Local microclimates can both amplify and mitigate extreme temperatures associated with climate change

Ashe-Jepson, E., Turner, E. C. and Bladon, A. J. ORCID: https://orcid.org/0000-0002-2677-1247 (2025) Local microclimates can both amplify and mitigate extreme temperatures associated with climate change. Frontiers in Biogeography, 18. e164843. ISSN 1948-6596 doi: 10.21425/fob.18.164843 Available at https://centaur.reading.ac.uk/128125/

Identification Number/DOI: 10.21425/fob.18.164843 <https://doi.org/10.21425/fob.18.164843>

Publisher: International Biogeography Society

FRONTIERS OF
BIOGEOGRAPHY
*The scientific journal of
The International Biogeography Society*

Frontiers of Biogeography 18, 2025,
e164843 | DOI 10.21425/fob.18.164843

RESEARCH ARTICLE

Local microclimates can both amplify and mitigate extreme temperatures associated with climate change

Esme Ashe-Jepson[1,2], Edgar C. Turner[2,3], Andrew J. Bladon[2,4]

1 *Chair of Global Change Ecology, Biocenter, University of Würzburg, Campus Hubland Nord, 97074, Würzburg, Germany*
2 *Department of Zoology, University of Cambridge, Downing Place, Cambridge, CB2 3EJ, UK*
3 *University Museum of Zoology, University of Cambridge, Downing Place, Cambridge, CB2 3EJ, UK*
4 *Ecology and Evolutionary Biology Division, School of Biological Sciences, University of Reading, Whiteknights, Reading, RG6 6EX, UK*

Corresponding author: Esme Ashe-Jepson (esme.ashe-jepson@uni-wuerzburg.de)

Editor Dan Gavin
Received 11 July 2025 ♦ **Accepted** 10 November 2025 ♦ **Published** 19 December 2025

Abstract

Climate change is a threat to global biodiversity, with changes to mean temperatures and increasing frequency and intensity of extreme weather events. Heatwaves in particular pose a threat to species' persistence, as temperatures may rise above physiological tolerance. However, individuals rarely experience temperatures measured at the macroclimatic scale: topographic or vegetation differences result in microclimates that provide cool refugia (local temperatures below ambient) or even result in heat traps (local temperatures above ambient) during heatwaves. However, little is known about the stability of microclimates through a period of regional warming. In this study, we recorded microclimate temperatures across different microhabitats within a calcareous grassland nature reserve in Bedfordshire, UK, in 2018, 2019 and 2022. During this time, six heatwave events occurred, including the highest air temperatures ever recorded in the UK. We found that the ability of microhabitats to offset air temperatures varied with topographic aspect, slope, amount of bare ground, shelter, vegetation height, and vegetation type, with encroaching scrub and north-facing slopes showing the strongest abilities to maintain relatively stable microclimate temperatures with increasing air temperatures, in contrast to short vegetation on south-facing slopes which became heat traps. However, no combinations of environmental structures consistently maintained cool refugia during heatwaves. Microclimate temperatures were amplified close to the ground, whereas at 50 cm height temperatures were more stable and similar to the macroclimate temperature, therefore surface-dwelling species, such as many insects, may be particularly vulnerable to extreme heat. We identified a breakdown in the ability of microhabitats to maintain cool refugia above 7 °C, implying cool refugia become increasing rare and unpredictable with increasing temperatures. Our results indicate that many microhabitats will amplify the effects of climate change rather than mitigate them.

Highlights

- The innate unpredictability and scarcity of extreme temperature events makes them an evolutionary challenge; instead, microclimatic refugia are often suggested as a way for species to cope under climate change.
- By comparing microclimate temperatures to macroclimate temperatures (from a nearby weather station) in central England, we highlight how variable local temperatures can be at fine scales relevant to small surface-dwelling organisms, with microclimate temperatures differing by as much as 20 °C.
- Microclimate performance changed with increasing temperature, with more heat traps (microclimate temperatures above ambient) and fewer cool refugia (microclimate temperatures below ambient).
- No environmental variables tested reliably maintained cool refugia at high temperatures.
- Ground-level microclimate temperatures were amplified compared to temperatures at 50 cm height, implying that surface-dwelling organisms in grasslands, including many insects, may be particularly vulnerable compared to species that fly, climb, or live in tall vegetation.

Keywords

Central England, climate change, cool refugia, data logger, extreme weather, heat trap, heatwave, landscape structure, microhabitat

Introduction

Climate change is a growing threat to global biodiversity, through changes in mean temperatures and increasing frequency and intensity of extreme weather events (IPCC 2022). Temperature directly impacts individuals by altering physiological processes, many of which are relevant to fitness, such as metabolism, oxygen demand, immune functioning, and hormone production (Karl et al. 2011; Verberk et al. 2016; González-Tokman et al. 2020). By altering internal processes, these upscale to individual and population-level responses, such as changes to species' behaviour (Hill et al. 2021), phenology (Inouye 2022), distribution (Pinsky et al. 2020; Soifer et al. 2025) and survival (Román-Palacios and Wiens 2020). Furthermore, temperature can indirectly impact interspecific interactions by causing a breakdown of close ecological relationships between species (Thackeray et al. 2010; Patterson et al. 2020), or through species' range shifts creating novel communities and interactions (Lurgi et al. 2012; Alexander et al. 2015). Therefore, understanding how species experience temperature, particularly extremes, is of critical conservation importance.

Most species, particularly small organisms such as insects, do not experience temperature at the macroclimate scale. Instead, small variations in topography and vegetation (microhabitats) can alter local climatic conditions across various scales in the form of microclimates, which can differ significantly from macroclimatic means (Bennie et al. 2008; Song et al. 2013). For example, temperatures can vary by 20 °C between north and south-facing mountainsides (Scherrer and Körner 2010). Landscape structure can therefore contribute to temperature differences within small areas, which can be similar to those found over large elevational or latitudinal gradients, and on one hand can act as climatic refugia for species to support persistence in otherwise adverse landscapes (cool refugia) (Suggitt et al. 2018). Alternatively, landscape structure can trap hot air or amplify temperatures experienced locally (heat trap), which would increase the prevalence of detrimental temperatures within landscapes. Cool microclimates may be particularly important for species with limited dispersal ability or physiological tolerance of high temperatures, or during extreme weather events such as heatwaves, where the direct temperature effects on many species will be most severe.

Heatwaves, defined by the Met Office in the UK as extended periods of hot weather relative to the expected conditions of the area at that time of year, are becoming increasingly common. In the UK, 2022 was the hottest year on record, with the highest air temperatures since records began, reaching 40 °C for the first time (Yule et al. 2023). There is growing evidence that extreme weather events such as heatwaves, rather than gradual changes in mean temperatures, drive species' responses to climate change (Bauerfeind and Fischer 2014; Ma et al. 2021). The evolutionary consequences of extreme temperature events are currently poorly understood (Grant et al. 2017), but can include strong selection in cases where specific phenotypes are affected (Van De Pol et al. 2010). This can be through truncation selection, whereby only individuals with a particular trait, such as thermal tolerance above or below a given temperature threshold survive or are fertile and contribute to the next generation. Such strong selection can increase the risk of population extinction (Vincenzi et al. 2012). Alternatively, should all individuals be equally affected by an extreme temperature event, or the impacts affect phenotypes randomly, there is little selective pressure to adapt. Adaptation to cope with temperature extremes can be inhibited by the innate unpredictability and scarcity of extreme events, particularly for species with short generation times. Therefore, selection imposed by these infrequent events can be eroded back to a phenotype that copes better with averages than extremes in subsequent generations (Bryant and Jones 1995). As such, microclimatic refugia may play a critical role in allowing species to cope with extreme conditions irrespective of adaptation, with long-term ecological and potentially evolutionary implications.

There is a growing body of knowledge as to how microhabitat structure alters the temperatures that species experience at very local scales, particularly relating to ground-shading structures such as topography or vegetation cover. For example, taller vegetation resulted in lower soil temperatures (Song et al. 2013), and micro-topographically complexity altered microclimate compositions in alpine systems (Opedal et al. 2015). Similarly, there is evidence that microclimatic conditions vary not only over the horizontal plane, but also the vertical plane, with large differences in thermal conditions with only minor changes in vertical height or distance from the ground, thereby altering the conditions experienced by species occupying different horizontal and vertical parts of the landscape (Kearney et al. 2021; Klinges and Scheffers 2021; Zellweger et al. 2024). Much recent research has demonstrated the importance of considering these variations in local climate when predicting species' responses to climate change (Scheffers et al. 2014; Baudier et al. 2015; Suggitt et al. 2018), particularly in relation to species distribution modelling (Lembrechts et al. 2019; Stark and Fridley 2022). However, although topography and vegetation structure are known to influence microclimate temperatures (Bennie et al. 2008), it is unclear whether microclimatic offsetting (the difference between microclimate temperature and ambient air temperature, following the definition of De Frenne et al. (2021))

changes during extreme weather events. Furthermore, improving understanding of which environmental structures provide the most reliable cool refugia (microclimate temperatures below ambient, which allow organisms relief or escape from high temperatures), or result in heat traps (microclimate temperatures above ambient, which put individuals that live in these areas at greater risk from high temperatures) during extreme weather events, can inform management of landscapes to promote climate resilience. With a greater understanding of which environmental characteristics influence microclimate composition, land-managers could develop landscapes that maximise species persistence under a changing climate, and focus limited resources on the management of characteristics that have the strongest influence.

