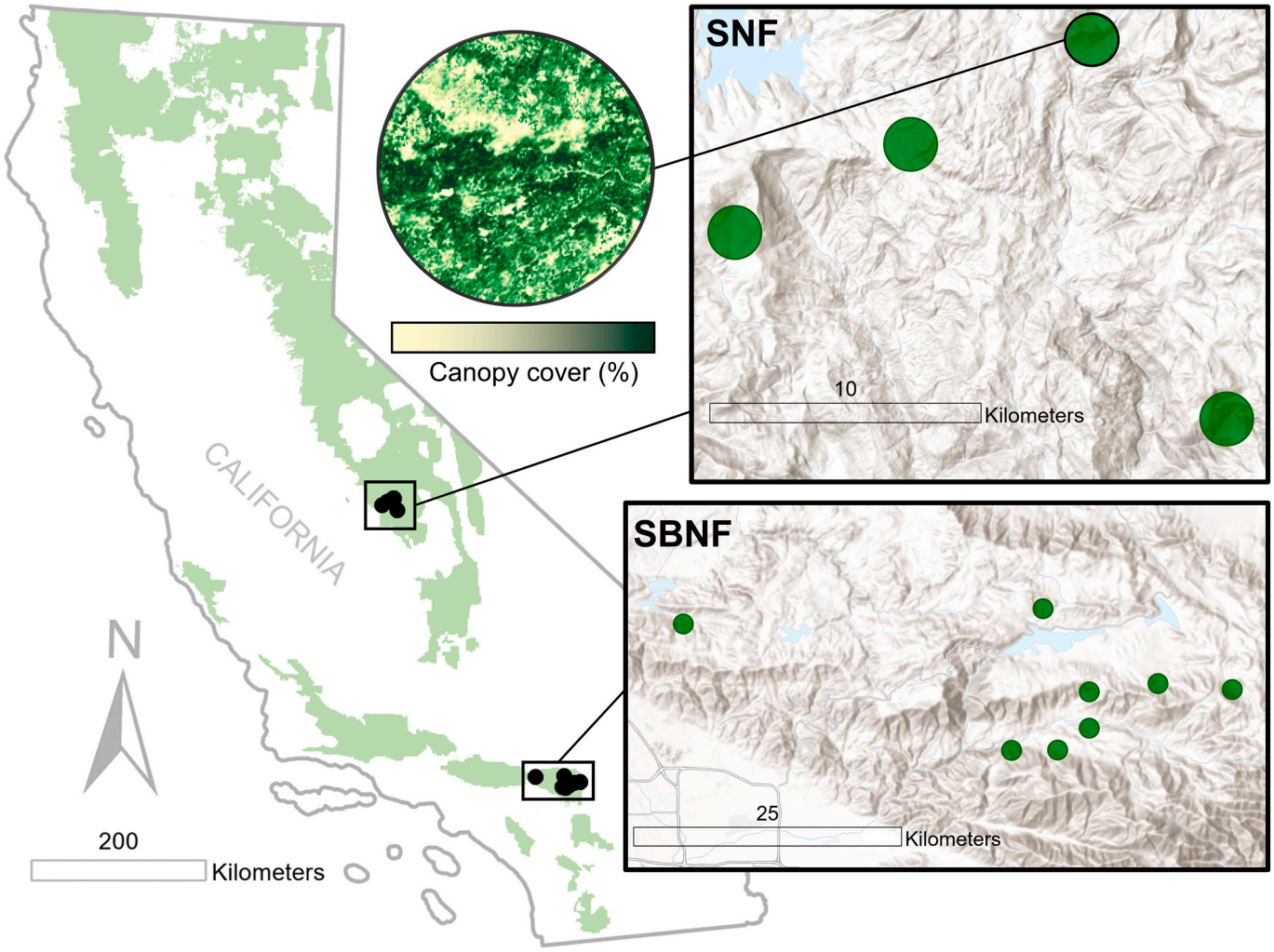

Fig. 1. Map showing study area and territories included in analyses. National Forests in California are indicated by green and territories are denoted by dark green circles. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

radiation (Lundquist and Huggett, 2008). Units lasted three to seven days, and we removed trackers upon recapture. Second captures were performed using the hand-grab technique, a snare-pole, or a pan trap, and tags were removed by breaking the adhesive seal on the tail mount. We aimed to minimize handling time, and birds were released in the same location as their capture. All handling of animals in this study were done by trained individuals under the proper permitting (IACUC A005367-R02-A01).

2.3. Site-level temperature sampling

We identified roost sites (n = 43) using radiotelemetry, tracking the location of tagged birds (n = 19) during daylight hours (Verner et al., 1992). Tags were programmed to transmit radio signals between 4:00–5:00, 11:00–13:00, and 18:00–20:00. Two researchers returned to capture locations and used a handheld Yagi antenna attached to a VHF receiver (R-1000 made by Communications Specialists, Orange, CA) to visually identify individuals on roost while tagged. For up to four consecutive days, we identified roost sites used by owls in each territory. Each individual or pair used 3–4 roosts in a singular stand (n = 12), which we will define below, during the sampling periods.

