# EXAMINING MICROCLIMATIC VULNERABILITY TO CLIMATE EXTREMES USING HIGH RESOLUTION REMOTE SENSING AND CLIMATIC TOLERANCES: METHODS AND APPLICATIONS

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# Abstract

Globally, species are experiencing geographical range shifts as a result of increased frequency and severity of extreme weather events exceeding their realized thermal niche boundaries. Using thermal limit approximations, relative heat indices can predict species extinction-colonization patterns over broad spatial scales. Locally, microclimate refugia can act as buffers against short term thermal extremes and improve species persistence probabilities. Opportunities to explore the role of microclimates in local species extinctions have recently emerged with advances in unmanned aerial vehicle (UAV) and thermal imaging technologies. My first chapter proposed a UAV-based methodology facilitating direct and accurate air temperature measurements at biologically relevant scales for butterfly species. These high-resolution microclimate measurements enabled broad-scale thermal limit approximation model applications to patch-level measurements using a verified thermal positioning index. In my second chapter, I evaluated the applicability of broad-scale models for predictions of local species distributions and abundances. The methodology proposed in Chapter 1 was used to generate patch-specific thermal position indices for butterfly species observed and surveyed in our study patches. Patch-level measurements of thermally tolerable area (overheating index) helped predict aspects of butterfly abundance, presence, and overall species richness, along with other environmental metrics that are relevant for butterfly biology. This thesis explores a frontier of direct UAV-based microclimate measurements and underscores the importance of considering thermal extremes to understand butterfly distribution and abundance, even in protected habitats.

# Résumé

À l'échelle mondiale, les espèces vivent des changements géographiques importants en raison de l'augmentation de la fréquence et de la gravité des événements météorologiques extrêmes surpassant leurs limites de niche thermique. En utilisant des approximations de limites thermiques, les indices de chaleur relative peuvent prédire des motifs d'extinction et de colonisation des espèces sur de larges échelles spatiales. Localement, les refuges microclimatiques peuvent agir comme tampons contre les extrêmes thermiques à court terme et améliorer les probabilités de survie des espèces. Des occasions d'explorer le rôle des microclimats sur les extinctions d'espèces locales ont récemment émergé avec la venue des véhicules aériens sans pilote (drones) et des technologies d'imagerie thermique. Mon premier chapitre propose une méthodologie basée sur l'utilisation des drones permettant d'effectuer des mesures directes et précises de la température de l'air à des échelles biologiquement pertinentes pour les papillons. Ces mesures de microclimat à haute résolution nous ont permis d'appliquer des modèles d'approximation de la limite thermique utilisés à grande échelle au niveau local à l'aide d'un indice validé de positionnement thermique. Dans mon deuxième chapitre, j'ai évalué l'applicabilité des modèles à grande échelle pour prédire la distribution et l'abondance des espèces au niveau locale. La méthodologie proposée dans le premier chapitre a été utilisée pour modéliser les indices de position thermique à chaque site d'étude pour les espèces de papillons observées et étudiées sur nos sites. Les mesures de la zone thermiquement tolérable dans nos zones d'échantillonnages (l'indice de surchauffe), ainsi que d'autres mesures environnementales pertinentes pour la biologie des papillons, ont aidé à prédire l'abondance, la présence et la richesse globale des papillons. Cette thèse explore une frontière de recherche pour des mesures directes des microclimats basées sur l'utilisation des drones et souligne l'importance de considérer les extrêmes thermiques pour comprendre la distribution et l'abondance des papillons, même dans les habitats protégés.

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# Introduction

Climate change is increasingly recognized as a global crisis. Consequences include warming global temperatures and increased frequency and severity of extreme weather (Harris et al. 2018). In addition to anthropogenic disturbances related to habitat degradation (Mantyka-pringle et al. 2012), such effects have been linked to species' population declines and extinction. Extinction rates have grown to mass extinction proportion (Wake & Vredenburg 2008), making research on strategies to mitigate biodiversity losses particularly critical. Many tools, such as species distribution models (SDMs; Algar et al. 2009; Kharouba et al. 2009; Porfirio et al. 2014), have been developed and refined to improve understanding of how species and biological communities respond to rapidly changing environmental conditions and to identify potential interventions that could improve their outlook in the future.

At local scales however, predicting species population trends has been more challenging. Microclimates provide thermal refuges from extreme weather over areas relevant to individual movement that can buffer organisms from negative effects of such extremes (Keppel et al. 2012; Suggitt et al. 2011; Suggitt et al. 2018). "Extreme" weather, for purposes of this thesis, consists of temperatures that exceed species' upper or lower realized thermal limits, which are the limits of their temperature tolerances after accounting for biotic interactions (e.g. with host plants, parasites, competitors, or predators). Extreme weather can also include heavy precipitation events, though I did not focus on such events in this thesis.

Refuges from extreme weather (and particularly from temperature extremes) may vary from kilometer to millimeter scales and depend on the biology and niche characteristics of individual species (Bramer et al. 2018; Suggitt et al. 2011). Species distribution models are often used to model geographical range shifts (Algar et al. 2009; Kharouba et al. 2009; Porfirio et al.

2014). However, such models typically rely on coarse, satellite-based observations or interpolated, modelled climatic data derived from widely spaced meteorological stations (Anderson & Gaston 2013; Ashcroft 2010; Potter et al. 2013; Zellweger et al. 2019). Use of such models at local scales may lead to highly generalized predictions of species persistence that lack the power to detect their responses to critical environmental characteristics that operate at spatial extents too small to be detectable using coarse-resolution models and data sources (Bramer et al. 2018; Milling et al. 2018). Thus, SDMs are more effective when estimating range shifts at broad scales and may only accurately predict local extinctions of species requiring large thermal refugia. Other models that downscale temperature observations and topographical data (Kearney et al. 2020; Maclean & Klinges 2021) offer strong potential but suffer from identical challenges: if the underlying satellite data is too coarse to detect environmental features that provide shelter to organisms, downscaled models necessarily will lack the power to identify microclimatic refugia that could be decisively important for species.

Emerging technologies, such as unmanned aerial vehicles (UAVs) and lightweight sensors (e.g. multispectral, visible light, and thermal imagery, LiDAR) present opportunities to develop microclimate modelling methodologies (Zellweger et al. 2019). These tools allow customisable fine-scale imagery that detected environmental conditions relevant for even very small-bodied organisms (Zellweger et al. 2019). In many environmental fields, UAVs rose to popularity before the development of efficient lightweight specialty sensors. Their ability to provide aerial imagery while simultaneously reducing the need for *in situ* observations in areas that are hard to access, lowering costs have streamlined their popularity (Linchant et al. 2015; Marris 2013).

In microclimatic research, the emergence of efficient lightweight sensors presents opportunities to expand the field. This includes LiDAR-based 3D ecosystem modelling (Guo et al. 2017), high resolution thermal mapping (Faye et al. 2016), and landscape change analyses (Gioia et al. 2021). While techniques that interpolate broad-scale remote sensing data will remain essential for broad-scale microclimatic estimations, direct thermal measurements using lightweight sensors could further improve habitat management with more accurate and detailed insight.

The thermal position index (TPI) has shown promise for global species extinction-colonization modelling (Kerr 2020; Soroye et al. 2020; Williams & Newbold 2021). By relating climate shifts to an estimate of each species' physiological thermal tolerances, this index predicts how each species is differentially impacted by climate change at global scales (Kerr 2020; Soroye et al. 2020; Williams & Newbold 2021). Multiple studies have proven species alter their historical ranges when temperatures exceed their physiological limitations (Hufnagel & Kocsis 2011; Soroye et al. 2020; Williams & Newbold 2021). However, this pattern has not been tested at microclimatic scales. Microclimate thermal buffering, the impact of which is still being studied, may alter thermal dynamics observable at global scales. Recent remote sensing advances present opportunities to study extinction-colonization dynamics at local scales. With efficient microclimate mapping methodologies and better understanding of local climate-based extinction-colonization patterns, more efficient and targeted conservation practices tailored to specific species can be developed.