This study takes place within a managed highly heterogenous calcareous grassland nature reserve in Bedfordshire, UK. As a calcareous grassland, this ecosystem contains high biodiversity, but is also innately exposed, with little shelter and dry soil (WallisDeVries et al. 2002). As a result, calcareous grasslands are at particular risk under future climate change, with the flora and fauna that occupy them particularly exposed to extreme weather events such as heatwaves.

Using a network of 131 temperature data loggers, this study addresses the following questions:

1. Does the offsetting effect of microhabitats change with environmental structure: topographic aspect, slope steepness, amount of bare ground, degree of shelter, vegetation type, or vegetation height, and which structures are the most important?
2. Does the offsetting effect of microhabitats change with increasing distance from the ground?
3. Does the offsetting effect of microhabitats change with increasing air temperature, and is there a particular temperature at which this relationship changes?
4. Which combinations of environmental structures that land-managers could alter result in the strongest microhabitat offsetting effect with increasing air temperatures?

We expect that microclimate temperatures will depend on microhabitat structure, but that particular characteristics will have stronger effects than others. We expect that topography (aspect, slope) and vegetation (type and height) will have strong effects on microclimate temperatures, as these are known to result in local temperature differences (Bennie et al. 2008; Song et al. 2013; Opedal et al. 2015). We expect that shelter may have a strong impact on the maintenance of cool refugia and heat traps as a result of reducing air mixing and trapping hot or cold air. We expect that percentage of bare ground will have an impact on heat traps due to the chalk in the soil reflecting solar radiation near the ground, resulting in amplified temperatures. However, the high albedo of the chalk should also reduce the amount of solar radiation absorbed, and so the impact of bare ground may be weaker than other environmental characteristics. Our aim is to identify key factors for land-managers and produce actionable advice to support nature within climate-resilient landscapes.

Methods

Study site

Data collection took place in Totternhoe Quarry, Bedfordshire, UK (51°53'30.75"N, 0°34'09.37"W) (Fig. 1), a highly heterogeneous nature reserve managed by the Wildlife Trust for Bedfordshire, Cambridgeshire and Northamptonshire (110–130 m above sea level). Totternhoe Quarry is an 8.9-hectare Site of Special Scientific Interest (SSSI), composed of a mixture of bare chalk, mixed length grasses, and scrub, with highly variable topography as a result of medieval quarrying. There is no natural surface water on site. The large variation in topography and vegetation structure within a small area generates a variety of microclimates which can be studied simultaneously while controlling for variations in local weather conditions. The reserve was originally mapped in 2009 with various updates in 2016–2017, as described in Hayes et al. (2018), and further updated in 2018. A backpack GPS (Trimble GeoExplorer 2008 Series Geographica Positioning System Handheld Recorder, running Fastmap Mobile 7, and Geobeacon Receiver) was used to map out blocks of continuous habitat by walking habitat perimeters, which were assigned slope, aspect, and vegetation type characteristics. In 2020, environmental characteristics (topographic aspect and vegetation type) across the whole site were updated using images from drone surveys and ground-truthed with on-the-ground surveys. High resolution digital elevation models were used to calculate aspect. There have been no general changes to the distribution of vegetation types since 2020.

Microclimate data

Microclimate data were collected continuously from May 2018 to August 2019 (with a gap from April 1st to 25th where data loggers were inactive, as they had to be collected and reset), and again from May to August 2022. In 2018, sampling locations were selected using R (R Core Team, 2018), by identifying the three largest continuous areas of each combination of four vegetation types (exposed chalk, short grass, long grass, encroaching scrub – see below for definitions) and five aspects (north, east, south, west, flat) based on fine-scale habitat maps of the reserve from Hayes et al. (2018). We chose to stratify our sampling in this way to capture the range of microclimatic conditions represented across the reserve in relation to both aspect and vegetation type, factors which are known to influence microclimatic conditions. Not all combinations of vegetation type and aspect had three replicates large enough to appear on the maps (at least 5 m^2), therefore a total of 51 locations were used. The geometric

Figure 1. Totternhoe Quarry nature reserve, with vegetation type (mapped from drone images in 2018 and updated in 2020, shown in colour) and topographic aspect (calculated from the OS Terrain 5 map at 5-m resolution, shown with hatching lines) illustrated. Points show locations with different combinations of topographic aspect and vegetation type where temperature data loggers were placed in 2018-2019 and 2022, and environmental structure was recorded. Base layer ESRI Satellite imagery, accessed via QuickMapServices plugin in QGIS 3.42.2. This includes imagery from Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community.

centroid of each polygon was calculated using R, and two data loggers (Thermochron iButton (DS1921G-F5), Maxim Integrated Products Inc) (accuracy ± 1 °C) were placed there, at 5 cm and 50 cm above the soil. These heights were chosen to represent near-ground conditions that organisms on low vegetation might experience (such as caterpillars), and conditions flying insects (such as adult butterflies) or insects climbing higher in the vegetation might experience. Data loggers recorded temperature hourly (on the hour) from April to October, and every two hours (to extend the time they could be left) from October to April. Data loggers were always orientated to face north to minimise direct sunlight on the temperature-sensing face and were wrapped in shiny metal foil to reflect rather than absorb solar radiation, reducing rapid temperature shifts due to short-term changes in solar radiation, and to protect them from water damage. They were then attached to wooden stakes (approximately 1 cm diameter) by zip ties (around the non-sensing outer edge) with a piece of shielded garden wire (in contact only with the zip tie), and they were suspended in the air (Suppl. material 1: fig. S1). We acknowledge that the exposed positions of the data loggers means that direct solar radiation hit the reflective surface, and may influence the temperatures recorded (Maclean et al. 2021). We view the large number of data loggers deployed as a compromise to more expensive radiation shields, and reduces the risk of artificial temperature amplification caused by shields heating in direct sunlight. We also note that animals, such as insects, will also experience direct solar radiation in this habitat, which will make our results perhaps more realistic than loggers housed in shields. In 2022, a different 45 sampling locations were randomly generated in QGIS version 3.36.3 (QGIS.org 2024) across three replicates of each combination of five aspects (north, east, south, west, flat) and three vegetation types (short grass, long grass, encroaching scrub), with a minimum plot size (consistent aspect and vegetation type) of 5 m^2, and a minimum distance of 10 m between each point. All data loggers were placed at 1 cm above the soil facing north, again shielded with shiny metal foil, and recorded temperature hourly. This height was chosen to represent near-ground conditions and was also partially chosen to reflect other data collected as part of a wider study. These temperatures should reflect the conditions that ground-dwelling organisms experience.

After placing the data loggers, environmental variables were recorded from the 5 m^2 surrounding each point. Topographic aspect was recorded as the predominant slope direction (assuming there was a slope, if not the point was recorded as Flat), recorded on a compass by the observer turning to face directly downhill. Slope was estimated in degrees in categories (0°, 1–10°, 11–20°, 21–30°, 31–40°, or > 40°). Shelter was recorded by scoring one point for each cardinal direction in which there was an obstruction (vegetation or topography) within 5 m of the point at chest height (from 1 (no obstructions) to 5 (obstructions in all directions), common obstructions included steep slopes and scrub). Vegetation type was recorded in three categories: encroaching scrub (25–75% of the surrounding 5 m^2 was scrub), short grass (<25% scrub, average grass height < 10 cm), long grass (<25% scrub, average grass height > 10 cm). In 2022, two additional variables were collected due to the likelihood of the ground-level data loggers being particularly affected by fine-scale local structure: the percentage of bare ground within 5 m^2 of the data logger was estimated by eye, and the average vegetation height at time of data logger deployment was recorded by gently lowering a clipboard onto the vegetation until it was supported, and the height of the clipboard above the ground was measured. After three months (or six months in winter), the data loggers were retrieved (and replaced in 2018–2019 to allow for continuous monitoring). Missing, moved, or tampered data loggers were noted and excluded from analysis. The temperature recordings were checked for outliers by visual inspection of the data, removing incomplete datasets, or complete datasets for data loggers where temperature recordings appeared nonsensical for the location and time of year (e.g. temperatures <-20 °C, n = 20).

Macroclimate data

Macroclimate data were acquired through the Met Office MIDAS Open database, where hourly air temperature data were acquired from a nearby weather station (Woburn, 52.01400, -0.59457) (approximately 16 kilometers from the study site) (Met Office, 2019) (89 metres above sea level). The weather station is positioned in a similar habitat composition to the landscape of interest (in that it is placed within an open grassy area comparable to a grassland). The weather station thermometer recorded air temperature at a height of 1.25 m (Met Office, personal communication, February 5th 2025), and was shielded with a Stevenson screen. A weather station was chosen for comparison rather than microclimate models due to weather station data still being commonly used in ecological studies, providing real-world temperature measurements for comparison, and its temperature recordings coming from a similar landscape. To date, microclimate modelling methods are still at relatively coarse resolution (e.g. ERA5 at 31 km, ERA5-Land at 9 km), which would incorporate a significant proportion of the surrounding landscape which is not similar in composition to the study site (being largely agricultural land and urbanised areas).