Because we wanted to sample from habitat that was forested and potentially suitable for spotted owls, we delineated forest stands according to typical spotted owl roosting habitat for each study area using NAIP aerial photography (National Agriculture Imagery Program, USGS, 2018) and a Gradient Nearest Neighbor Forest structure dataset for our study area (LEMMA Lab, Oregon State University, Corvallis, OR, 2017; Ohmann and Gregory, 2002). Stands were defined as groups of trees reasonably uniform in species composition, dominant-tree age class, and canopy cover. In the Sierras, we limited sample locations to conifer/mixed conifer habitat with canopy cover of at least 40 % (Moen and Gutiérrez, 1997) and large trees typical of older forests (Bias and Gutiérrez, 1992) with at least 50-cm QMD (Quadratic Mean Diameter) of dominant and codominant trees, which are the two tallest crown classes and form the forest canopy. In SBNF, we limited sample locations to hardwood, conifer, or mixed stands with QMD of dominant trees of at least 20 cm in diameter and >40 % canopy cover, which included at least 70 % of historical roost/nest locations in the SNBF (Supplemental Table 1).

To obtain estimates of temperatures in a roost stand, we also sampled at “available” sites (n = 43) within delineated stands. Using ArcMap (v10.7.1), we established a random “available” site for every known roost site.

At each known roost and random “available” site, we used a tree climbing sling shot to deploy a line of two iButtons into the canopy to span the range of heights spotted owls roost (~3 and ~ 20 m). We deployed loggers in known roosts while owls were not actively roosting in those locations. After deployment, we let iButtons collect temperature every 30 min for at least 20 days to increase the probability of capturing anomalous temperatures. The iButtons were secured in combined cone/

tube solar shields made from insulated, reflective foil with passive ventilation that prevented UV degradation and minimized radiation from direct sunlight (Tarara and Hoheisel, 2007).

2.4. Spatial covariates

At each location (both known roosts and random "available" sites within stands) where temperature sensors were distributed, we obtained both field and remotely sensed measurements for habitat covariates that prior research has shown to be important for driving microclimates (Supplemental Table 2). We measured diameter at breast height (DBH) of the tree in which sensors were deployed and the height at which sensors were deployed (TH) using a clinometer. We measured the orientation of sensors, which we categorized into eight groups describing cardinal direction (N, NE, E, etc.). We obtained remotely sensed habitat data from California Forest Observatory (CFO: https://forestobservatory.com) for canopy cover and canopy height. These fine-scale estimates (10 m) are created by imputing airborne lidar estimates of forest structure across the landscape using deep learning models that recognize forest structure patterns in satellite imagery (Salo Sciences Inc, 2020). We obtained estimates for elevation from a digital elevation model (3D Elevation Program, United States Geological Survey). To classify microtopography, we used a remotely sensed dataset with delineations for six topography groups: ridges, drainages, >30 % NE-facing slopes, <30 % NE-facing slopes, >30 % SW-facing slopes, and <30 % SW-facing slopes, in which percentage indicates slope angles (Underwood et al., 2010; North et al., 2012).

For daytime GPS locations, we considered only GPS points with HDOP (horizontal dilution of precision) of 10 or less and with at least 4 satellites, which yielded 658 locations, ~41 locations per individual, and ~10 locations per day for each individual. We established a minimum convex polygon (MCP) surrounding the remaining locations, grouped by individual and Julian day, and buffered the polygons by 50 m to account for potential GPS error (Zulla et al., 2022). Within each MCP, we estimated mean canopy cover, mean canopy height, and the most prevalent TOPO category.

2.5. Temperature processing

We estimated average daily maximum temperatures during a sampling period (~20 days) at known roost locations (T_R), averaging values between iButtons in an array. We obtained the same estimate of average daily maximum temperatures for the random "available sites" in stands (T_S). We also estimated average daily maximum operative temperature at the surface of owls (T_O). All temperature variables are denoted in Supplemental Table 3. We removed outliers prior to analyses using the interquartile range method (Tukey, 1977), which offered an unbiased way to remove temperatures that exceeded a realistic range of thermal conditions. A point was considered an outlier if it was above the 75th or below the 25th percentile by a factor of 1.5 times the interquartile range. We estimated differences between maximum temperatures at roosts and available maximum temperatures (ΔT_{RS}, [−8.7 °C, 6.1 °C], $\mu_{\Delta TRS}$ = −0.34 °C) using the following equation:

$$\Delta T_{RSi,j} = T_{Ri,j} - \frac{1}{n}\sum_{i}^{n} T_{Si,j,t}$$

where i is unique for each site, j indicates Julian date, t indicates territories, and n indicates the number of available sites in selected stands. We performed the same calculations to obtain estimates for differences between maximum operative temperatures and available maximum temperatures (ΔT_{OS}, [−6.0 °C, 8.5 °C], $\mu_{\Delta TRO}$ = 1.55 °C).