Butterflies are useful model organisms in climate change research. They are diverse and the distributions of individual species are relatively well-characterized spatially and temporally in many regions (Wilson & Maclean 2011). They are small-bodied and ectothermic, making them particularly vulnerable to temperature extremes (Beirão & Cardoso 2020; Wilson & Maclean 2011). As a taxon, they also exhibit considerable interspecific variation in heat tolerances, further recommending them for research on biotic responses to changing thermal conditions. As a result, the effects of climate change on butterflies are well established regarding their response to direct (e.g. thermal changes; Beirão & Cardoso 2020; Hufnagel & Kocsis 2011; Mattila et al. 2011; Wilson & Maclean 2011) and indirect (e.g. host plant and nutritional availability; Braschler & Hill 2007; Geister et al. 2008; Jain et al. 2021; Lancaster 2020; Patterson et al. 2020) effects. While evidence suggests that even specialist butterflies can show some flexibility in host plant use (Lancaster 2020), rapid adaptation for higher heat tolerance seems physiologically unlikely (Bennett et al. 2021). Understanding thermal dynamics at small scales becomes crucial for future mitigation efforts, particularly as it relates to ectothermic species.

The first chapter of this thesis explores remote sensing opportunities to develop microclimate modelling methodologies. It proposes a methodology that enables direct and detailed air temperature measurements at organism-relevant scales (in our case butterflies) using UAV-based thermal remote sensing. The methodology adapts realized thermal niche approximation methods successfully used at global scales to measure microclimatic thermal position. The second chapter of this thesis uses the methodology developed in Chapter 1 to assess abundance and distribution patterns of observed butterfly species at microclimatic scales. The objective was to examine whether microclimate buffering altered thermal dynamics observed globally. This chapter also explores whether niche level processes (e.g. realized thermal niche boundaries) could inform patch use at microclimatic scales.

# Chapter 1 - High resolution thermal remote sensing and the limits of species' tolerance

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## Abstract

Extinction risks for many insect species, particularly across very broad spatial extents, have been linked to the growing frequency and severity of temperatures that exceed the boundaries of their realized niches. Measurement and mitigation of such impacts is hindered by the availability of high-resolution measurements of species-specific severity of extreme weather, especially temperature. While techniques enabling interpolation of broad-scale remote sensing metrics are vital for such efforts, direct remote sensing measurements of thermal conditions could improve habitat management by providing detailed insights that interpolative approaches cannot. Advances in unmanned aerial vehicle (UAV) technology have created opportunities to better evaluate the role of microclimates in local species extinctions. Here, we develop a method to create high-resolution maps of microclimates using UAV and thermal imaging technology that use species' realized niche boundaries to assess potential effects of severity of extreme temperatures. We generated air temperature maps (5cm resolution) and canopy height maps (1cm resolution) for 15 sites in a rare alvar ecosystem in eastern Ontario. We validated these remote sensing observations against independent, *in situ* temperature observations using iButtons. Temperature observations were accurate and related to physical heterogeneity in alvar habitats. We converted temperature measures into estimates of proximity of thermal niche boundaries for three butterfly species found during field surveys. This is the first time that this method has been applied to high resolution remote sensing observations and offers potential to

assess the availability and adequacy of microclimates within habitats at resolutions relevant for conservation management.

## Introduction

Climate change exposes species to abiotic conditions that may exceed their tolerances (Kerr et al. 2015; Urban et al. 2016), leading to growing frequencies and severities of extreme weather events (Harris et al. 2018; Kerr 2020). Such changes contribute to the declines of many species (Riddell et al. 2021; Soroye et al. 2020). Over broad geographical areas, such extreme events are increasing extinction risks for populations of key pollinator species (Soroye et al. 2020) and vertebrates at global extents (Williams & Newbold 2021). Distinguishing between effects of "press" events (e.g. shifts in average climatic conditions that can progressively change the suitability of an environment for particular species) vs. "pulse" events (e.g. short duration extreme weather that can cause population decline; Harris et al. 2018), temperature extremes ("pulse" events) in particular have been linked to changes in species colonization-extinction dynamics, contributing to declines for many species across broad geographical areas. Translating broad-scale models to direct local measurements that assess species' exposures to extreme temperature, relative to their individual tolerances, could improve habitat management and species' conservation prospects.

Microclimate refugia are areas where species can find shelter from extreme weather (Rull 2009). The size of these refugia depends on the body size and niche boundaries of each species (Keppel et al. 2012). Species distribution models (SDMs) are often used to forecast impacts of climate change on species' ranges (Algar et al. 2009; Kharouba et al. 2009; Porfirio et al. 2014). However, such methods rely heavily on long term climate data and are more appropriate for use at large biogeographical extents (Anderson & Gaston 2013; Ashcroft 2010; Potter et al. 2013).

Species experience temperatures at very localized spatial extents (Suggitt et al. 2011). While some studies have measured microclimatic variation of complex local landscapes at scales relevant to the movement and habitat use of individual organisms, fewer studies have assessed this microclimatic variability relative to individual species' thermal boundaries comprehensively throughout habitats (Milling et al. 2018; Pincebourde et al. 2016; Rebaudo et al. 2016; Slavich et al. 2014; Suggitt et al. 2011; Suggitt et al. 2018). A key challenge is that many habitats exhibit considerable thermal heterogeneity (e.g. Milling et al. 2018), which can enable species to find shelter from short duration temperature extremes (Suggitt et al. 2011; Suggitt et al. 2018). Techniques to measure microclimate heterogeneity relative to the limits of species' tolerances are essential for predicting extinction risks of small-bodied species (Pincebourde et al. 2016; Potter et al. 2013; Rebaudo et al. 2016; Suggitt et al. 2018), but are likely to require emerging remote sensing technologies (Zellweger et al. 2019).

Unmanned aerial vehicles (UAVs, or drones) show considerable promise in ecological research (Christie et al. 2016; Duffy et al. 2021; Zellweger et al. 2019). The availability of powerful, lightweight sensors, including thermal, multispectral, visible light, and LiDAR, create opportunities to translate broad-scale models to particular habitats, which could help predict movements or presences of individual species within habitats (Anderson & Gaston 2013; Duffy et al. 2021; Zellweger et al. 2019). Satellite thermal infrared (TIR) imagery and topographical data have been used in broad-scale ecological models (Zellweger et al. 2019). However, most satellite TIR imagery resolution is too coarse to detect and measure microclimates directly, particularly for small-bodied organisms, which may limit their application to air and soil microclimatic temperature measurements in some cases (Anderson & Gaston 2013; Zellweger et al. 2019). Radiometric thermal cameras mounted on UAVs provide measurements at very high resolutions that can complement broader-scale remote sensing measurements of temperature (Anderson & Gaston 2013; Brenner et al. 2018; Byerlay et al. 2020; Maes et al. 2017; Messina & Modica 2020; Milling et al. 2018). Prior to the onset of UAV and thermal camera technologies, microclimate studies required temperature loggers, such as iButtons (George et al. 2015; Holden et al. 2011). Such loggers are vital for calibrating and validating thermal remote sensing observations, but remote sensing provides unique advantages in terms of synoptic environmental measurement that greatly expands the reach of *in situ* ecological measurement (George et al. 2015; Holden et al. 2011; Kerr & Ostrovsky 2003).

The thermal limits of each species could predict the response of small-bodied species to climate change (Sunday et al. 2012). There is mounting evidence of species altering their historical range in response to habitats exceeding their thermal limitations (Hufnagel & Kocsis 2011; Soroye et al. 2020; Williams & Newbold 2021). When temperatures exceed a species' thermal tolerances, their fecundity and survival declines because they must expend energy on behavioural or physiological thermoregulation rather than resource gathering or reproduction (e.g. Buckley et al. 2021). The newly-developed and tested Thermal Position Index (TPI; Kerr 2020; Soroye et al. 2020; Williams & Newbold 2021) relates species' realized thermal niches to their extinction-colonization dynamics. This method measures thermal tolerances using historical observations of air temperatures in areas where species have successfully persisted over time. Species' upper thermal limits evolve slowly, so adaptation rates are likely to be insufficient to permit many species to tolerate rapid warming (Araújo et al. 2013; Bennett et al. 2021).

This paper proposes a new methodological framework to measure landscape-scale microclimatic profiles with UAV and thermal infrared imaging technology, and illustrates their use in a practical conservation setting. We simultaneously outline a method of translating the

Thermal Positioning Index, previously validated at global scales, to microclimatic applications. This framework includes five steps: data collection, assessment of species' thermal limits, map building, mapping of thermal conditions relative to species' measured tolerances, and interpretation (*sensu* Faye et al. 2016). We present examples of how individual species' tolerances can be linked to remotely sensed thermal data to describe habitat suitability for three butterfly species: *Hesperia sassacus* (Indian skipper), *Speyeria aphrodite* (Aphrodite fritillary), and *Coenonympha tullia* (Common ringlet).