Data analysis

Data analysis took place in R version 4.3.3 (R Team, 2024). The data were initially prepared using the ‘dplyr’ (Wickham and Romain, Francois 2023) and ‘lubridate’ (Grolemund and Wickham 2011) packages. Plots were produced in ‘ggplot2’ (Wickham 2016) and ‘sjPlot’ (Lüdecke 2021). All temperature recordings (microclimate and macroclimate) were cut to the same date-times, starting from midnight after the last data logger was placed out, and running to midnight before the first data logger was collected.

The difference in temperature between each microclimate recording and the macroclimate was calculated for each date-time (hereafter: microclimate offset). A positive value indicated that the microclimate was warmer than the macroclimate (a ‘heat trap’), and so the weather station underestimated the temperatures species would experience locally. A negative value indicated the microclimate was cooler than the macroclimate (a ‘cool refugia’), and so the weather station overestimated the temperatures species would experience. A value of zero indicated that the microclimate and macroclimate temperatures were the same, and so the weather station accurately reflected the local conditions species would experience.

Does the offsetting effect of microhabitats change with environmental structure: topographic aspect, slope steepness, amount of bare ground, degree of shelter, vegetation type, or vegetation height, and which structures are most important?

Due to the large number of variables and data points, and the possibility of complex interactions between variables, a random forest classification model was implemented to predict which environmental structures had the highest predictive power when it came to microclimate offsetting, and the highest probability of maintaining cool refugia, using the ‘randomForest’ package (Liaw and Wiener 2002). Note that only temperature records from the 1 and 5 cm height data loggers was used, with the 50 cm loggers excluded from the random forest model.

To understand which environmental variables were important in altering the offsetting capacity of the microhabitats, the first random forest classification model was trained on the environmental variables; aspect, slope steepness, shelter, vegetation type, and macroclimate temperature, with the response variable as microclimate offsetting above or below zero (a binary categorical response). Above zero indicated a heat trap, whereby microclimate temperatures were hotter than ambient (amplified), and below zero indicated cool refugia, whereby microclimate temperatures were cooler than ambient (buffered). We chose to use a binary approach to specifically focus on what land-managers invest time and resources in to benefit nature (cool refugia), or should be avoided (heat traps). A second model was also trained on only the 2022 data to include all previously mentioned environmental variables and also percentage bare ground and vegetation height, which were only recorded in that year. The random forest models were built using 500 decision trees. These models then ranked each variable in importance in improving the predictions by calculating the mean decrease in accuracy. This metric quantifies how much the model accuracy drops when each variable is permutated: a higher mean decrease in accuracy corresponds to a variable that is more important for accurately predicting offsetting capacity. Model performance was checked using out-of-bag (OOB) error estimations. The model was trained on a bootstrap sample (67%) with the remaining (33%) used to test tree predictions. Each tree in the model was trained on equal-sized class samples, which slightly elevated the OOB (from 33.5% to 34.7%), but resulted in more balanced prediction accuracy across classes (55.2% and 17.8% to 36.0% and 33.8% respectively). To account for minor fluctuations in variable importance due to the random sampling inherent in random forests and bootstrapping, we re-ran the model 10 times and averaged the mean decrease in accuracy for each variable to produce more stable importance rankings.

Similar random forest models were fitted with the same structure, except that all categorical variables were transformed to dummy variables. This was done to more specifically test how each different level of each environmental variable influenced the likelihood of a microhabitat maintaining cool refugia specifically. Again, a separate model was run for 2022 to include vegetation height and percentage bare ground (as continuous variables these were not dummied). The difference in predictive power within each variable was then visualised using partial dependence plots, which show differences within variables while holding all other variables constant (for example to identify differences in the dependent variable (positive or negative microclimate offsetting) between north and south facing slopes with all other variables held constant). This was done by calculating log-odds of microclimate offsetting by averaging the models' predicted probabilities of a microclimate being cooler than ambient (cool refugia) while changing a single variable and holding all other variables constant. A higher log-odds value indicates a greater likelihood that the model predicts cool refugia in that microhabitat.

Does the offsetting effect of microhabitats change with increasing height above the ground?

To test whether microclimate offsetting varied with height above the ground, a linear mixed effects model was fitted with microclimate offsetting as the response variable, and macroclimate temperature, data logger height and their two-way interaction as explanatory variables, and data logger identity as a random effect. A significant interaction would imply that microclimate offsetting differs across air temperatures at different heights above ground. Model assumptions and performance of the random effect were checked before fitting.

Does the offsetting effect of microhabitats change with increasing air temperature, and is there a particular temperature at which this relationship changes?

To test whether microclimate offsetting changed with increasing air temperatures, and whether there was a particular macroclimate temperature which altered this relationship, a segmented linear mixed effects model was fitted using the 'segmented' package (Fasola and Muggeo 2018). First, a linear mixed effects model was fitted using the 'nlme' package (Pinheiro et al. 2023) with the microclimate offset as the response variable, and macroclimate temperature as the explanatory variable. As it is likely that environmental structure will influence this relationship, environmental variables were also included in the model: aspect, slope, shelter, vegetation type, vegetation height, and percentage bare ground. Interaction terms were also included between all environmental variables and macroclimate temperature. By including these environmental variables, the effect of macroclimate temperature on microclimate offsetting could be estimated independently of these variables. Data logger identity was included as a random effect. Performance of the random effect was checked using the 'lmerTest' package (Kuznetsova et al. 2017). The model was then tested for evidence of a change in slope using a Davies test, and the optimal breakpoint was extracted using the 'segmented' package (Fasola and Muggeo 2018). The segmented and non-segmented models were compared with AIC. To account for low heteroscedasticity, robust coefficients were calculated with the 'broom.mixed' package (Bolker and Robinson 2024).

Which combinations of environmental structures result in the strongest microhabitat offsetting effect with increasing air temperatures?

To determine which combinations of environmental variables were most effective in maintaining cool refugia during heatwaves, a linear mixed effects model was fit to the data from all years (therefore excluding the variables percentage bare ground and vegetation height, to reduce the number of models run and missing values impacting the results), with microhabitat offsetting as the response and all possible combinations of all environmental variables, macroclimate temperature, and an interaction term between the macroclimate temperature and environmental variables. Data logger identity was included as a random effect. Note that temperature recordings at 50 cm height were excluded from this analysis. We extracted the slope of the relationship between macroclimate air temperature and the microhabitat offset for all models. These slopes were then ranked according to the lowest slope value, as this would indicate combinations that could maintain either cool refugia (negative slopes), or microclimate temperatures close to ambient temperatures without heat amplification (slopes close to zero).

Results

In total, 629,503 microclimate temperature recordings were recovered from 131 data loggers (309,072 in 2018 (172,436 at 5 cm, 136,636 at 50 cm), 270,600 in 2019 (154,161 at 5 cm, 116,439 at 50 cm) (Suppl. material 1: fig. S2A), and 49,831 in 2022 (all at 1 cm)) (Suppl. material 1: fig. S2B). Microclimate temperatures ranged from -16.0 to 63.0 °C, with a mean ± standard deviation of 14.8 ± 7.6 °C. Across 10,155 records, the macroclimate temperatures ranged from -7.1 to 39.3 °C, with a mean ± standard deviation of 14.5 ± 6.0 °C. Six heatwave events (as defined by the Met Office as extended periods of hot weather relative to the expected conditions of the area for that time of year) were captured during recording (June 22nd to August 8th in 2018, February 21st to 28th, July 21st to 29th, August 23rd to 30th in 2019, and June 15th to 17th, July 17th to 19th, and August 9th to 10th in 2022). During these heatwaves, microclimate temperatures ranged from 17.2 °C below ambient temperature to 36.0 °C above ambient. However, high temperatures were not only recorded during heatwave events, with 3,078 microclimate temperature recordings over 40 °C recorded during the surveyed period, 1,585 of which occurred outside of the defined heatwave events (51.3%).

Does the offsetting effect of microhabitats change with environmental structure: topographic aspect, slope steepness, degree of shelter, vegetation type, amount of bare ground, or vegetation height, and which structures are most important?

Overall, macroclimate temperature was the most influential variable in determining whether microhabitats became heat traps or maintained cool refugia, followed by vegetation type, aspect, and shelter score, which all performed similarly well, followed by slope steepness (Fig. 2A). In 2022, which included the variables vegetation height and percentage bare ground, vegetation height ranked the highest of all the environmental variables, and percentage bare ground the lowest. The inclusion of these extra variables also changed the ranking of vegetation type and aspect, though they performed relatively similarly in their impact on model accuracy. In all cases, all environmental variables tested improved the model's ability to predict whether microhabitats buffered or amplified temperatures.