To quantify ambient temperature, which reflect regional spatio-temporal variation in temperature, we located the nearest remote automated weather station (RAWS) to each stand and obtained daily maximum ambient temperatures for each day sensors were active (T_A; Western Regional Climate Center cited 2020, 2021).

2.6. Statistical analysis

We examined the general effect of vegetation and topography on maximum temperature using a linear mixed effects model (Bolker et al., 2009). The response variable was average daily maximum temperature at the four "available" locations in each stand (T_S), the predictors were all habitat covariates, and Julian day and site nested within stands were random effects.

To examine whether temperatures at known roost locations differed from temperatures in available habitat within stands, we fit a linear mixed effect model in which the difference in daily maximum temperatures between known roosts and available habitat (ΔT_{RS}) was the response. We treated Julian day and site nested within stand as random intercepts. The magnitude, directionality, and significance of the intercept term was indicative of differences in temperatures between roost and available sites. To examine the effects of spatial variables and ambient conditions on differences in temperature between roost sites and available sites (ΔT_{RS}), we established a series of a priori linear mixed effects models in which ΔT_{RS} was the response variable and spatial covariates and interactions with maximum ambient temperature (T_A) were predictors (Table 2). We first fit univariate models for spatial covariates that contributed to competitive models compared to the null model, and then we examined the effect of those covariates and two-way interactions with T_A on ΔT_{RS}. We added variables in order of rank until resulting models were no longer competitive. We ranked models using sample corrected Akaike Information Criteria (AIC_C) and considered competitive models as those within 2 ΔAIC_C units of the top-ranked model (Burnham and Anderson, 2002). Random intercepts for all models included Julian day and site nested within stand to account for lack of independence between visual observations of an owl/pair of owls.

Finally, we tested for the effect of ambient conditions and spatial covariates on the difference between temperature at the surface of owls (operative temperature) and temperatures in available stand locations (ΔT_{OS}) using linear mixed-effects models. Operative temperatures were shielded only by the conifers under which spotted owls roost and recorded ambient temperature as well as radiant energy. Thus, we were specifically interested in the relative rate of change, which is captured by ΔT_{OS}. As above, we fit a series of a priori models in which we identified habitat covariates that contributed to competitive models compared to a null model, and then we examined the effect of those covariates and two-way interactions with T_A. Again, we ranked models using Akaike Information Criteria (AIC_C) and considered competitive models as those within 2 ΔAIC_C units of the top-ranked model. Random intercepts for all models included Julian day and owl identity.

For all models, we standardized predictors using a z-transformation. We tested for multicollinearity and did not include habitat variables that were highly correlated in the same model (Spearman's rank coefficient, $r_s > 0.7$; Dormann et al., 2012). All analyses were implemented in the lme4 package (v1.1.31, Bates et al., 2015) in R 4.2.2 (R Core Team, 2022). All β estimates and 95 % confidence intervals are reported in parentheses in the results section.

3. Results

3.1. Environmental predictors of temperatures in roost stands

Elevation, canopy height, and canopy cover explained most of the variation in daily maximum temperatures in roost stands (Supplemental Fig. 1). Specifically, maximum temperatures were cooler at sampling sites within roost stands at higher elevations (β_{elev} = −1.71, 95 % CI [−2.03, −1.38]), with higher canopy cover (β_{CC} = −0.41, [−0.79, −0.02]), and under taller canopies (β_{CH} = −0.41, [−0.79, −0.03]). Tree size and microtopography did not have a significant influence on

maximum temperatures in stands, though stands on steep NE-facing slopes tended to be warmer than stands on SW-facing slopes.

3.2. Environmental predictors of temperature differences between roosts and roost stands

Maximum daytime temperatures were cooler in roost sites compared to the surrounding forest stand (Table 1; $\beta_0 = -0.46$, [−0.80, −0.11]). Both microtopography and canopy structure were strong predictors for differences in temperature between known roost sites and available habitat in stands. The top two models for differences in maximum temperatures included slope characteristics (TOPO) and an interaction between maximum ambient temperature (T_A) and canopy height (CH; Table 2). Maximum temperatures at roost sites were cooler than available habitat on SW-facing slopes with gentle slopes (Fig. 2a; $\beta_{<30SW} = -1.79$ [−2.89, −0.76]). We found that ambient temperatures alone did not affect the difference between roost and stand temperatures. However, the relationship between ambient temperature and temperature offsets depended on the height of canopies at roost sites and was negative when canopies were tall (Fig. 2b; $\beta_{CH*TA} = -0.087$, [−0.15, −0.024]).

3.3. Predictors of temperature differences between owls and roost stands

All top models for differences in maximum temperatures between operative temperature and available habitat included ambient temperature as a covariate, but only our top model outperformed the null model ($\Delta AIC_C > 2.00$, Table 2). Based on the top model, which carried 0.25 of the model weight, spotted owls were cooler relative to roost stands on warmer days (Fig. 3a; $\beta_{TA} = -1.17$, [−2.09, −0.25]). Differences between operative temperature and roost stand temperature tended to decrease with canopy height (Fig. 3b; $\beta_{CH} = -0.77$, [−1.67, 0.13]), but models that included canopy height did not outperform the null model. Competitive model parameter estimates were similar to those reported in the top model, and the interaction between T_A and CH and CC were both uninformative.