## Methods

### STEP 1 - DATA COLLECTION

***Study Site.*** Field sites were located in Burnt Lands Provincial Park situated 30km west of Ottawa, ON, which hosts an alvar ecosystem interspersed with mostly coniferous tree stands. Fifteen sites of varying sizes separated by a minimum of 20 m of forested area were selected (Gordon & Kerr 2022). All sites consisted of open areas and clearings. Only two were not surrounded by trees. Research and UAV use permits were provided by Ontario Parks. Recognized as rare and imperiled ecosystems by the Nature Conservancy of Canada, alvars are characterized by open and barren areas with little to no soil, and often host rare species (NCC 2020). During summer, these landscapes can experience highly localized extreme heat in areas with exposed limestone, while vegetated areas nearby might have considerably lower temperatures. The spatial variability in these thermal conditions has not previously been measured.

***UAV and Sensor.*** A DJI Matrice 300 quadcopter with real-time kinetic (RTK) positioning was deployed. This drone carried a Zenmuse XT2 dual sensor with thermal (13mm focal length;

640x512 image capture) and visual (8mm focal length, 12 megapixel resolution) imaging capabilities (DJI Inc., Shenzhen, China). A RTK base station was deployed in the field, which increased the positioning accuracy of the UAV by providing real-time differential corrections, and eliminated the need for ground control points. The quadcopter was equipped with the DJI pilot program, which included a mission function allowing execution of automated flight and camera control sequences. Imaging was acquired during missions programmed in the DJI pilot program using satellite imagery. The thermal camera captured images in the thermal infrared (TIR) spectral range in the radiometric-jpeg (R-JPEG) format. Each pixel was embedded with temperature data. The in-camera emissivity value was set to 1 for TIR images and adjusted in the GIS workflow step outlined below. The visual camera captured images in the red, green, and blue spectral bands (RGB). Both cameras captured images simultaneously. Every image was geotagged with the RTK-corrected GPS coordinates.

***Flight Plan.*** Image acquisition flight plans were programmed with a 90% image overlap on all sides to optimize mapping accuracy, as recommended by the Pix4DMapper software used in the mapping step (Pix4D SA, Lausanne, Switzerland). The UAV was programmed to capture images at 1 second intervals and fly at a constant 2.5 m/s speed to maximize survey area, given a 37-minute battery life limitation, while minimizing motion blur. All missions were performed at 37 meters altitude to achieve 5 cm thermal imaging resolution and 1 cm RGB imaging resolution. All flights were restricted to days above 15°C with <50% cloud cover between 10:30am and 3:30pm to ensure the accuracy and comparability of the thermal imagery gathered (Dai et al. 1999). Cloud cover alters TIR-based temperature measurement, so all flight missions were paused during cloudy periods and resumed after they cleared. Missions were aborted if conditions remained cloudy. Butterfly surveys were conducted in parallel to our UAV surveys.

While the data were not used in this paper, the butterfly monitoring methodology's temporal and temperature requirements (i.e. between 10:45am and 3:45pm, and over 13℃) had to be respected for the drone surveys as well (Pollard 1977). As the method was designed for British summer conditions, mild liberties were taken with the methodology (i.e. earlier start but higher temperature requirement).

***In situ Temperature Measurements.*** To calibrate temperature readings captured by the thermal imaging, temperature loggers were placed *in situ*. At each site, an iButton (DS1922L-F5#, Maxim, Dallas, USA; accuracy: ±0.5℃) coated in clear plastic (Roznik & Alford 2012) was placed on the ground approximately 1 meter into the tree line in full shade near each site's access point for convenience. The plastic coating provided a waterproofing barrier (Plasti Dip, Blaine, MN, USA) for the iButton but is not expected to significantly affect the air temperature readings in the shade (Roznik & Alford 2012). Statistical comparisons of coated and uncoated logger data supported this assumption. These coated temperature loggers (hereafter referred to as ground loggers) were assumed to measure near surface air temperature as tree shade blocked most direct solar radiation and acted as solar shields, thus limiting the effect of solar radiation on temperature readings (Gies et al. 2007). Three ground loggers were lost in the field, likely due to wildlife interference. At three sites, three poles each containing three uncoated iButtons at 0.05 m, 0.75 m, and 1.5 m (total of 27 iButtons) were placed to record air temperature variations at different heights (Fig. 1.1). These poles were constructed out of white PVC pipes (Mittra et al. 2013). The three sites were chosen for their variation in dominant surface type (limestone, grass, and mix of both). Temperature loggers (hereafter referred to as pole loggers) were positioned on the tip of each protrusion and rested on wire mesh to allow ventilation. Additional holes were drilled along the main pole and on each protrusion to allow better ventilation. These temperature loggers were used to model the relationship between UAV captured remotely sensed soil surface temperatures and air temperatures as air temperature is the metric adult lepidopterans, our study group, are most exposed to. Every iButton was programmed to record temperature at 30-minute intervals and was placed in the field to be retrieved at the end of the field season. Air temperature was also measured before every UAV mission in a shaded area using a handheld HT-86 humidity meter (Wal Front, USA; accuracy: ±0.5°C, ±3% RH).

## STEP 2 - GENERATING THERMAL LIMITS

We extracted data on the five hottest and coldest locations in the ranges of butterfly species that were detected in our study sites based on a historical air temperature dataset (Harris et al. 2014). As in Soroye et al. (2020), we used a baseline observation period to estimate thermal limits. Only occurrences between 1901 and 1975 were considered when estimating species' upper and lower thermal limits. Climate change has accelerated rapidly after that baseline period. By using the location-month combinations, only the months where a species observation had occurred were considered to extract monthly maximum and minimum air temperatures. Therefore, the summer months of the overwintering sites would not be considered when extracting thermal limits. Location-month combinations were used in lieu of location-day combinations due to lack of historical daily temperature data. These values have previously been shown to be informative with respect to insect and other species' vulnerabilities to changing frequencies of extreme weather (Outhwaite et al. 2022; Soroye et al. 2020; Williams & Newbold 2021). Historical air temperatures were obtained from the Climate Research Unit dataset (Harris et al. 2014). Lepidoptera occurrence information was extracted from the eButterfly citizen science program (Prudic et al. 2017) and from longer term butterfly observations assembled through the activities of systematists and biological surveyors (Soroye et al. 2018). Each species observation is traceable to a curated museum specimen or to a submitted observation that has been approved by a team of butterfly experts.

## STEP 3 - MAPPING

A total of 30 drone surveys were conducted from May 17 to August 26, 2021. One survey was discarded due to a brief malfunction with the RTK base station, which caused georeferencing discrepancies. As a result, every raster output was produced 29 times for each of the drone surveys. Raw TIR and RGB images collected in the field were used to generate TIR, RGB, digital surface model (DSM), and digital terrain model (DTM) orthomosaics (i.e. a georeferenced aerial image geometrically corrected; Faye et al. 2016) using the Pix4Dmapper software. The software used the embedded GPS information in each image and detected characteristic objects in the images to generate tie points and create densified point clouds. These clouds were then used to blend overlapping images and create an orthomosaic (hereafter referred to as map) with the original pixel information still intact. The software algorithm relies on machine-learning techniques that employ geometric features and colour information (Becker et al. 2017). For each of the 29 surveys, one map of each type (TIR, RGB, DSM, DTM) was created. TIR maps had an approximate resolution of 5 cm/pixel, while RGB, DSM, and DTM maps had an approximate resolution of 1 cm/pixel.

## STEP 4 - GIS PROCESSING

***Classified Surface Type Map.*** The RGB maps were then imported into ArcGIS Pro software (Esri, Redlands, CA, USA). Thermal cameras estimate soil temperature by measuring the amount of infrared energy being reflected from the ground (Madding 1999). However, each surface reflects, absorbs, and emits re-radiated light differently (i.e. emissivity). To better estimate soil surface temperature, correcting for surface emissivity is essential (Madding 1999). To correct the remotely sensed soil surface temperature TIR maps for emissivity, each RGB map had to be classified by surface type (Becker 1987; Faye et al. 2016). This was accomplished using the *Classification Wizard* tool. Its algorithm uses a feature class, developed with training samples, to identify the map's surface classes. The following surface types were included in the classification schema: debris, forest, grass, tall grass, limestone, shrub, soil, water, and wood. An object-based classification type was used using a supervised classification method to identify training samples. This classification type accelerated the training sample process by allowing the selection of objects (based on geometric features and colour information) instead of individual pixels. In each RGB map, approximately 25% of each surface type was identified using the *Segment Picker* tool. This process generated a classified raster with each pixel identified as the appropriate surface type. These maps were validated by matching ground truth data about major landscape features to the land cover classification.