All environmental variables tested influenced the ability of microhabitats to maintain cool refugia specifically (Fig. 3). In particular, aspect (Fig. 3A), shelter (Fig. 3C), and vegetation type (Fig. 3D) performed well, with north-facing slopes, medium shelter scores, and encroaching scrub having the highest probabilities of maintaining cool refugia. To a lesser extent, intermediate slopes (Fig. 3B), low percentages of bare ground (Fig. 3E), and high vegetation height (Fig. 3F) also contributed to increased probabilities of maintaining cool refugia.

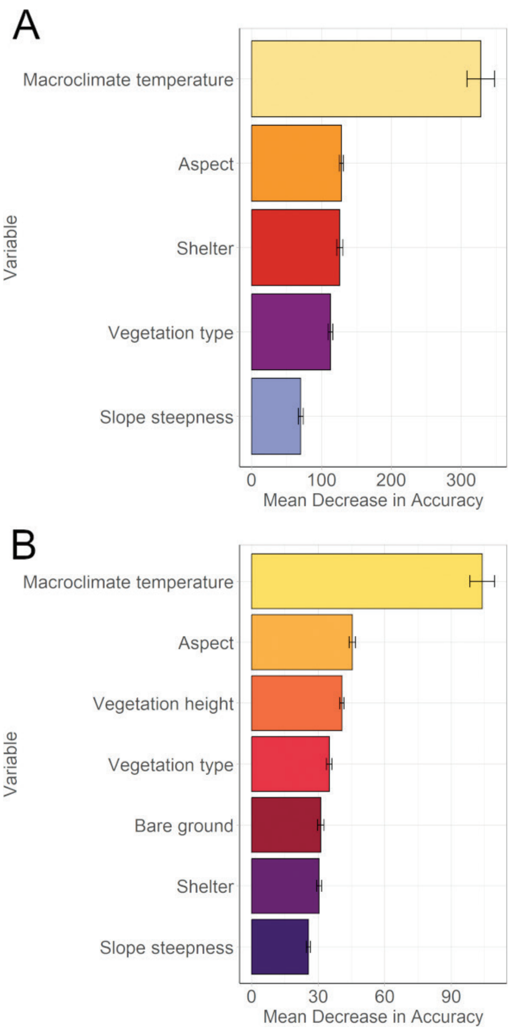

Figure 2. Environmental variables ranked in importance according to how much they contributed to the prediction accuracy of the random forest models in all years (**A**) and only 2022 (**B**), which was tested separately due to including two new variables (vegetation height and percentage bare ground). All decrease in accuracy values are averaged from 10 models. Error bars show the standard deviation in the decrease in accuracy values across the 10 models.

Does the offsetting effect of microhabitats change with increasing distance from the ground?

There was a significant change in microclimate offsetting with distance from the ground ($\chi^2 = 11.082$, d.f. = 1, $p < 0.001$) (Fig. 4, Suppl. material 1: fig. S3), with temperatures at 50 cm above the ground being similar to macroclimate temperatures and remaining relatively stable with increasing air temperatures, whereas temperatures near the ground (1 and 5 cm) were increasingly warm as air temperatures increased.

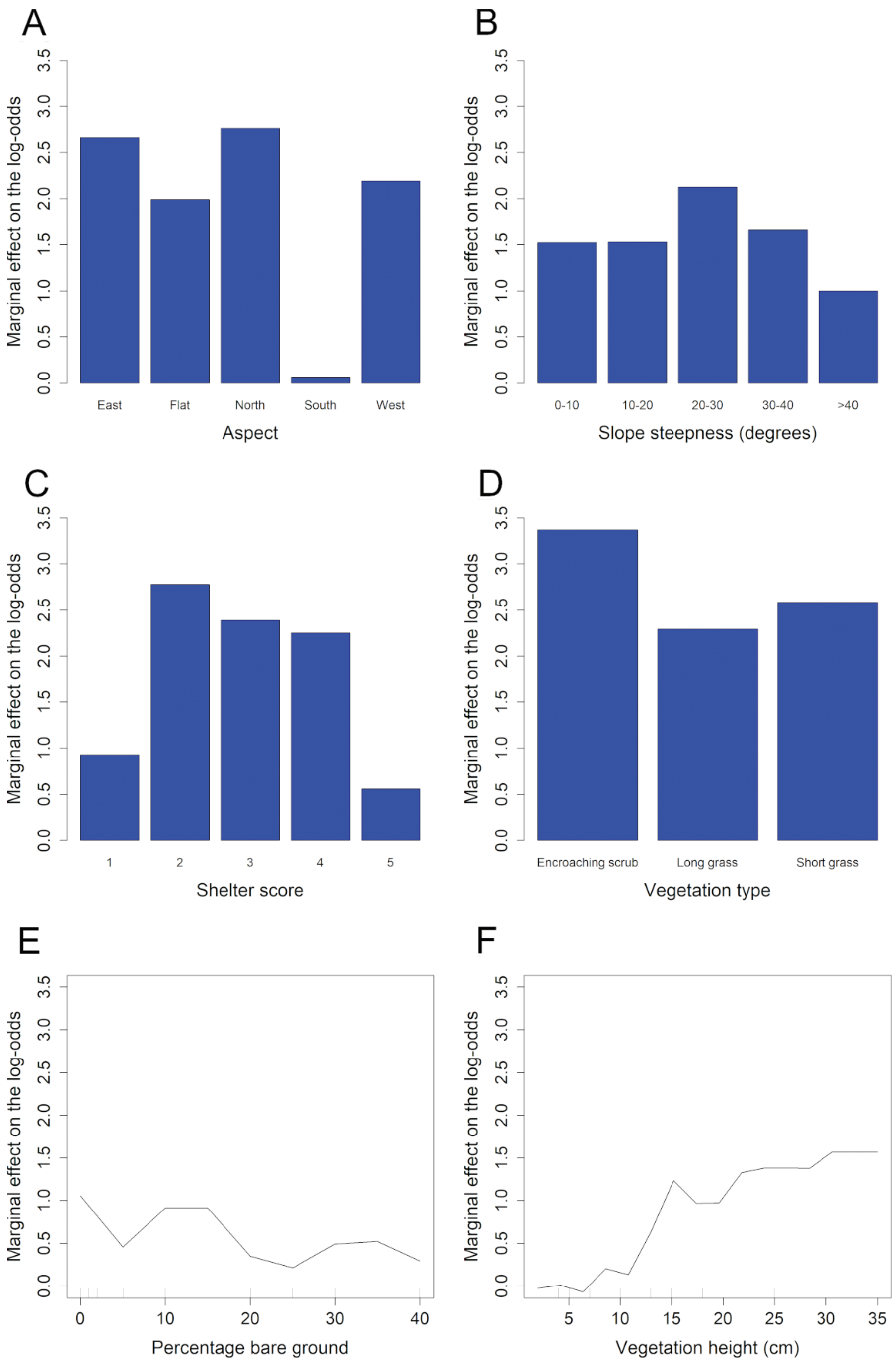

Figure 3. The marginal effects on the log-odds of a microhabitat having temperatures below ambient conditions (cool refugia) from the random forest model. Each environmental variable's effect is shown separately with all other variables held constant, with scale bars standardised to ease comparisons. Higher marginal effects indicate a higher probability of a microhabitat being below ambient temperature (cool refugia).

Does the offsetting effect of microhabitats change with increasing air temperature, and is there a particular temperature at which this relationship changes?

There was a significant change in the relationship between macroclimate temperature and microclimate offsetting at a macroclimate temperature of 7.24 °C ± 0.07 (d.f. = 323217, $p < 0.001$), which results in a significant change in slope at this temperature ($\Delta\beta = 0.357$, SE = 0.006, t = 62.00), this was confirmed by the Davies test ($p < 0.001$) (Fig. 5). Below this temperature, microclimate offsetting decreased (i.e. microclimate temperatures got marginally cooler relative to macroclimate temperatures) as macroclimate temperature increased ($\beta = -0.159$, SE = 0.006, t-value = -25.079, d.f. = 376329, $p < 0.001$). Above the breakpoint, microclimate offsetting increased (i.e. microclimate temperatures got warmer relative to macroclimate temperatures) as macroclimate temperature increased ($\beta = 0.198$).