4. Discussion

In rapidly changing climates, organisms will face extirpation without the availability of, and capacity to use, suitable microclimates (De Frenne et al., 2021). Pockets of habitat that retain stable climate conditions offer vital refugia for sensitive species, especially when conditions at broader scales become unsuitable (Keppel et al., 2012). Such microclimates are driven by a variety of topographic and vegetation structures, many with nuanced effects on fine-scale temperatures (Dobrowski, 2011). While understanding the extent to which species access and use microclimates is challenging, doing so is necessary to understand species vulnerability to climate change and mitigate the potential effects of a warming climate. Focusing on a climate-vulnerable species in western North America during a period in which individuals experienced extreme thermal conditions, we examined the features that structure forest microclimates and the subsequent ability of individuals to access such refugia. We found that high canopy cover and tall forests, elements typically selected by spotted owls for roosting habitat, supported cool microclimates. Indeed, individuals actively sought out cooler microclimates when ambient conditions were warmer, but only when they had access to tall canopies. This work emphasizes the value of conserving forest structures that create cooler microclimates, especially where temperatures consistently approach thermal extremes.

Table 1
Intercept model for the difference in daily maximum temperatures between known roosts and available habitat in stands (ΔT_{RS}); with estimates for β_0 and σ^2 (ΔT_{RS}) and standard errors for β_0 and variance σ^2 (SE).

Model	ΔT_{RS}	SE
Intercept	−0.46	0.18
σ^2_{jdate}	0.12	0.35
$\sigma^2_{number:stand}$	0.60	0.78
σ^2_{stand}	0.16	0.40
$\sigma^2_{residual}$	0.75	0.87

Table 2
Models for the difference in daily maximum temperatures between known roosts and available habitat in stands (ΔT_{RS}) and the differences in maximums between operative temperatures and available habitat in stands (ΔT_{OS}); with number of parameters (K) Akaike Information Criterion adjusted for small sample sizes (AIC_c), Delta AIC (ΔAIC_c), model weight (ω_i), and log likelihood (LL).

Model	K	AIC_c	ΔAIC_c	ω_i	LL
Response: ΔT_{RS}					
TOPO[a] + CH[b] * T_A[c]	12	2998.87	0.00	0.40	−1487.29
TOPO	8	3000.27	1.40	0.20	−1492.07
CH * T_A	8	3000.41	1.54	0.19	−1492.14
TOPO * T_A	13	3003.74	4.88	0.04	−1488.70
null	5	3003.85	4.98	0.03	−1496.90
CC[d]	6	3004.10	5.23	0.03	−1496.01
TH[e] * T_A	8	3004.47	5.60	0.02	−1494.17
T_A	6	3004.84	5.97	0.02	−1496.38
CH	6	3004.90	6.04	0.02	−1496.41
TH	6	3005.13	6.26	0.02	−1496.53
DBH[f]	6	3005.33	6.46	0.02	−1496.63
CC * T_A	8	3006.49	7.62	0.01	−1495.18
DBH * T_A	8	3007.34	8.47	0.01	−1495.60
Orientation	6	3012.60	13.74	0.00	−1494.16
Response: ΔT_{OS}					
T_A	5	233.84	0.00	0.25	−111.19
CH + T_A	6	234.02	0.18	0.22	−109.96
CH * T_A	7	235.14	1.30	0.13	−109.13
CC + T_A	6	235.94	2.10	0.09	−110.92
null	4	235.99	2.16	0.08	−113.52
CC + CH + T_A	7	236.69	2.85	0.06	−109.91
CH	5	236.78	2.94	0.06	−112.66
CC	5	237.53	3.69	0.04	−113.03
CC + CH * T_A	8	237.88	4.05	0.03	−109.05
CC * T_A	7	238.18	4.34	0.03	−110.65
CH + CC*T_A	8	239.27	5.44	0.02	−109.74
TOPO	9	242.41	8.57	0.00	−109.77

[a] Topography.
[b] Canopy height.
[c] Ambient temperature.
[d] Canopy cover.
[e] Tree height.
[f] Diameter at breast height.

4.1. Temperature variation in microclimates

Elevation was the strongest driver of maximum temperatures in roost stands, which corroborates prior research in topographically complex regions and forests where temperatures are cooler at higher elevations (Dobrowski, 2011; Frey et al., 2016b). Canopy height and cover also created cool microclimates available to individuals in roost stands (Supplemental Fig. 1), supporting the body of work demonstrating that temperature sensitive species preferentially roost in older forests with large trees and high canopy cover (Bias and Gutiérrez, 1992; Kramer et al., 2021). Contrary to prior research that shows SW-facing slopes sustain warmer microclimates, driven largely by more direct sunlight and xeric conditions (Frey et al., 2016b), roost stands on SW-facing slopes in our study were similar in maximum temperatures to roost stands in drainages and NE-facing slopes. That is, when owls roosted on SW-facing slopes, they sought out stands that were cooler – presumably to reduce exposure to warm temperatures.