***Emissivity Map.*** To create emissivity rasters, an "Emissivity" field was added to the classified maps' attribute tables. The emissivity values were added manually based on a literature review (Table 1). Objects identified as debris were given an emissivity value of 1 as their composition was not always known. Each map was then resampled to match the pixel size of the classified maps to the pixel size of the thermal maps. The emissivity values were extracted into a new raster and turned into floating point rasters to ensure the emissivity map was in the same raster format as the TIR maps.

***Emissivity-Corrected Remotely Sensed Soil Surface Temperature Map.*** Emissivity-corrected soil surface temperature maps were created by first extracting the radiance value in each TIR maps using Planck's law. Thermal cameras estimate surface temperature by assuming a surface emissivity of one. By extracting radiance values, we can re-estimate radiance values, and subsequently surface temperatures, given the emissivity values obtained in the emissivity maps. The difference in focal length between the TIR and visual cameras caused occasional misalignments between the RGB and TIR maps. As such, the emissivity and TIR maps were first manually aligned.

***Modelling Air Temperature.*** To transform the remotely sensed soil surface temperature maps into air temperature maps, we modelled the relationship between the air temperatures (ground and pole logger data) and soil surface temperatures (emissivity-corrected remotely sensed soil surface temperature maps) at a given position. We ensured air temperature data of different logger heights was not statistically different before performing the model. Thus, elevation had no effect on air temperature. The mean temperature in a 30cm radius around the iButton locations were extracted and used as soil surface temperature proxy on the corrected soil surface temperature maps. The iButton temperature recorded nearest the time of the UAV survey was used as air temperature. A simple linear regression model with 76 data points was constructed in R to relate air temperature to remotely sensed soil surface temperature used here as the independent variable (R Core Team 2019). Although air temperature data recorded via iButtons was considered to represent "true" temperatures, it was used as the dependent variable. This allowed for an easier calibration of remotely sensed soil surface temperatures into air temperatures. As this regression model was statistically strong, we used the model slope's equation to calibrate drone-based ground temperature maps into air temperature measurements.

Soil surface temperatures differ greatly between shaded and open areas, primarily due to solar radiation. The effects of radiation on organismal body temperatures are complex, depending on factors such as behaviour, body size, and coloration (Stelbrink et al. 2019;

Stevenson 1985). To avoid systemic biases due to variability in solar radiation, we limited UAV operation to cloud-free times around mid-day and treated radiation as a constant in our subsequent modelling (Dai et al. 1999). We opted to measure *in situ* air temperature in the shade, as convention dictates when measuring ambient air temperature, to find a single generalized conversion factor for soil surface to air temperature over our study sites. This methodology was developed to require minimal microhabitat temperature modelling. Therefore, pole loggers were placed in sites with varying surface types to account for the landscape variability, and data were pooled together to generalize the model across the study sites. The resulting air temperature model remained statistically strong and facilitates its reproducibility in different ecosystems. A main objective of our study was to adapt a verified global index of species vulnerability to microclimatic scales. A big component of this index uses historical air temperature data captured from meteorological stations to estimate species thermal niche boundary. As such, air temperature measurements needed to be used to generate the thermal positioning index and overheating index of each species.

***Air Temperature Map.*** Air temperature maps were extrapolated from the emissivity-corrected remotely sensed soil surface temperature maps using the aforementioned air temperature model equation (Fig. 1.2). These maps were used in step 5 (see below) as they better represent the thermal conditions experienced by animals and airborne insects such as *Lepidoptera*.

***Thermal Positioning Map.*** Thermal positioning maps were generated using the historical thermal limits of the study species (*H. sassacus*, *S. aphrodite*, and *C. tullia*) and the air temperature maps. Thermal positioning maps estimate a species' proximity to its thermal limits in every pixel. These maps were estimated as

$$P = \frac{N_m - N_{Smin}}{N_{Smax} - N_{Smin}},$$

developed by Soroye, Newbold, and Kerr (2020), where P is the species' thermal position at a given location or pixel, $N_\mathrm{m}$ is the air temperature of a given pixel in the air temperature map, $N_\mathrm{Smax}$ is the species' upper thermal limit, and $N_\mathrm{Smin}$ is the species' lower thermal limit (Fig. 1.2). This index has previously been shown to predict extinction risk among bumblebees, aspects of population dynamics among mammals, and insect declines more generally (Kerr 2020; Outhwaite et al. 2022; Soroye et al. 2020; Williams et al. 2022; Williams & Newbold 2021). A value of 1 represents a pixel with a temperature value equal to the upper thermal limit. Values exceeding 1 represent pixels with temperature readings greater than the upper thermal limit of the species.

***Canopy Height Map.*** Canopy height maps were generated by subtracting the digital terrain maps from the digital surface maps. Terrain maps represent ground topography (the algorithm detects soil and removes above-ground objects), while surface maps represent an elevation map of both natural and artificial features in addition to ground topography. The resulting canopy height maps represent the height of the natural and artificial features.

## STEP 5 - ECOLOGICAL INDICES

***Overheating Index.*** The overheating index was used as a landscape-scale relative heat indicator. It was calculated as the proportion of pixels within the UAV temperature measurement area where that species' thermal position was ≥ 1. For thermal position index, such values indicate that temperatures exceed the boundaries of that species' upper thermal limits.

***Foliage Height Diversity.*** Foliage height diversity represents the canopy height diversity and is used as a landscape heterogeneity index (MacArthur & MacArthur 1961). We classified canopy height maps to the nearest 0.5m interval and calculated the inverse Simpson index to assess this aspect of heterogeneity. We did not test the accuracy of canopy height maps. However, the resulting foliage height diversity metrics provided meaningful statistical results that aligned with past research. Therefore, canopy height estimated provided by the Pix4D software were considered sufficiently accurate for the purpose of our study.

***Thermal Diversity.*** Lastly, we assessed thermal diversity in a similar manner to foliage height diversity. First, we classified temperature data according to the nearest 0.5 °C temperature interval, and then calculated the standardized inverse Simpson index for each site (Faye et al. 2016; Fig. 1.3).

## STUDY SPECIES

Butterflies were used as focal species. Butterflies are useful model organisms for small-scale climate change research (Beirão & Cardoso 2020). Due to their small size and dependence on temperature to regulate body heat, insects are considered good model organisms to predict species response to climate change (Beirão & Cardoso 2020; Wilson & Maclean 2011). However, few insect species have detailed contemporary and historical datasets like *Lepidoptera* (Wilson & Maclean 2011). As a result, the impact of climate change on butterflies has been well documented (Beirão & Cardoso 2020; Hufnagel & Kocsis 2011; Mattila et al. 2011; Wilson & Maclean 2011). We assessed thermal position indices for three butterfly species (*Hesperia sassacus*, *Speyeria aphrodite*, and *Coenoympha tullia*) that account for microclimatic variation at scales relevant to these species' individual movements and thermoregulation. These species were selected for their variation in body size, taxonomy, and thermal tolerance (5.40°C to 28.56°C, -

14.78°C to 32.37°C, and -12.65°C to 36.04°C respectively). Each species was observed during transect based butterfly surveys. Beyond confirming the presence of our case study species at our study sites, results from these surveys are outside the scope of this paper.

## Results

Foliage height diversity (which was log-transformed) exhibited a peaked relationship with thermal diversity ($R^2 = 0.2883$, $F(1,27) = 12.34$, $p = 0.0016$; Fig. 1.4). Visual inspection indicated that model residuals were normally distributed and homoscedastic.

Air temperature was measured at four different heights with iButton temperature loggers (0 m, 0.05 m, 0.75 m, 1.5 m) and related to surface temperature measurements using an ANCOVA. Temperature measurements did not differ statistically within this height range, so all air temperature measurements, regardless of height, were pooled for calibration and validation of remotely sensed soil surface temperature. Air temperature, as measured using *in situ* iButton instruments, related strongly to UAV-based remotely sensed temperatures ($R^2 = 0.4975$, $F(1,72) = 71.29$, $p << 10^{-4}$). Therefore, we used the resulting regression equation, $y = 0.4466x + 11.99544$, to calibrate air temperature values and map them (Fig. 1.5).