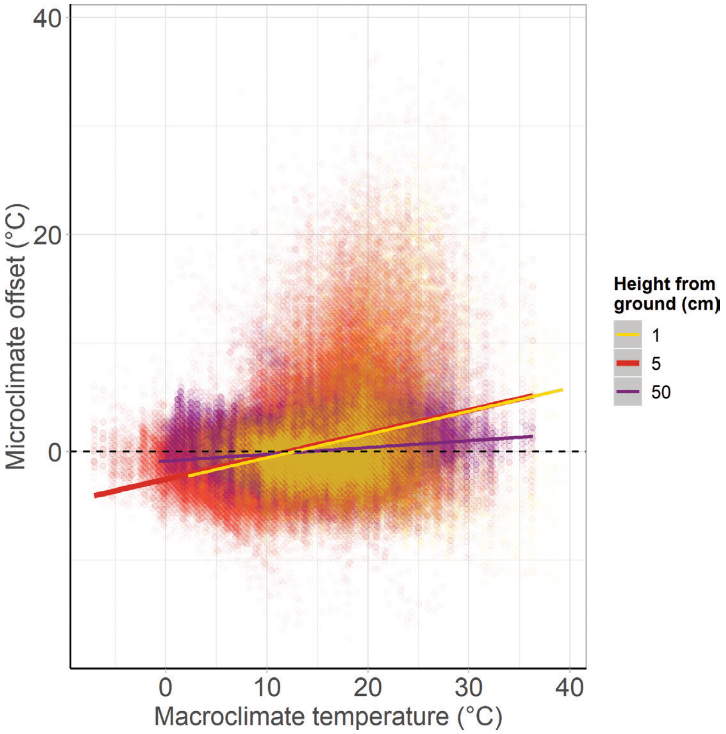

Figure 4. The relationship between air temperature (macroclimate temperature, from nearby weather station) and microclimate offsetting (the difference between the microclimate temperature and macroclimate temperature) at different heights from the ground (1 cm, 5 cm, and 50 cm). Points represent individual data logger hourly temperature recordings, and are plotted semi-transparent to illustrate where data overlap.

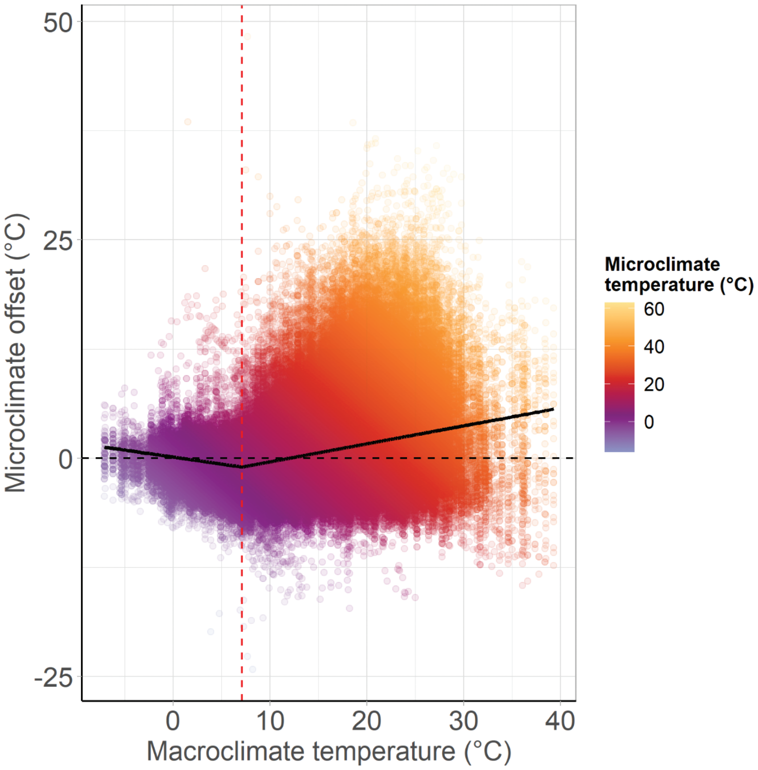

Figure 5. The relationship between air temperature (macroclimate temperature, from nearby weather station) and microclimate offsetting (the difference between the microclimate temperature and macroclimate temperature). Points represent individual data logger hourly temperature recordings and are coloured by the microclimate temperature. The black line illustrates the fitted segmented linear relationship, with the breakpoint highlighted with a vertical red dashed line. The dashed horizontal line highlights the microclimate offset values of zero (where the macroclimate and microclimate temperatures are the same). Above this line indicates the microclimate was hotter than the macroclimate, and below the line indicates where the microclimate was colder than the macroclimate.

Which combinations of environmental structures result in the strongest microhabitat offsetting effect with increasing air temperatures?

Overall, north facing slopes in combination with encroaching scrub performed best at maintaining microhabitat temperatures close to the macroclimate temperature with increasing air temperatures (Table 1), however note that the slope value is positive, indicating that there is still minor heat amplification even in these habitats. Slope steepness and shelter scores did not impact this relationship, with all combinations resulting in the same slope value. Overall, the vegetation type 'encroaching scrub' tended to provide the most microclimate offsetting in combination with all other environmental variables, followed by aspect (with north-facing slopes performing particularly well). In regard to heat traps, south-facing slopes with short grass had the strongest temperature amplification effect, followed by long grass, and then flat ground with short grass.

Table 1. The ranked coefficient values of linear mixed effects models of all combinations of environmental variables (Aspect: North, South, East, West, Flat), slope steepness (0–10°, 10–20°, 20–30°, 30–40°, > 40°), shelter (ordinal scale from 1–5), vegetation type (SG = short grass, LG = long grass, ES = encroaching scrub), ranked by the lowest slope value. The coefficient indicates the change in microclimate offset for every 1 °C increase in macroclimate air temperature. Note that in cases where different levels within a variable (e.g. slope steepness categories) resulted in the same slope value, they have been collapsed into a single row (with 'All' indicating all categories of that variable are combined).

Rank	Aspect	Slope steepness	Shelter	Vegetation type	Coefficient
1	North	All	All	ES	0.017
2	East	All	All	ES	0.095
3	West	All	All	ES	0.106
4	Flat	All	All	ES	0.131
5	South	All	All	ES	0.162
6	North	All	All	LG	0.181
7	North	All	All	SG	0.183
8	East	All	All	LG	0.259
9	East	All	All	SG	0.261
10	West	All	All	LG	0.270
11	West	All	All	SG	0.272
12	Flat	All	All	LG	0.295
13	Flat	All	All	SG	0.296
14	South	All	All	LG	0.326
15	South	All	All	SG	0.328

Discussion

The local landscape structure altered microhabitat temperatures across space and time, with aspect, slope, amount of bare ground, shelter, vegetation type, and vegetation height all contributing to changes in microclimate offsetting across air temperatures. Within the relatively small study area, we found substantial variation in microclimate temperatures, showcasing how small areas without extreme changes in topography or vegetation can contain high thermal complexity. The strongest microclimatic offsetting occurred in areas with encroaching scrub, north-facing slopes, high shelter, with tall vegetation. Microhabitats with these structures maintained microclimate temperature more similar to the macroclimate. The offsetting effect changed with increasing distance from the ground, with microclimate temperatures at 50 cm height being more similar to the macroclimate temperature, whereas temperatures at ground level (1 and 5 cm) showed stronger deviations from the weather station temperatures, with high temperatures being particularly amplified. The offsetting effect of microhabitats across increasing air temperatures showed a change in relationship at approximately 7 °C. Below this, microclimate temperatures got cooler relative to macroclimate temperatures as macroclimate temperatures increased. Above 7 °C, microclimate temperatures got warmer and more variable relative to macroclimate temperatures as macroclimate temperatures increased, implying that the offsetting capacity of microhabitats changes with increasing air temperatures, with fewer cool refugia and more heat traps, ultimately amplifying extreme temperatures. However, the increase in variation in microclimate temperatures with increasing air temperature indicates some potential for complex landscapes such as the study site to maintain some level of microclimate complexity, even at high temperatures, despite the general tendency of microclimates to amplify ambient temperatures. There were microhabitat temperatures below the macroclimate temperature even at high temperatures and so cool refugia should still exist within landscapes during high temperature events, however these are increasingly rare and less predictable with increasing temperatures.

Many of the environmental variables that we tested can be manipulated via management (e.g., Yates et al. 2000). Small ectothermic organisms, such as insects, for which the site is famous (for example it contains regionally rare butterfly species such as *Hamearis lucina*, and specialist calcareous grassland species such as *Polyommatus coridon*) are known to be sensitive to temperature change (Pollard 1988), and so would benefit from small-scale manipulations of the site based on promoting microhabitat combinations than confer microclimate complexity and, in particular, cool refugia. This study took place in a relatively small grassland nature reserve with active management that has promoted microhabitat diversity. Our results suggest that this diversity of environmental structures has also produced high microclimate diversity, which in turn should promote resilience to extreme temperatures for the species living there (Suggitt et al 2018). However, though there were cases of microhabitat temperatures being below ambient across all air temperatures, none of the environmental variables we measured were able to consistently or reliably reduce microclimate temperature below ambient conditions, with temperature differences being particularly pronounced during heatwaves. This means that, if ambient temperatures exceed an organism's thermal tolerance, microclimates may have a limited capacity to provide consistent climatic refugia. Microclimate offset changed with increasing air temperatures and so may not be sufficient to protect species from the impacts of extreme temperature events. Our study highlights the value of considering microclimate composition in species distribution models or when making extinction risk predictions (Lembrechts et al. 2019), as even in a relatively small and consistent habitat, minor variations in microhabitat structure resulted in changes to the temperatures organisms experience at fine scales.