Individual owls in our study located and used cooler daytime roost sites, which can result from fine-scale variation in forest microclimates (Chen et al., 1993; De Frenne et al., 2021; Frey et al., 2016b). Within

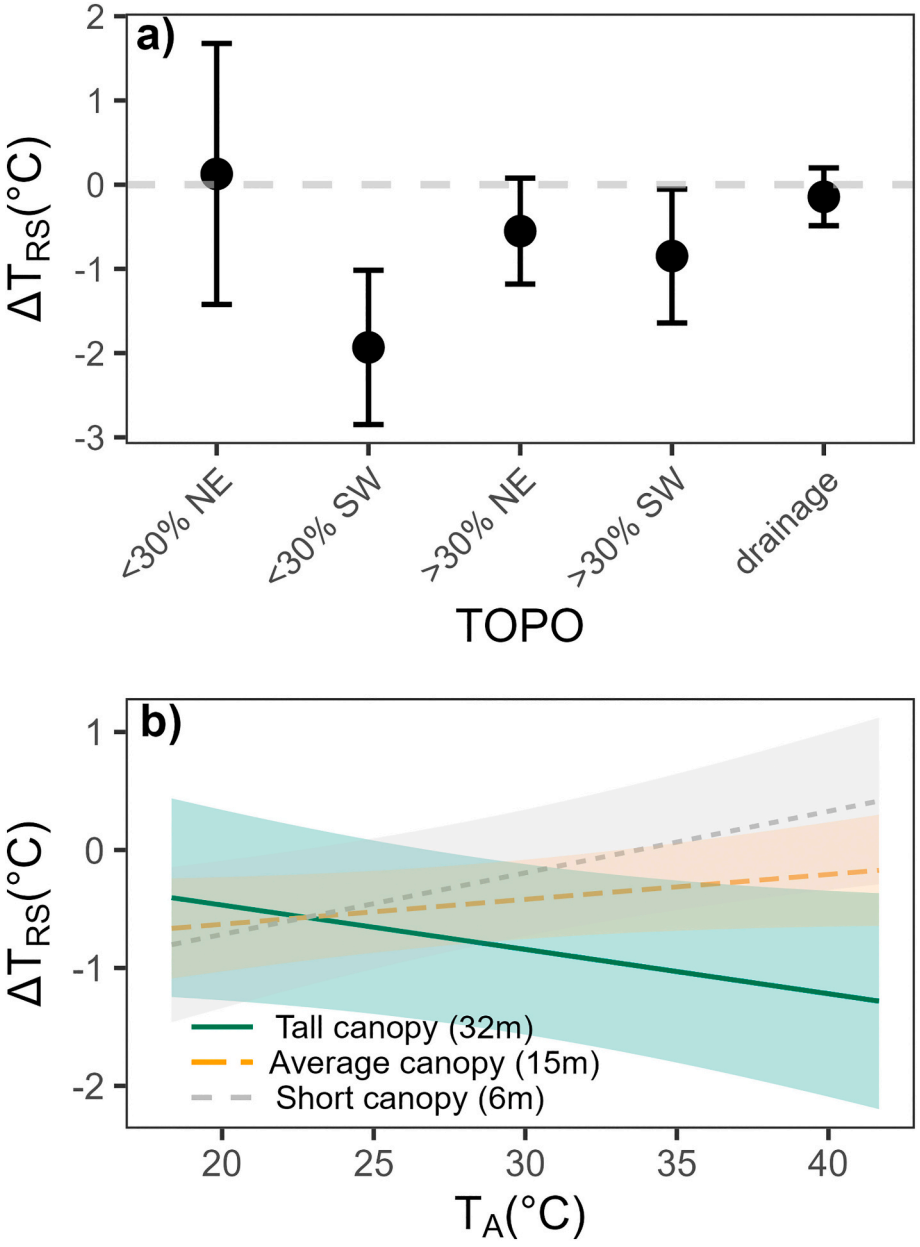

Fig. 2. Predicted differences between roosts and available habitat in stands. a) Differences in maximum temperatures were strongest on gentle (< 30 %) SW-facing slopes. b) Roosts were cooler than stand temperatures on warmer days, but only when roosting habitat was in forests with taller canopies. Here, we show this interaction with three levels. Grey, short dash lines show the predicted relationship between ambient temperatures and ΔT_{RS} for roosts in shorter forests; orange, long dash lines show the predicted relationship for roosts in forests with the average canopy height in this study; and emerald, solid lines show the predicted relationship in forests with tall canopies. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

forest stands, roost sites were indeed cooler than available habitat by as much as 5 °C, especially on SW-facing slopes. This suggests a multi-scaled strategy of habitat selection on SW-facing slopes, where individuals first identify a cooler stand and, within those cooler stands, identify roost sites that support cooler microclimates (Fig. 2a). Canopy height also shaped differences in maximum temperature between known roost locations and available habitat in stands when conditions were warmer. On these warmer days, roost sites under higher canopies were generally more buffered (i.e., cooler) from surrounding conditions. Higher, more complex forest structure associated with canopy height can create more stable microclimates by reducing solar radiation (Frey et al., 2016b). However, sites with lower canopies were often warmer than surrounding habitat on hotter days. With an absence of complexity in the overstory, air temperatures heat up faster, creating relatively warmer microclimates. This suggests that roosts with higher canopies are particularly valuable when temperatures are hot.