Coarse air temperature was a significant predictor of the overheating index for *H. sassacus* ($R^2 = 0.175$, $F(1,27) = 6.945$, $p = 0.0138$), *S. aphrodite* ($R^2 = 0.068$, $F(1,27) = 3.071$, $p = 0.091$), and *C. tullia* ($R^2 = 0.157$, $F(1,27) = 6.218$, $p = 0.0191$). The overheating index position of our three example species diverged increasingly with increasing coarse air temperature (Fig. 1.6). Handheld humidity meter observations (which measure temperature and humidity) collected *in situ* were assumed to be a validated method of capturing locality-specific air temperature data, while drone-based temperature measurements provide the basis for the site-level metric of overheating and spatial heterogeneity in thermal position. Site level average overheating potential for these species relates to contemporary *in situ* temperature measurements (Fig. 1.6). These *in situ* values are on the x axis as thermometer measurements of temperature should have very small errors relative to any other technique we employed, including remote sensing measures. Overheating indices for each species were not statistically related to thermal diversity or foliage height diversity.

## Discussion

Here, we demonstrate the feasibility of direct, synoptic measurements of seasonal temperature extremes relative to individual species tolerances using a UAV-borne thermal sensor. Landscape heterogeneity relates strongly to variation in temperature extremes within habitats, relative to the limits of species' thermal tolerances (see also Carroll et al. 2016; Milling et al. 2018; Suggitt et al. 2018) that are known to affect insect species persistence at broader spatial extents (Kerr 2020; Outhwaite et al. 2022; Soroye et al. 2020). The method developed here complements temperature measurements that can be interpolated from coarse resolution remote sensing and from meteorological station data (Kearney et al. 2020; Maclean & Klinges 2021; Fig. 1.4). While previous work demonstrates that some insect species' extinction risks depend on the frequency and intensity of temperature extremes, as measured using the thermal position index (Soroye et al. 2020) or derivatives (Outhwaite et al. 2022), this is the first demonstration that these metrics can be assessed using remote sensing methods within individual habitats.

The importance of microclimatic variation and microclimatic refugia in protecting species from the growing risks of extreme weather has been demonstrated empirically (Bladon et al. 2020; Milling et al. 2018; Riddell et al. 2021). The foundations of such work rely on observed habitat characteristics (Bladon et al. 2020) and frequently employ coarse resolution remote sensing imagery (Riddell et al. 2021) to estimate landscape heterogeneity relative to species' habitat use. Those techniques are essential for ongoing assessments of microclimatic refugia within habitats because they can provide broad coverage relative to higher resolution, but relatively localized, UAV-based measurements. Nevertheless, more detailed remote sensing at very high resolution (in this study, 5cm), provides accurate temperature measurements that demonstrate the extent and magnitude of thermal refugia that result from physical heterogeneity within particular habitat patches. These measurements are consistent with observations made at much broader spatial scales (Carroll et al. 2016; Suggitt et al. 2018), though previous work has not assessed microclimatic variation in the context of thermal position. As all survey sites were within the same landscape, and most were very similar in their landscape features, landscape heterogeneity results were very similar. Repeating this methodology in more varied physical landscapes and ecosystems would likely produce more diverse results (Carroll et al. 2016; Gies et al. 2007). We believe the approach we have described here represents a step toward assessing fine-grained thermal constraints in real-world habitats.

The overheating indices for the three study species (*H. sassacus*, *S. aphrodite*, and *C. tullia*; Fig. 1.2) highlighted the relative impact of localized temperature extremes on individual species relative to species' thermal limits. Variance in the within-habitat overheating index increased as temperatures rose for each of the three species for which thermal position index (and its spatial average, the overheating index) was measured, suggesting that microclimates persisted in these areas through the warmest periods we observed. As these microclimates depended on structural habitat heterogeneity (e.g. partial canopy cover and shrubs, for example), maintenance of these habitat characteristics and potentially the restoration or addition of those characteristics to habitats could improve species' resilience to warming conditions, even through the hottest periods observed within this region. Additional work is needed to assess how individual species' movements and persistence within and among these habitats might relate to thermal conditions, independent from other landscape characteristics, such as habitat connectivity.

Infrared imagery has frequently been used to study surface temperatures in agricultural and geological studies (Faye et al. 2016; Harvey et al. 2016; Maes & Steppe 2019; Sener et al. 2019). However, in ecological studies, air temperature is the primary metric for many species, including adult butterflies. Transformation of UAV-acquired soil surface temperature measurements into air temperature measurements is necessary to transform these remote sensing tools' outputs into measurements that have the greatest biological relevance for organisms, like butterflies, that spend relatively little time on exposed ground (though, we note that many butterfly species sometimes obtain nutrients from moisture on soil surfaces). Butterfly species are more likely to be vulnerable to surface temperature extremes during egg and larval phases of development (Pincebourde et al. 2021). It is likely to be possible to alter the framework we have applied here to measure temperatures most relevant to butterflies during those life stages, but more work would be needed to understand temperature variability within the areas through which caterpillars moved as well as on the temperature dependence of ovipositioning behaviour of adult butterflies. Because *in situ* air temperature measurements matched remote sensing metrics quite closely (Fig. 1.5), we expect that UAV-based thermal measurements, especially if related to thermal tolerances of eggs and larvae, could inform risks of extreme temperatures for butterflies during these earlier life stages.

We found that air temperatures showed little variation from ground level to a height of 1.5 metres within the alvar habitats where we collected *in situ* temperature values. Our measurements were made over areas with vegetated ground cover, which might have reduced temperature variability over this small range. Limestone pavement surface temperatures can be extremely hot in this habitat. Our results would have differed had our ground surface temperatures focused on those areas. Butterflies were not observed to settle onto such surfaces during hot periods. Different habitat types may exhibit other relationships between ground and air temperatures than that observed here, depending on vegetation type, vegetation density, and solar radiance (Gies et al. 2007). Our results suggest species that must engage in behavioural or physiological thermoregulation in hot conditions may face challenges escaping extreme heat by moving upward along vegetated surfaces or adjusting flight heights during foraging. Instead, such species (including the study species) will likely need to rely on heterogeneity within the habitat to find localities where vegetation creates cooler temperatures from ground to canopy and to adjust their activity periods away from the hottest times of day. Disturbances in these habitats that create more homogeneous conditions, such as removing small patches of trees or shrubs, or perhaps even mowing, may eliminate critical thermal microrefugia (Larsen 2012), and reduce the likelihood of species' persistence. We predict such effects to become more pronounced as extreme temperatures become more frequent and severe. Remote sensing-based measurements of temperatures within particular habitats will be more relevant and reliable for conservation applications if calibrated by *in situ* temperature measurements. Calibration is necessary as UAV-based estimates of temperature, though strong ($R^2 = 0.7129$), tended to be slightly lower than *in situ* iButton measurements, perhaps owing to UAV thermal measurements integrating more variable air temperatures above ground level.

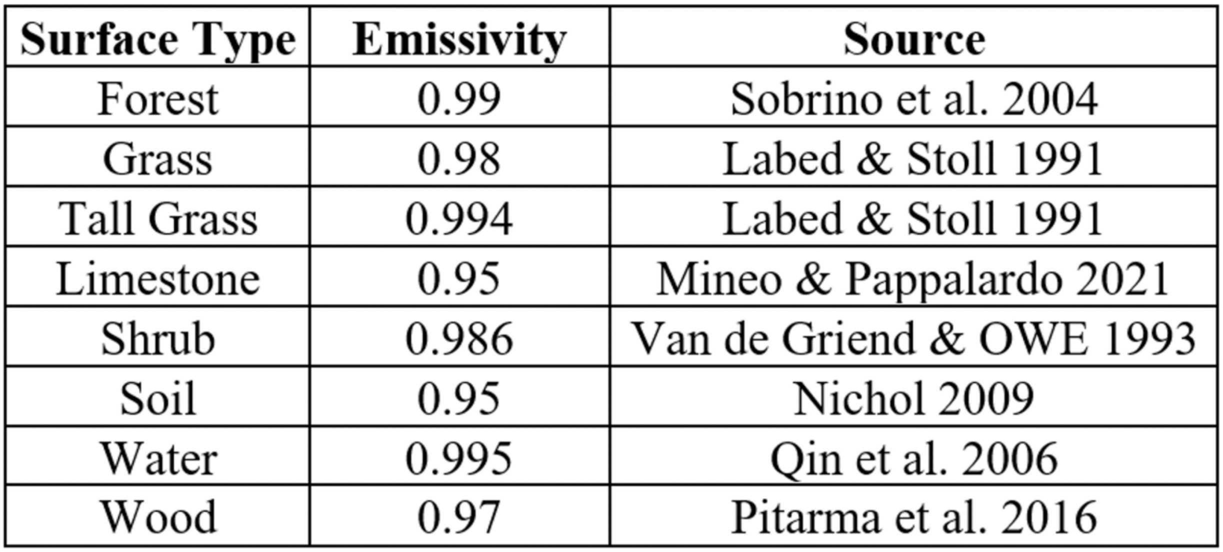
Estimates of the thermal position index focused on peak flight seasons for three butterfly species with divergent thermal tolerances. A more thorough estimate of the effects of temperature extremes on butterfly, or other species', biology would require temperature monitoring throughout the year. We do not discount the potential importance of microclimates at other times of year, but our main focus was on measuring thermal position of habitats during the warmest periods of butterfly activity. Consequently, repeated surveys at each site assessed different temperature regimes, separated by several weeks, which we treated as independent data points. Growing frequency and severity of extreme weather is expected to cause negative population growth among many species, but local losses of species might require several years of such climate-driven declines.