At the ground-level, extreme macroclimate temperatures were amplified, whereas at 50 cm above ground microclimate temperatures more closely followed the weather station temperature, which records temperature at a height of 1.25 m (Met Office, personal communication, February 5th 2025). Therefore, species that live close to the ground may be particularly vulnerable to extreme temperatures compared to species that live above the ground, for example in trees or on tall vegetation, or which are more mobile vertically, such as flying insects. Moreover, species that can climb or fly would benefit from maintaining patches of tall vegetation where they can escape extreme heat, but it is unclear what measures would benefit strictly surface-dwelling organisms. Further study is needed to determine whether surface-dwelling organisms in grasslands have shown stronger responses to extreme temperatures than species that live further from the ground. The rate of change in microclimate offsetting with distance to the ground also warrants further study. Across our randomly selected sampling locations there were none with an average vegetation height of 50 cm, the highest being 35 cm. There may be challenges in maintaining very tall vegetation whilst also protecting grasslands from scrub and woodland encroachment, however our results suggest that patches of tall herbaceous vegetation should be encouraged, which can be achieved, for example, by grazer exclusion (Pardo et al. 2015). Our results also highlight the value of scrub in grasslands for maintaining cool refugia, though we recognise the difficulty in allowing scrub encroachment without compromising sensitive and specialised grassland communities. The lack of importance of high shelter when it comes to the impact of scrub implies that even low-density scrub can provide sufficient microhabitat buffering of high temperatures.

We detected a change in how microhabitats offset macroclimatic conditions across ambient temperatures. At cooler air temperatures (below 7 °C), microclimates got relatively cooler as macroclimate temperature increased. This could be due to cool air sinking to ground level, with complex topography and vegetation trapping cold air longer and causing a lag in temperature change compared to what was recorded by the more exposed and elevated weather station (Sheridan et al. 2014, Jemmett-Smith et al. 2018), and therefore a negative trend. Weather stations tend to be in open locations and above the ground and so can detect changes in air temperature faster than in complex microhabitats in natural systems. The weather station used in this study is located on a nearby farm, in a relatively open grassy area. Another possible explanation could be radiative cooling at night, whereby the ground cools at night and then cools air in contact with it by conduction. Microhabitat structure could also alter microclimate temperatures in a variety of ways not directly linked to temperature. For example tall vegetation or topographic complexity may obstruct wind and prevent air mixing, resulting in slower changes in temperature compared to the exposed and elevated weather station (Szkordilisz and Zöld 2016). Ultimately this could result in a lag between microclimate temperatures and the macroclimate temperature. Above 7 °C, we detected a rapid increase in variation in microclimate temperatures and an overall increase in the difference between microclimate and macroclimate temperature. This could similarly be the result of the complex microhabitat structures, whereby some surfaces (such as bare earth or vegetation) absorb and radiate heat for periods of time, particularly during extended periods of direct solar radiation, and result in microhabitats taking longer to cool down. In calcareous grasslands, exposed chalk may be a particularly strong reflector of solar radiation compared to other surfaces such as vegetation or other soil types, meaning that these ecosystems may be particularly vulnerable to extreme temperatures due to reflection of radiation from bare ground during high heat events. However, the high albedo of exposed chalk should also reduce the radiation absorbed and result in dynamic temperatures that may not persist for long once the radiation has ceased (e.g. rapid cooling at night). This combination of effects may explain why percentage bare ground did not have a strong effect on microclimate offsetting compared to the other environmental characteristics. The complex topography and vegetation diversity in the reserve may act to trap heat similarly as it traps cold air, trapping hot air which cannot dissipate quickly. Moreover, our results come from a calcareous grassland, which tend to be particularly dry habitats with little moisture available for evaporative cooling. The nature reserve this study took place in had a history of medieval quarrying resulting in particularly thin soils and highly heterogenous landscape structure. Therefore, the patterns identified in this study are relevant to calcareous grasslands, which are particularly biodiverse habitats, but may not be applicable to other ecosystems. It would be valuable to test whether the trends identified in this system are similar to those in other damper or more sheltered habitats. Ultimately, the increased difference between microclimate and macroclimate temperatures above 7 °C results in an amplification of warming effects, and an underestimation of microclimate temperatures by weather stations in extreme heat conditions.

Over 3,000 microclimate recordings from 58 data loggers exceeded 40 °C, higher than the maximum recorded air temperature from the weather station (39.3 °C).

Temperatures this high reach the upper thermal limits of organisms (e.g. Clusella-Trullas et al. 2011; Cabello-Vergel et al. 2022; Diamond et al. 2024). This implies that extreme temperatures have been occurring within landscapes relatively commonly. Half of these recordings occurred outside of heatwave events, meaning that heatwave frequency may underestimate the true frequency at which species are exposed to extreme temperatures. Temperatures were particularly amplified close to the ground, which could be the result of several processes. Firstly, reflected radiation from the ground surface are likely to be intercepted by the data loggers and warm them relative to ambient conditions. Secondly, the ground absorbs radiation and warms and can then directly heat the air in close contact with it by conduction. Lastly, complex topography or vegetation structures can reduce air mixing or wind movement, resulting in pockets of air close to the ground that vary more in temperature than air further from the ground, which can mix more readily and will therefore be less variable. It is however also possible that this is partially due to recording error. For example prolonged exposure to strong direct sunlight may result in inaccurate air temperature recordings across various different temperature sensing devices (Maclean et al. 2021), however it is worth noting that the data loggers at 50 cm height recorded air temperatures similar to the weather station, on average, while exposed to the same amount of sunlight as the data loggers at the ground-level (which were placed in the same locations). This implies that the higher temperatures recorded by the ground-level data loggers were genuinely the result of higher ambient air temperature rather than this effect being caused by direct sunlight exposure, although caution should be exercised when detecting extreme air temperatures with any recording devices. Though care was taken to reduce the chance of inaccurate readings (covering the data loggers in reflective metal foil, facing the temperature-sensing side north to reduce direct sunlight exposure), there is always the risk of inaccurate readings. We attempted to mitigate this by checking the data for outliers and excluding suspicious recordings. However, it is worth noting that organisms do experience direct solar radiation and therefore warming, particularly within open habitats such as calcareous grasslands that often contain little shade, so data loggers are reflecting realistic conditions for organisms living within this environment.

The differences between the microhabitat temperatures and the weather station temperatures highlights the importance of considering microclimate availability when predicting species' responses to extreme weather events; the temperatures that individuals experience at the local scale can differ dramatically from macroclimate recordings. Furthermore, many of the highest microclimate temperature recordings occurred outside of heatwaves, implying that animals may encounter inhospitable temperatures more frequently than previously suspected, at least at small scales and in exposed habitats such as calcareous grasslands. Microclimates are often predicted to help support species' persistence in a landscape by providing climatic refugia and mitigating non-tolerable temperatures (e.g. Suggitt et al. 2018), but our findings also indicate that many microhabitats can also amplify extreme temperatures, meaning that particular microhabitat compositions may exacerbate climate change, particularly for small or sessile organisms that have a limited ability to move between microclimates. We may therefore expect species assemblages to alter under climate change according to species' capacity to locate and compete for increasingly rare and unpredictable suitable climatic refugia. This may be particularly the case in homogenous landscapes with limited microclimatic variation, or in landscapes composed of a large proportion of microhabitats that become heat traps under high temperatures (e.g. those with short vegetation or very little shelter). Our result also implies that species may have been experiencing extreme temperatures near the ground for longer than previously suspected and therefore have had more time to adapt. Further study is needed to determine whether species with limited abilities to move between microclimates within landscapes have shown stronger responses to extreme weather events than more mobile species.

As topography is challenging to manipulate (though see Hayes et al. 2024), landscapes containing north-facing slopes should be highly valued for conservation going into the future, as they have a greater chance of providing climatic refugia during increasingly frequent and intense heatwaves. In addition, land managers could consider constructing artificial topographies in areas of flat land as a potential mitigation method for extreme temperatures. Indeed, constructing artificial topographies is becoming an increasingly common management practice in the UK; artificial topographies have been built in nature reserves by the RSPB (https://www.rspb.org.uk/days-out/reserves/winterbourne-downs, accessed 08/07/2025), Butterfly Conservation (https://butterfly-conservation.org/our-work/reports-and-factsheets/habitat-creation, accessed 08/07/2025), and the Wildlife Trust (https://www.wildlifebcn.org/banking-butterflies-project, accessed 08/07/2025). Compared to topography, vegetation is more easily managed. Encroaching scrub performed particularly well at supporting microclimates that did not trap heat in high air temperatures, likely by providing a combination of shade and shelter, and possibly also higher evapotranspiration. Scrub clearance is a common management technique to maintain grasslands (Redhead et al. 2012), but our results suggest that retaining some scrub would help provide climatic refugia for species in calcareous grasslands during extreme temperature events. As low shelter score areas composed of scrub performed similarly well to areas with high shelter scores, out results indicate that even at low densities scrub would be effective and so may become an increasingly important component of the landscape under future climate change. Tall vegetation also supported relatively stable microclimates and would not compromise vulnerable grassland flora communities by allowing scrub encroachment. As such, allowing vegetation to grow long, protecting some areas from grazers, or not mowing throughout the hottest summer months, could provide refugia for small ground-dwelling organisms should a heatwave occur. Ultimately, a combination of environment structures within relatively small areas could help support species and populations during high temperature events, though we express caution in an over-reliance on microclimates as a solution to protect species from heatwaves.