While spotted owls managed to access cooler microclimates for roosting, the fact that some individuals roosted in warmer stands contradicts prior research that shows that spotted owls actively roost in cooler forests (Barrows, 1981). The fraction of spotted owls in this study using warmer habitat may have lacked access to forests with cooler characteristics, especially individuals limited to roost sites at low elevations. Higher orders of habitat selection confer available microclimates, and an individual's territory may have constrained available roosting habitat to forests on warmer slopes or those with lower canopies (Johnson, 1980; Boyce et al., 2002). In the SNF and SBNF, tree mortality and recent large-scale, high-severity fire has potentially limited available habitat at the scale of stands. Additionally, individual daytime behavior is likely driven by phenology and energetic requirements of reproduction. Most of the owls in this study were active breeders, and temperature sampling occurred post-fledging. Like many avian species, adult roosts are determined in part by offspring locations, which are located near nest sites for the first few weeks post-fledge (LaHaye et al., 1997). Thus, while some individuals have access to cool microclimates, the location of their offspring may constrain where individuals choose to roost.

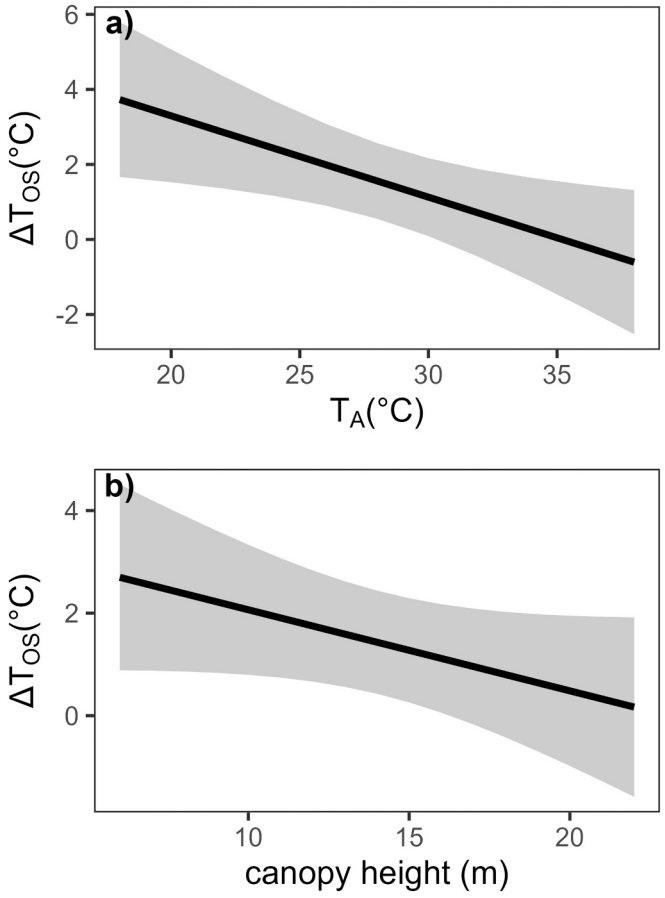

Fig. 3. Predicted differences between operative temperature and stand temperature. a) Differences between operative and stand temperatures decreased with ambient temperatures.
b) Differences between operative and stand temperatures decreased with canopy cover.

4.2. Spotted owl behavior as a response to warm temperatures

Spotted owls seemed to display behavioral flexibility in response to warmer ambient temperatures. Operative temperatures were nearly ubiquitously warmer than stand temperatures, but offsets decreased as ambient temperatures increased, indicating that spotted owls successfully located microclimates that were more buffered. The loggers on the owls were unshielded and measured ambient air temperature as well as long- and short-wave radiation, wind, and humidity (Dzialowski, 2005), quantifying thermal conditions individuals experience in nature (Bakken and Gates, 1975). Long-wave radiation is partially driven by ambient temperature; if individuals randomly used available sites within stands, then differences between operative temperatures and stand temperatures would be greater when ambient conditions were warmer. However, temperature offsets in our study were smaller and even negative when conditions were generally warmer, suggesting individuals choose daytime roosts to avoid potentially stressful temperatures.