## Conclusion

Monitoring the biological impacts of extreme weather will require a broad array of remote sensing tools and techniques, ranging from broad-scale models drawing on coarse resolution remote sensing to UAV-based measurements that can directly observe within-habitat variation at scales relevant to site-level habitat management. Exposure to extreme temperatures that exceed species' tolerances increase their extinction risk across broad regions. This study demonstrates that such models can be translated to within-habitat scales, and identify microclimatic variability that is validated by *in situ* temperature measurements for individual species. We believe this work offers one avenue to expand monitoring efforts for biological diversity that can inform practical conservation management. For example, this methodology can assess the microclimate refugia availability of various areas and inform which would serve as the most efficient protected area for a target species.

## Figures and Tables

Table 1. Emissivity values used for different land surfaces.



| **Surface Type** | **Emissivity** | **Source** |
|---|---|---|
| Forest | 0.99 | Sobrino et al. 2004 |
| Grass | 0.98 | Labed & Stoll 1991 |
| Tall Grass | 0.994 | Labed & Stoll 1991 |
| Limestone | 0.95 | Mineo & Pappalardo 2021 |
| Shrub | 0.986 | Van de Griend & OWE 1993 |
| Soil | 0.95 | Nichol 2009 |
| Water | 0.995 | Qin et al. 2006 |
| Wood | 0.97 | Pitarma et al. 2016 |

Figure 1.1. Image of a PVC pole containing iButtons at 0.05 m, 0.75 m, and 1.5 m deployed in the field. Photo credit: Gabrielle Ednie.

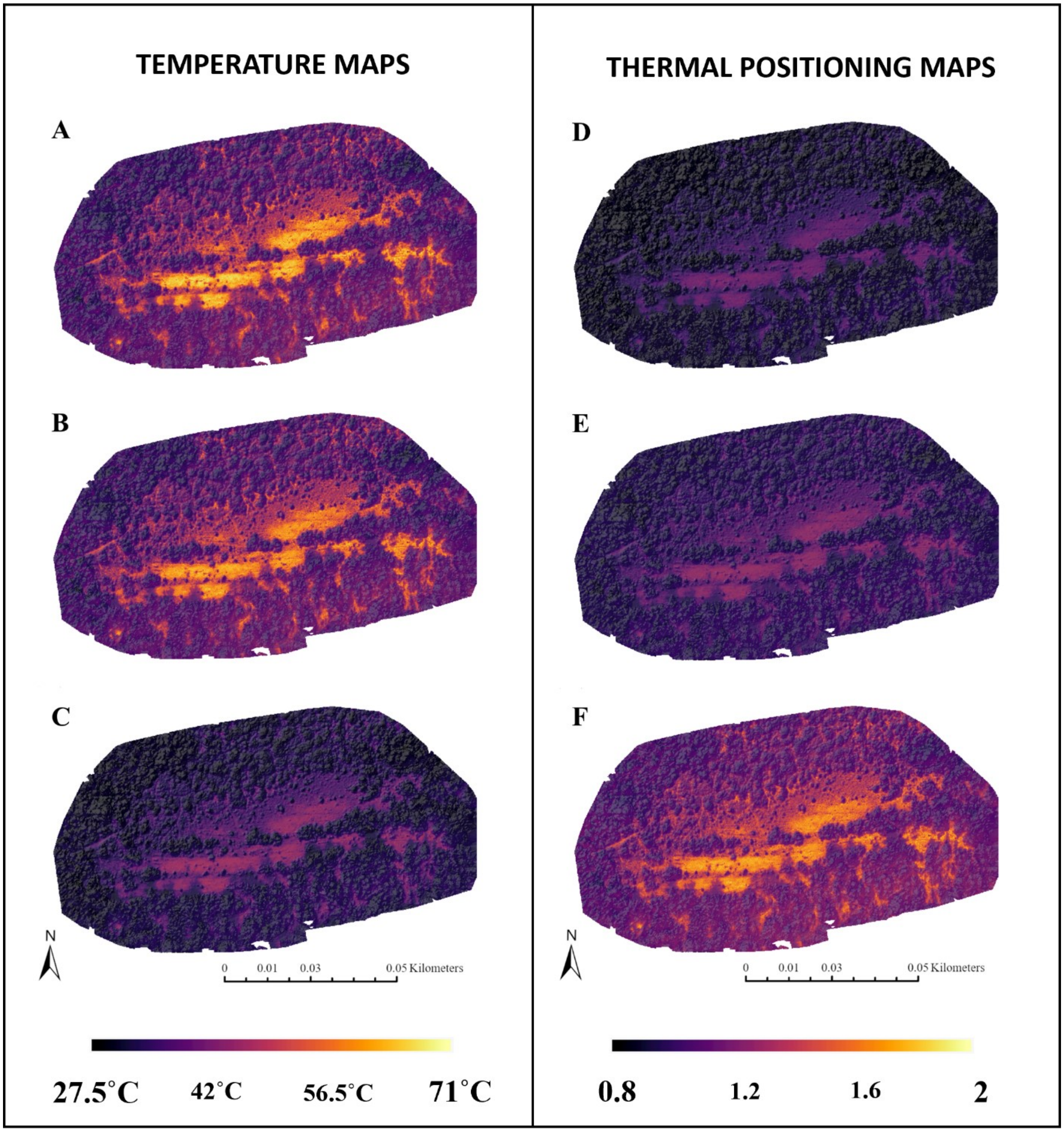


Figure 1.2. Three temperature maps and three thermal positioning maps of a survey completed on August 3rd, 2021. The maps were rendered slightly transparent and overlaid on a shaded relief map of its canopy height map to depict topographic variation also. The maps shown are as follows: (A) raw remote sensing temperature map, (B) emissivity-corrected remote sensing map, (C) air temperature map, (D) *C. tullia* thermal positioning map, (E) *S. aphrodite* thermal positioning map, and (F) *H. sassacus* thermal positioning map. For the thermal positioning maps, a value of 1 represents a pixel with a temperature value equal to the upper thermal limit. Values exceeding 1 represent pixels with temperature readings greater than the upper thermal limit of the species.