Conclusion

Overall, variation in environmental structure resulted in large differences in the microclimate temperatures that small organisms may experience compared to macroclimatic temperatures. In particular, macroclimate temperature under-estimated the temperatures species could experience during heatwave events, with some microclimates being as much as 20 °C hotter than the record-breaking macroclimate temperatures experienced during the summer of 2022. Based on our findings, we encourage land managers to maintain some scrub on grasslands, to prioritise the protection of north-facing slopes for climatic refugia, or to explore the possibilities of constructing artificial topographies on flat land to protect species from the increasingly frequent and intense extreme temperature events predicted under climate change. However, ultimately the capacity of microhabitats to create cool microclimates diminished with increasing air temperatures, and all environmental variables tested had a substantially weaker impact on microhabitat offsetting than the macroclimate temperature, implying that there is only so much that local environmental structure can do to offset extreme temperatures. Understanding the role and value of microclimates as climatic refugia, and in particular whether this value changes during extreme weather events, will improve our ability to predict species and population responses to future climate change.

Acknowledgements

EAJ was supported by the Cambridge Conservation Initiative (CCI) Evolution Education Trust (EET) Knowledge-Studentship. AJB was funded by a NERC Highlight topic grant (GLiTRS project NE/V007173/1) and the project was developed from an Isaac Newton Trust/Wellcome Trust ISSF/University of Cambridge Joint Research Grants Scheme grant (RG89529) to AJB and ECT. We thank the Wildlife Trust for Bedfordshire, Cambridgeshire, Northamptonshire and Peterborough for permission to collect data at their sites. We would also like to thank Dan Gavin, David Klinges, and an anonymous reviewer for their constructive comments on the manuscript.

Conflict of interest disclosure

None to declare.

Author contributions statement

Study was designed by EAJ, AJB, and ECT. Data were collected by EAJ and AJB. EAJ conducted analyses and wrote the first draft of the manuscript. All authors contributed substantially to revisions.

Data accessibility statement

The data and associated code can be found at: https://doi.org/10.5281/zenodo.17633199

References

Alexander JM, Diez JM, Levine JM (2015) Novel competitors shape species' responses to climate change. Nature 525: 515–518. https://doi.org/10.1038/nature14952

Baudier KM, Mudd AE, Erickson SC, O'Donnell S (2015) Microhabitat and body size effects on heat tolerance: implications for responses to climate change (army ants: Formicidae, Ecitoninae). Journal of Animal Ecology 84: 1322–1330. https://doi.org/10.1111/1365-2656.12388

Bauerfeind SS, Fischer K (2014) Simulating climate change: Temperature extremes but not means diminish performance in a widespread butterfly. Population Ecology 56: 239–250. https://doi.org/10.1007/s10144-013-0409-y

Bennie J, Huntley B, Wiltshire A, Hill MO, Baxter R (2008) Slope, aspect and climate: Spatially explicit and implicit models of topographic microclimate in chalk grassland. Ecological Modelling 216: 47–59. https://doi.org/10.1016/j.ecolmodel.2008.04.010

Bolker B, Robinson D (2024) broom.mixed: Tidying Methods for Mixed Models. R package version 0.2.9.6. https://CRAN.R-project.org/package=broom.mixed

Bryant DM, Jones G (1995) Morphological changes in a population of Sand Martins Riparia riparia associated with fluctuations in population size. Bird Study 42: 57–65. https://doi.org/10.1080/00063659509477149

Cabello-Vergel J, González-Medina E, Parejo M, Abad-Gómez JM, Playà-Montmany N, Patón D, Sánchez-Guzmán JM, Masero JA, Gutiérrez JS, Villegas A (2022) Heat tolerance limits of Mediterranean songbirds and their current and future vulnerabilities to temperature extremes. Journal of Experimental Biology 225: jeb244848. https://doi.org/10.1242/jeb.244848

Clusella-Trullas S, Blackburn TM, Chown SL (2011) Climatic Predictors of Temperature Performance Curve Parameters in Ectotherms Imply Complex Responses to Climate Change. The American Naturalist 177: 738–751. https://doi.org/10.1086/660021

De Frenne P, Lenoir J, Luoto M, Scheffers BR, Zellweger F, Aalto J, Ashcroft MB, Christiansen DM, Decocq G, De Pauw K, Govaert S, Greiser C, Gril E, Hampe A, Jucker T, Klinges DH, Koelemeijer IA, Lembrechts JJ, Marrec R, Meeussen C, Ogée J, Tyystjärvi V, Vangansbeke P, Hylander K (2021) Forest microclimates and climate change: Importance, drivers and future research agenda. Global Change Biology 27: 2279–2297. https://doi.org/10.1111/gcb.15569

Diamond SE, da Silva CRB, Medina-Báez OA (2024) A multicontinental dataset of butterfly thermal physiological traits. Scientific Data 11: 1348. https://doi.org/10.1038/s41597-024-04191-2

Fasola S, Muggeo V (2018) A heuristic, iterative algorithm for change-point detection in abrupt change models. Computational Statistics 33: 997–1015. https://doi.org/10.1007/s00180-017-0740-4

González-Tokman D, Córdoba-Aguilar A, Dáttilo W, Lira-Noriega A, Sánchez-Guillén RA, Villalobos F (2020) Insect responses to heat: physiological mechanisms, evolution and ecological implications in a warming world. Biological Reviews 95: 802–821. https://doi.org/10.1111/brv.12588

Grant PR, Grant BR, Huey RB, Johnson MTJ, Knoll AH, Schmitt J (2017) Evolution caused by extreme events. Philosophical Transactions of the Royal Society B: Biological Sciences 372: 20160146. https://doi.org/10.1098/rstb.2016.0146

Grolemund G, Wickham H (2011) Dates and Times Made Easy with lubridate. Journal of Statistical Software 40: 1–25. https://doi.org/10.18637/jss.v040.i03

Hayes MP, Rhodes MW, Turner EC, Hitchcock GE, Knock RI, Lucas CBH, Chaney PK (2018) Determining the long-term habitat preferences of the Duke of Burgundy butterfly, Hamearis lucina, on a chalk grassland reserve in the UK. Journal of Insect Conservation 22: 329–343. https://doi.org/10.1007/s10841-018-0065-9

Hayes MP, Ashe-Jepson E, Hitchcock GE, Clark R, Hellon J, Knock RI, Bladon AJ, Turner EC (2024) Heatwave predicts a shady future for insects: impacts of an extreme weather event on a chalk grassland in Bedfordshire, UK. Journal of Insect Conservation 28: 923–933. https://doi.org/10.1007/s10841-024-00556-5

Hill GM, Kawahara AY, Daniels JC, Bateman CC, Scheffers BR (2021) Climate change effects on animal ecology: butterflies and moths as a case study. Biological Reviews 96: 2113–2126. https://doi.org/10.1111/BRV.12746

Inouye DW (2022) Climate change and phenology. WIREs Climate Change 13: e764. https://doi.org/10.1002/wcc.764

IPCC (2022) Climate Change 2022: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Pörtner HO, Roberts DC, Tignor M, Poloczanska ES, Mintenbeck K, Alegría A, Craig M, Langsdorf S, Löschke S, Möller V, Okem A, Rama B (Eds). Cambridge University Press, Cambridge, UK and New York, USA. https://doi.org/10.1017/9781009325844

Jemmett-Smith B, Ross AN, Sheridan P (2018) A short climatological study of cold air pools and drainage flows in small valleys. Weather 73: 256–262. https://doi.org/10.1002/wea.3281

Karl I, Stoks R, De Block M, Janowitz SA, Fischer K (2011) Temperature extremes and butterfly fitness: conflicting evidence from life history and immune function. Global Change Biology 17: 676–687. https://doi.org/10.1111/j.1365-2486.2010.02277.x

Kearney MR, Porter WP, Huey RB (2021) Modelling the joint effects of body size and microclimate on heat budgets and foraging opportunities of ectotherms. Methods in Ecology and Evolution 12: 458–467. https://doi.org/10.1111/2041-210X.13528

Klinges DH, Scheffers BR (2021) Microgeography, Not Just Latitude, Drives Climate Overlap on Mountains from Tropical to Polar Ecosystems. The American Naturalist 197: 75–92. https://doi.org/10.1086/711873

Kuznetsova A, Brockhoff PB, Christensen RHB (2017) lmerTest Package: Tests in Linear Mixed Effect Models. Journal of Statistical Software 82: 1–26. https://doi.org/10.18637/jss.v082.i13

Lembrechts JJ, Nijs I, Lenoir J (2019) Incorporating microclimate into species distribution models. Ecography 42: 1267–1279. https://doi.org/10.1111/ecog.03947

Liaw A, Wiener M (2002) Classification and Regression by randomForest. R News 2: 18–22.