Taller canopies tended to be associated with smaller or more negative offsets between stand and operative temperatures as well (Fig. 3b), but top models that considered canopy height did not outperform the null model. Microclimates under tall canopies in forests are extremely variable, and even small movements to large trees may offer temporary refuge from warm conditions (De Frenne et al., 2021) or refuge from direct sunlight and short-wave radiation (Carroll et al., 2016). When tall forest is readily available, spotted owls may seek out cooler microclimates to avoid potential consequences of heat or solar exposure. While other endotherms have been shown to actively use more stable microclimates during periods of anomalous conditions (Wolff et al., 2020; Shipley et al., 2020), we were unable to discern whether spotted owls sought relatively cooler microclimates created by tall canopies for their thermal characteristics, their shade, or both.

4.3. Microclimates, behavioral flexibility, and climate change

Our study documented important connections between microclimates and individual behavior during a period of historic warming. It was also the first to characterize microclimate use for this climate-vulnerable species near its southern range boundary as well as for old forest species (like martens and pacific fishers) more broadly. When spotted owls had access to habitat with cooler microclimates and ambient conditions were warm, they actively located and used roosts that were cooler than surrounding temperatures. This finding emphasizes the value of conserving large trees and forests with higher canopies and canopy cover that sustain cooler microclimates, a strategy that may benefit a suite of less well-studied forest associated species as the climate continues to warm.

Despite their behavioral response to warm temperatures, spotted owls were still exposed to conditions that exceeded presumed physiological thresholds when ambient maximums were high (Fig. 4). Over two-thirds of the roosts in this study reached maximum temperatures of at least 30 °C, a threshold over which individuals show signs of heat stress, and over a quarter of roosts reached maximum temperatures over 35 °C, the upper critical limit for the species (Weathers et al., 2001). Consecutive days consistently exceeded thermal thresholds, especially at lower elevations, pointing to potential cumulative exposure, which has been shown to reduce reproductive success and survival in similar species (Cruz-McDonnell and Wolf, 2016). In our study, we exclusively found lower elevation roost sites in habitat with higher canopy cover. Even when greater canopy cover was available, temperatures still exceeded thermal thresholds (Fig. 4e). As documented in the SBNF, many low elevation territories, where temperatures are warmer, large trees are absent, and canopy cover is low, have gone extinct and are more likely to contribute to population declines (Tempel et al., 2022). Given a future climate with a higher likelihood and frequency of extreme heat events that approach and exceed thermal extremes for forest-dwelling species, some areas may be lost regardless of management efforts aimed at promoting cool microclimates. This may limit potential refugia to higher elevations, cementing the value of managing for cooler habitat at mid-elevations. Our results potentially explain one aspect of the rapid extirpation of spotted owls from lower elevations and a mechanistic explanation for the species shifting its distribution upslope to track its abiotic niche (Peery et al., 2012).

Forest microclimates that support climate refugia are likely important to a suite of other canopy-dwelling species in addition to spotted owls. For example, northern goshawks (*Accipiter gentilis*), great grey owls (*Strix nebulosa*), martens (*Martes americana*) and Pacific fisher (*Martes pennanti*) have been identified as potentially vulnerable species to climate change (Siegel et al., 2014). Fisher, like spotted owls, likely use cooler forests during daytime resting activity to avoid thermal stress (Zielinski et al., 2005; Purcell et al., 2009). Given current rates of forest loss due to high-severity forest fire and drought-induced tree mortality (Keyser and Westerling, 2017), identifying and conserving the existing features that promote climate resiliency will be important for promoting the viability of these species. Fuel-treatments, including prescribed fire and removal of vegetation, can reduce the spread and intensity of large fires (Stephens et al., 2012), and potentially reduce the loss of important habitat (Jones et al., 2022). While such treatments may be necessary to minimize the extremity of unprecedented wildfires and habitat loss, management that also promotes large, tall trees and denser canopy cover may better sustain important microrefugia and promote climate resiliency for forest-dwelling species.