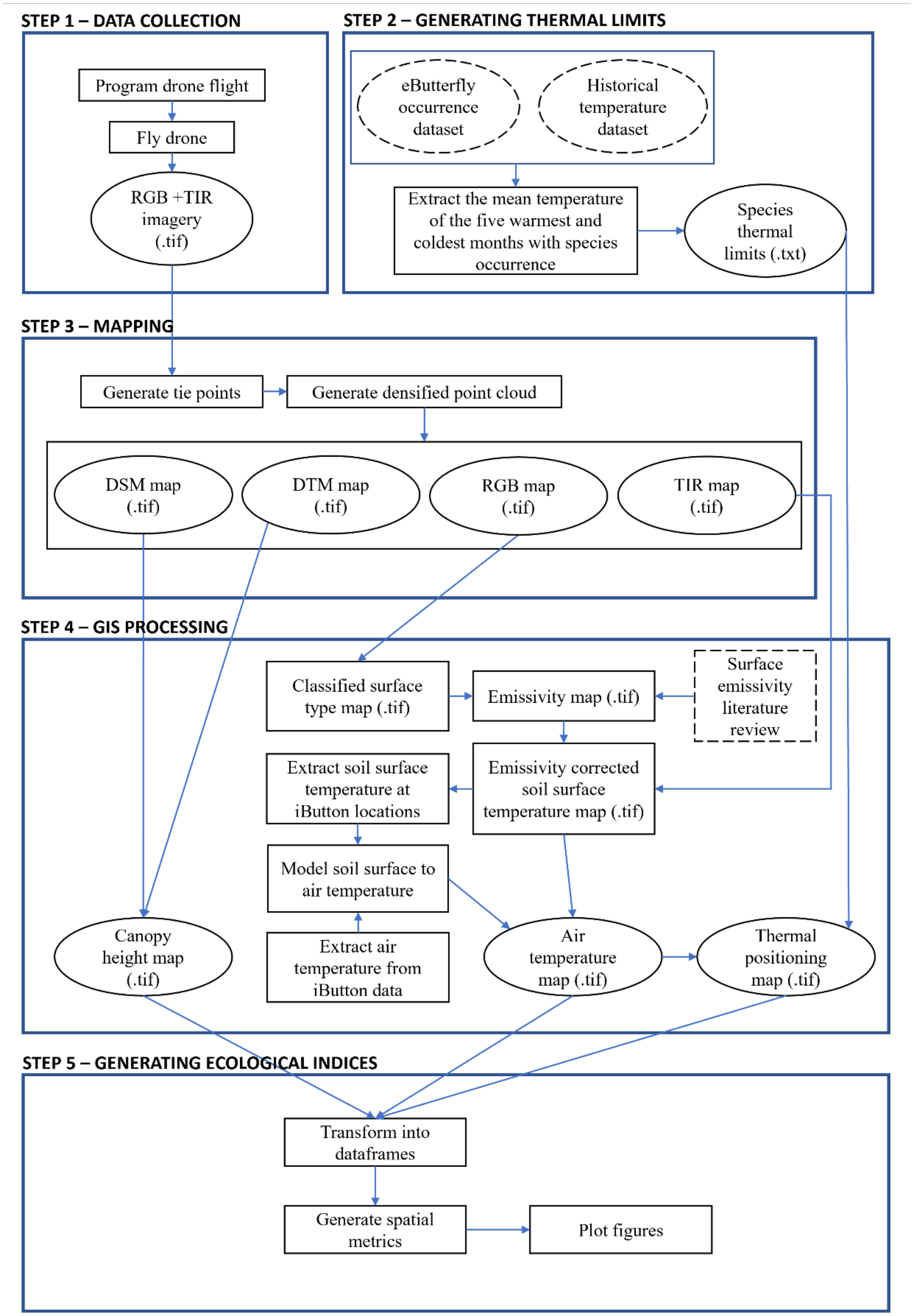


Figure 1.3. Flowchart of the proposed methodological framework. Dashed lines represent data from outside sources. Rectangular shapes represent intermediate outputs and steps. Oval shapes represent primary outputs from each step. All soil surface temperatures were remotely sensed.

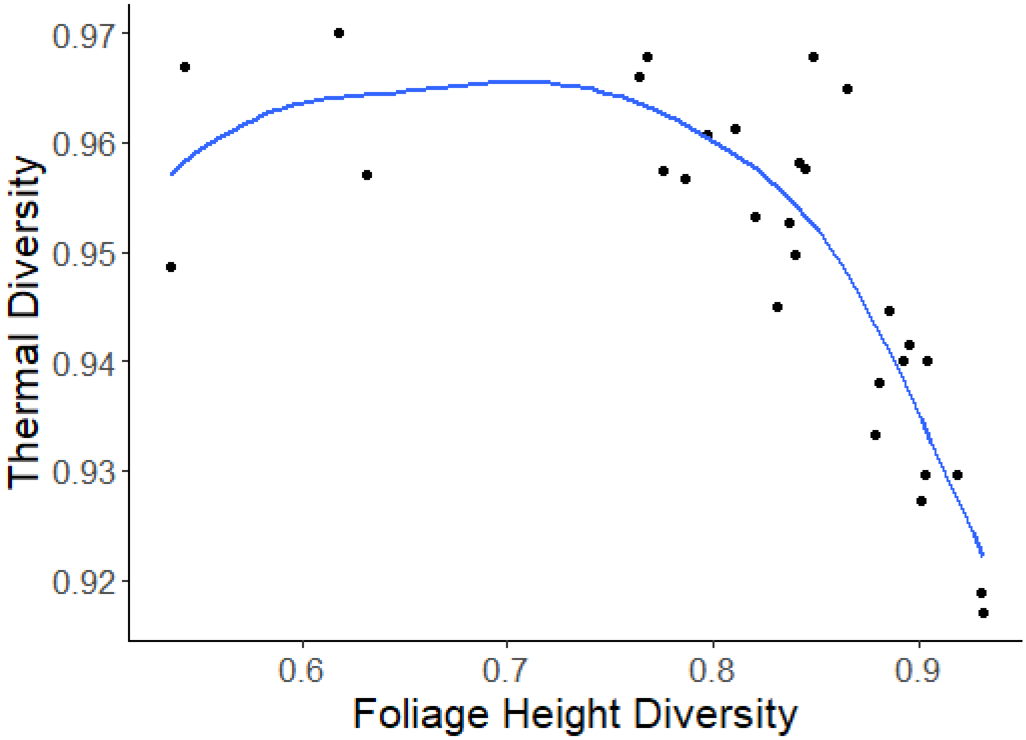


Figure 1.4. Plot of the relationship between the log of foliage height diversity and thermal diversity. Each point represents one UAV survey.

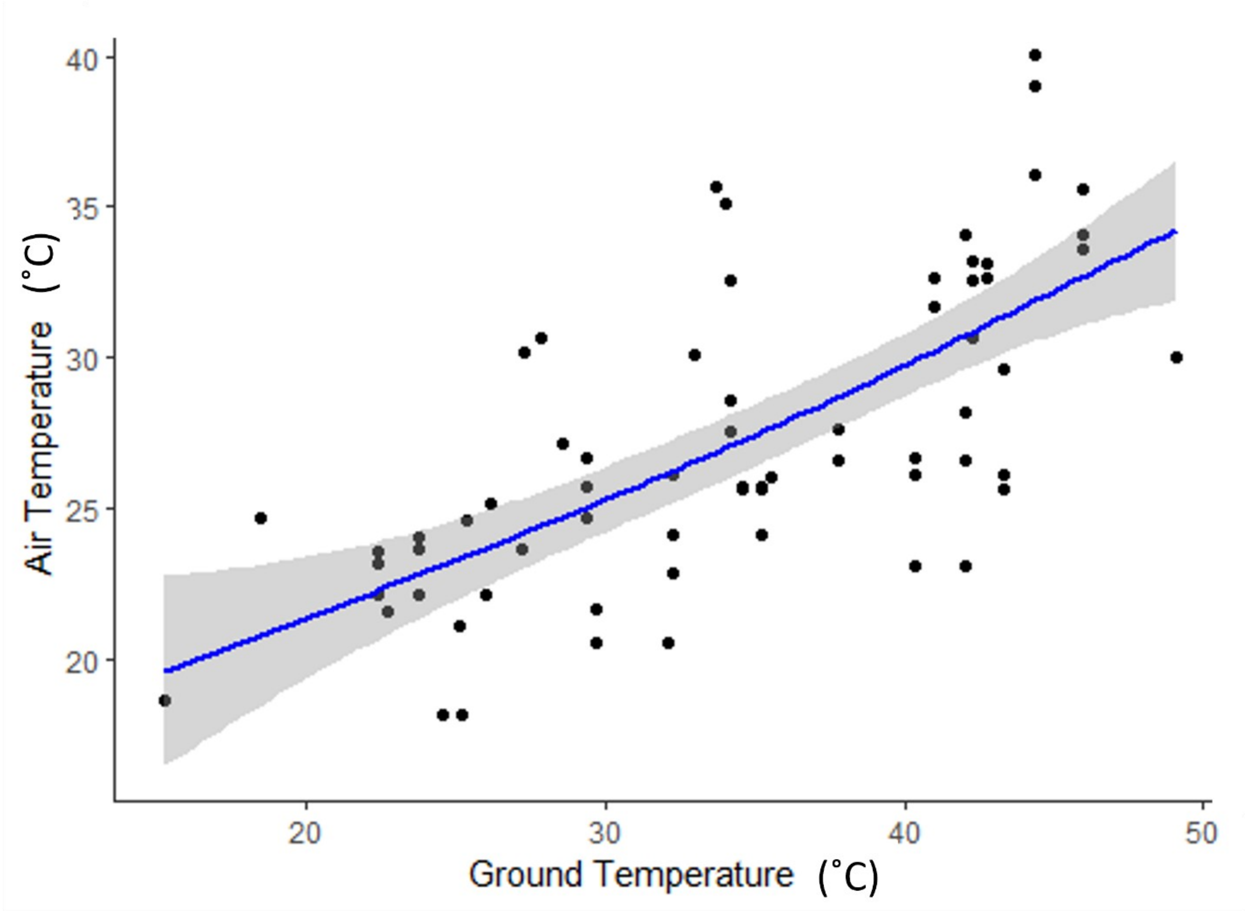


Figure 1.5. Relationship between remote sensing temperature and air temperature. Remote sensing temperature was extracted from emissivity-corrected remote sensing temperature maps. Air temperature was extracted from *in situ* iButton temperature loggers launched in the study sites.