Lüdecke D (2021) sjPlot: Data Visualization for Statistics in Social Science. R package version 2.8.10. https://cran.r-project.org/package=sjPlot

Lurgi M, López BC, Montoya JM (2012) Novel communities from climate change. Philosophical Transactions of the Royal Society B: Biological Sciences 367: 2913–2922. https://doi.org/10.1098/rstb.2012.0238

Ma C-S, Ma G, Pincebourde S (2021) Survive a Warming Climate: Insect Responses to Extreme High Temperatures. Annual Review of Entomology 66: 163–184. https://doi.org/10.1146/annurev-ento-041520-074454

Maclean IMD, Duffy JP, Haesen S, Govaert S, De Frenne P, Vanneste T, Lenoir J, Lembrechts JJ, Rhodes MW, Van Meerbeek K (2021) On the measurement of microclimate. Methods in Ecology and Evolution 12: 1397–1410. https://doi.org/10.1111/2041-210X.13627

Met Office How we measure temperature. Met Office. https://www.metoffice.gov.uk/weather/guides/observations/how-we-measure-temperature [visited on February 5, 2025]

Met Office (2019): Met Office MIDAS Open: UK Land Surface Stations Data (1853-current). Centre for Environmental Data Analysis, September 25 2024. http://catalogue.ceda.ac.uk/uuid/dbd451271eb04662beade68da43546e1

Opedal ØH, Armbruster WS, Graae BJ (2015) Linking small-scale topography with microclimate, plant species diversity and intra-specific trait variation in an alpine landscape. Plant Ecology & Diversity 8: 305–315. https://doi.org/10.1080/17550874.2014.987330

Pardo I, Doak DF, García-González R, Gómez D, García MB (2015) Long-term response of plant communities to herbivore exclusion at high elevation grasslands. Biodiversity and Conservation 24: 3033–3047. https://doi.org/10.1007/s10531-015-0996-3

Patterson TA, Grundel R, Dzurisin JDK, Knutson RL, Hellmann JJ (2020) Evidence of an extreme weather-induced phenological mismatch and a local extirpation of the endangered Karner blue butterfly. Conservation Science and Practice 2: e147. https://doi.org/10.1111/csp2.147

Pinheiro J, Bates D, R Core Team (2023) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-164. https://CRAN.R-project.org/package=nlme

Pinsky ML, Selden RL, Kitchel ZJ (2020) Climate-Driven Shifts in Marine Species Ranges: Scaling from Organisms to Communities. Annual Review of Marine Science 12: 153–179. https://doi.org/10.1146/annurev-marine-010419-010916

Pollard E (1988) Temperature, Rainfall and Butterfly Numbers. The Journal of Applied Ecology 25: 819. https://doi.org/10.2307/2403748

QGIS Development Team (2009) QGIS Geographic Information System. Open Source Geospatial Foundation. http://qgis.org

Redhead J, Cuevas-Gonzales M, Smith G, Gerard F, Pywell R (2012) Assessing the effectiveness of scrub management at the landscape scale using rapid field assessment and remote sensing. Journal of Environmental Management 97: 102–108. https://doi.org/10.1016/j.jenvman.2011.12.005

Román-Palacios C, Wiens JJ (2020) Recent responses to climate change reveal the drivers of species extinction and survival. Proceedings of the National Academy of Sciences 117: 4211–4217. https://doi.org/10.1073/pnas.1913007117

Scheffers BR, Edwards DP, Diesmos A, Williams SE, Evans TA (2014) Microhabitats reduce animal's exposure to climate extremes. Global Change Biology 20: 495–503. https://doi.org/10.1111/gcb.12439

Scherrer D, Körner C (2010) Infra-red thermometry of alpine landscapes challenges climatic warming projections. Global Change Biology 16: 2602–2613. https://doi.org/10.1111/j.1365-2486.2009.02122.x

Sheridan PF, Vosper SB, Brown AR (2014) Characteristics of cold pools observed in narrow valleys and dependence on external conditions. Quarterly Journal of the Royal Meteorological Society 140: 715–728. https://doi.org/10.1002/qj.2159

Soifer LG, Lockwood JL, Lembrechts JJ, Antão LH, Klinges DH, Senior RA, Ban NC, Evengard B, Fadrique B, Falkeis S, Fredston AL, Guralnick R, Lenoir J, Neate-Clegg MHC, Palacios-Abrantes J, Pecl G, Pinsky ML, Smith JE, Stys B, Tingley MW, Scheffers BR (2025) Extreme events drive rapid and dynamic range fluctuations. Trends in Ecology & Evolution 40: 862–873. https://doi.org/10.1016/j.tree.2025.06.009

Song YT, Zhou DW, Zhang HX, Li GD, Jin YH, Li Q (2013) Effects of vegetation height and density on soil temperature variations. Chinese Science Bulletin 58: 907–912. https://doi.org/10.1007/s11434-012-5596-y

Stark JR, Fridley JD (2022) Microclimate-based species distribution models in complex forested terrain indicate widespread cryptic refugia under climate change. Global Ecology and Biogeography 31: 562–575. https://doi.org/10.1111/geb.13447

Suggitt AJ, Wilson RJ, Isaac NJB, Beale CM, Auffret AG, August T, Bennie JJ, Crick HQP, Duffield S, Fox R, Hopkins JJ, Macgregor NA, Morecroft MD, Walker KJ, Maclean IMD (2018) Extinction risk from climate change is reduced by microclimatic buffering. Nature Climate Change 8: 713–717. https://doi.org/10.1038/s41558-018-0231-9

Szkordilisz F, Zöld A (2016) Effect of Vegetation on Wind-Comfort. Applied Mechanics and Materials 824: 811–818. https://doi.org/10.4028/www.scientific.net/AMM.824.811

Team RC (2024) R: A language and environment for statistical computing. https://www.r-project.org/

Thackeray SJ, Sparks TH, Frederiksen M, Burthe S, Bacon PJ, Bell JR, Botham MS, Brereton TM, Bright PW, Carvalho L, Clutton-Brock T, Dawson A, Edwards M, Elliott JM, Harrington R, Johns D, Jones ID, Jones JT, Leech DI, Roy DB, Scott WA, Smith M, Smithers RJ, Winfield IJ, Wanless S (2010) Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. Global Change Biology 16: 3304–3313. https://doi.org/10.1111/j.1365-2486.2010.02165.x

Van De Pol M, Ens BJ, Heg D, Brouwer L, Krol J, Maier M, Exo K-M, Oosterbeek K, Lok T, Eising CM, Koffijberg K (2010) Do changes in the frequency, magnitude and timing of extreme climatic events threaten the population viability of coastal birds? Journal of Applied Ecology 47: 720–730. https://doi.org/10.1111/j.1365-2664.2010.01842.x

Verberk WCEP, Bartolini F, Marshall DJ, Pörtner HO, Terblanche JS, White CR, Giomi F (2016) Can respiratory physiology predict thermal niches? Annals of the New York Academy of Sciences 1365: 73–88. https://doi.org/10.1111/NYAS.12876

Vincenzi S, De Leo GA, Bellingeri M (2012) Consequences of extreme events on population persistence and evolution of a quantitative trait. Ecological Informatics 8: 20–28. https://doi.org/10.1016/j.ecoinf.2011.12.001

WallisDeVries MF, Poschlod P, Willems JH (2002) Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. Biological Conservation 104: 265–273. https://doi.org/10.1016/S0006-3207(01)00191-4

Wickham H (2016) ggplot2: Elegant Graphics for Data Analysis. In: Springer-Verlag, New York, USA. https://doi.org/10.1007/978-3-319-24277-4_9

Wickham H, Romain, Francois (2023) dplyr: A Grammar of Data Manipulation. R package version 1.1.4. https://CRAN.R-project.org/package=dplyr

Yates CJ, Norton DA, Hobbs RJ (2000) Grazing effects on plant cover, soil and microclimate in fragmented woodlands in south-western Australia: implications for restoration. Austral Ecology 25: 36–47. https://doi.org/10.1046/j.1442-9993.2000.01030.x

Yule EL, Hegerl G, Schurer A, Hawkins E (2023) Using early extremes to place the 2022 UK heat waves into historical context. Atmospheric Science Letters 24: e1159. https://doi.org/10.1002/asl.1159

Zellweger F, Sulmoni E, Malle JT, Baltensweiler A, Jonas T, Zimmermann NE, Ginzler C, Karger DN, De Frenne P, Frey D, Webster C (2024) Microclimate mapping using novel radiative transfer modelling. Biogeosciences 21: 605–623. https://doi.org/10.5194/bg-21-605-2024

Supplementary materials

Supplementary material 1

Supplementary Information (.pdf)
Link: https://doi.org/10.21425/fob.18.164843.suppl1

Supplementary material 2

Dataset used in analysis, contains microclimate temperature recordings (from the datalogger network), and macroclimate temperature recordings (from a nearby weather station), as well as microhabitat structure (.RData)
Link: https://doi.org/10.21425/fob.18.164843.suppl2

Supplementary material 3

R code used to analyse the dataset (.R)
Link: https://doi.org/10.21425/fob.18.164843.suppl3