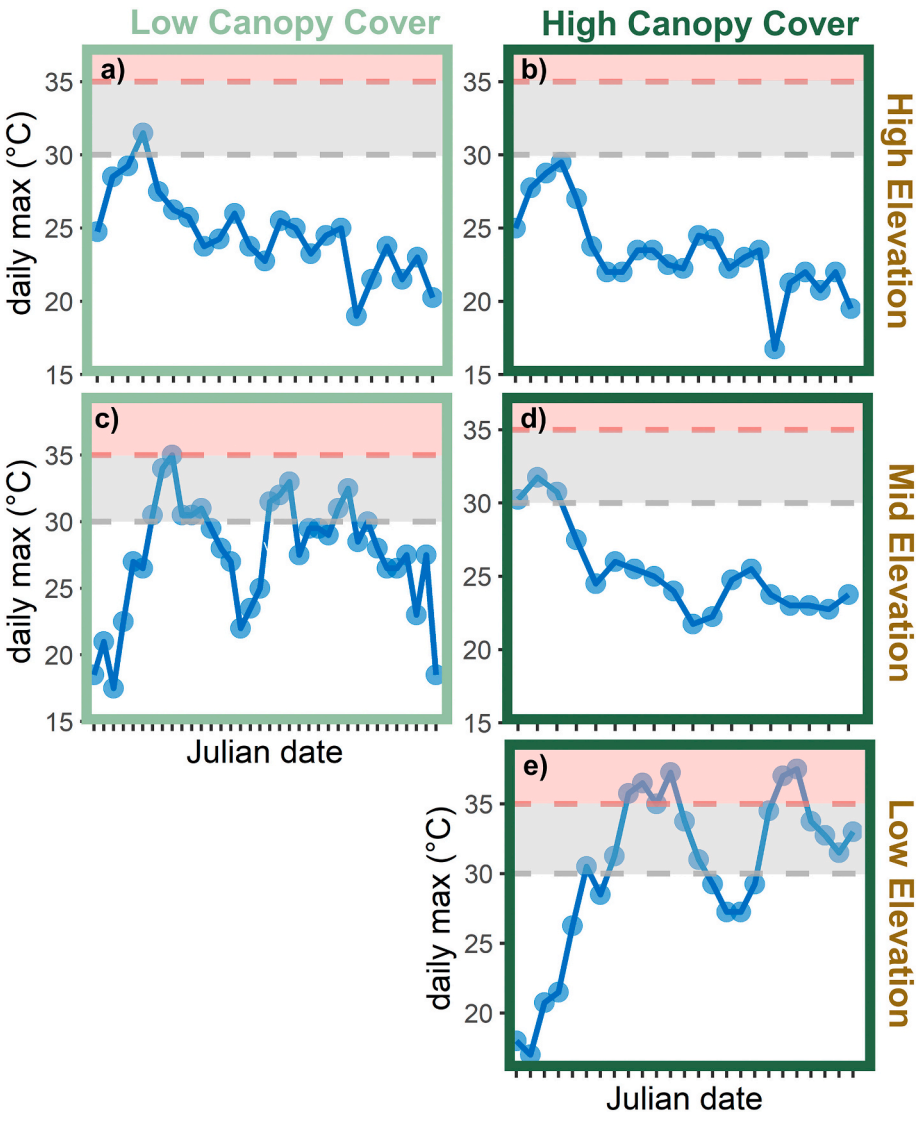

Fig. 4. Daily maximum temperatures at five roost sites during sampling periods (20–30 days), where thresholds (dashed lines) indicate species-specific physiological thresholds. At 30 °C, spotted owls begin to experience heat stress (grey) and 35 °C is the upper critical temperature for spotted owls (red). A) At a high elevation roost site (2500 m) where canopy cover was relatively low (29 %), maximum temperatures generally did not exceed thermal thresholds. B) A high elevation roost site (2500 m) with high canopy cover (54 %) had similar conditions. C) Low canopy cover (39 %) at a mid-elevation site (1900 m) yielded conditions that often exceeded the lower thermal threshold. D) A roost sites with high canopy cover (71 %) at mid-elevation (2000 m) experienced cooler maximum temperatures. E) At a low elevation (1200 m), even high canopy cover (88 %) did not buffer the site when conditions were extremely warm, where daily maximum temperatures consistently exceeded the species' thermoneutral zone and surpassed the upper critical threshold. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

5. Conclusion

Climate change will alter the availability and distribution of suitable microclimates for many species and ecosystems, including the spotted owl (De Frenne et al., 2021; Jones et al., 2016). Over the next two to five decades, average temperatures in some regions may become comparable to present-day maximum temperatures (Diffenbaugh and Field, 2013; Trisos et al., 2020; Armstrong McKay et al., 2022). Large-scale, high-severity wildfire and tree mortality due to drought threaten temperate forests globally and cause the loss of canopy cover and large trees, which will exacerbate projected temperature increases (Millar and Stephenson, 2015). Increasing temperatures, canopy loss and large tree reductions comprise a deadly cocktail to further restrict the distribution of suitable microclimates and potentially lead to local and regional extirpations of climate-vulnerable species. In the context of such rapid changes in both climate and land cover, conserving existing refugia, and restorating and propagating future refugia in areas that may buffer against climate-driven thermal stress, are important strategies for biodiversity conservation planning. Regardless of management that promotes cooler microclimates, some historic habitat will no longer be suitable for the spotted owl and other iconic forest species.

CRediT authorship contribution statement

Kate A. McGinn: Conceptualization, Methodology, Formal analysis, Data curation, Writing – original draft, Funding acquisition, Investigation, Visualization. **M. Zachariah Peery:** Conceptualization, Funding acquisition, Writing – review & editing, Resources, Supervision. **Ceeanna J. Zulla:** Investigation, Data curation, Resources. **William J. Berigan:** Project administration, Resources. **Zachary A. Wilkinson:** Investigation, Resources. **Josh M. Barry:** Investigation, Data curation. **John J. Keane:** Resources, Project administration. **Benjamin Zuckerberg:** Conceptualization, Funding acquisition, Writing – review & editing, Supervision.

Declaration of competing interest

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

Data availability statement

All temperature data used in this paper are available on Dryad doi: https://doi.org/10.5061/dryad.xksn02vjq.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2023.110132 and https://datadryad.org/stash/share/Msj0ITxCCP5mGmzryFM_6WCtwdF_YK4dSzArBhyzvVU.

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