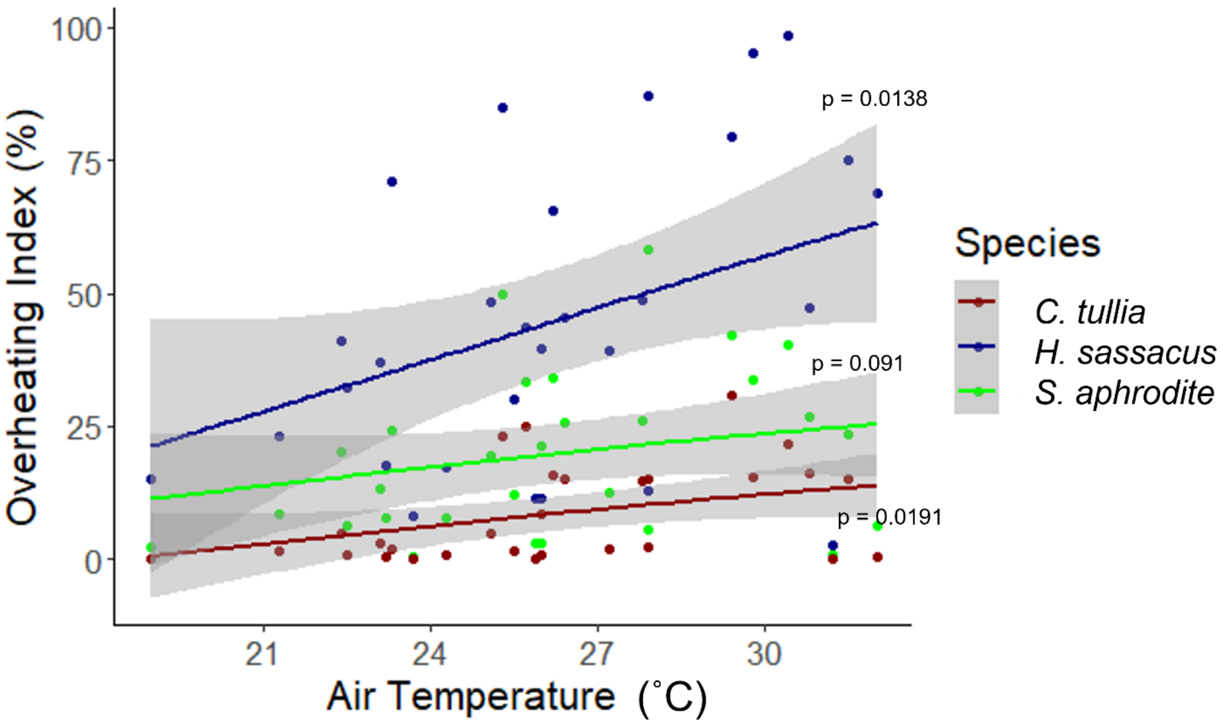


Figure 1.6. Plot of the overheating index of *H. sassacus*, *S. aphrodite*, and *C. tullia* in relation to coarse air temperature. Coarse air temperature was measured using a handheld humidity meter at the time of each UAV survey.

# Chapter 2 - Microclimatic scale thermal extremes limit butterfly patch use in a protected ecosystem

*To be submitted to: Global Change Biology*

## Abstract

Globally, many species have altered their ranges as environmental conditions exceed the boundaries of their realized thermal niche. Relative heat indices have been able to predict these shifts successfully over broad spatial scales using thermal limit approximations. It is unclear whether those models, which rely on realized thermal niche limits, can also predict species' distributions and abundances within individual landscapes and habitats. A key limitation in enabling such model translation across scales is powerful measurement of species-specific microclimate availability and the frequency and severity of extreme events relative to the limits of species' tolerances. Recent technological advances with unmanned aerial vehicles (UAV) and thermal imaging have begun to permit direct measurements of environmental and thermal conditions, creating opportunities to evaluate the relationship between species' measured thermal tolerances and their distributions within and among habitats in a landscape. Here, we use new high resolution remote sensing methods to assess the severity of extreme temperatures on patch level habitat use with thermal limit approximation methods successfully used to predict global species range shifts. We used new methodologies that utilize UAV and thermal imaging technology to map air temperatures (5cm resolution) and canopy height (1cm resolution) of 15 patches in a rare alvar ecosystem in eastern Ontario. We extracted relative heat and landscape heterogeneity indices from the remote sensing maps. In parallel, we conducted transect-based butterfly surveys at each patch to use as a biological response variable. We then assessed the predictive ability of relative heat indices for species abundance, occurrence, and richness using generalized mixed linear models. Relative heat indices were found to be a significant predictor of

butterfly patch use and offers microclimatic insight into site and species-specific conservation potential.

## Introduction

Locally, microclimate refuge availability heavily influences species persistence by buffering against short term climate extremes (Riddell et al. 2021; Suggitt et al. 2011; Suggitt et al. 2018). Refuges refer to natural shelters from changing environmental conditions that enable species survival (Ashcroft 2010; Keppel et al. 2012; Rull 2009; Suggitt et al. 2011). Refuge extent is taxon specific (Keppel et al. 2012; Suggitt et al. 2011). Finding and studying these refuges requires measurement of temperature at organism-relevant resolutions (i.e. microclimatic scales; Milling et al. 2018).

Assessing species' vulnerabilities to climate change includes understanding of their thermal tolerances. While climate change implies shifts in temperature or precipitation norms, the frequency and severity of extreme weather is also rising. A new model of species-specific exposure to such extremes – the thermal position index (TPI) – helps predict extinction-colonization dynamics and aspects of population growth for groups of insects and many vertebrate populations at continental-to-global extents (Kerr 2020; Soroye et al. 2020; Williams & Newbold 2021). This index uses historical climate data and known species observations to estimate species' realized niches throughout the year. Then, it relates seasonal temperatures to estimates of thermal niche boundaries to predict whether populations are likely to decline in an area or colonize a new one. A key strength of this index is its focus on the frequency and severity of extreme events relative to approximated thermal tolerances, which is more relevant than long term shifts in average conditions for most species' life histories, especially at local spatial extents (Acevedo et al. 2020). It is uncertain whether broad-scale metrics of extreme event intensities (which incorporate both severity relative to species' tolerances and event frequencies) can be translated to within-habitat metrics of abundance or population persistence.

Microclimatic variation can create buffers against climate change by attenuating potentially harmful extreme weather events (Suggitt et al. 2011). Topographical heterogeneity and habitat structural complexity can create microclimates at highly localized scales. Topographical effects on microclimate alone reduce extirpation risks for plants and insects (Suggitt et al. 2018). Yet, species with comparable physiological and ecological characteristics could differ substantially in their respective capacities to make use of microclimatic refuges (Riddell et al. 2021). Assessment methods for microclimatic variability within individual habitats have been developed based on the use of *in situ* temperature sensors, such as iButtons (and conventional thermometers), that can be placed in sheltered localities. Microclimates within habitats cannot be comprehensively measured using networks of individual sensors unless the habitat is very small or point-based measurements are used statistically to predict unobserved areas elsewhere within habitats. Downscaling from moderate resolution satellite data to predict microclimatic variability is also possible, permitting predictions of microclimatic variation spatially and seasonally. Yet, direct, high-resolution measurement of microclimatic variation that is synoptic across entire habitats remains uncommon (Bramer et al. 2018; Suggitt et al. 2011). Rapid advances in remote sensing have increased the capacity to measure microclimates within habitats, leading to predictions of a renaissance in the accessibility and use of such data (Zellweger et al. 2019). Whether these data will translate to effective predictions of variation in species' persistences remains a frontier relative to existing knowledge.

Butterflies are valuable study species in microclimatic and climate change research (Beirão & Cardoso 2020). As ectotherms, they depend strongly on variation in climate across broad scales, they are relatively easily identified in many regions, and their distributions have been well characterized in both the present and recent past (Beirão & Cardoso 2020; Wilson & Maclean 2011). Butterflies depend strongly on their host plants as larvae and on nectar (and sometimes mineral) sources as adults (Braschler & Hill 2007; Geister et al. 2008; Jain et al. 2021). Lack of such resources can impact a species' abundance and potential persistence in particular habitats (Johansson et al. 2020). Extreme heat can cause their host plants to decline or for wildflower resources to produce little or no nectar (Lancaster 2020), which has contributed to extinction of butterfly populations in the past (Patterson et al. 2020). Yet, butterflies are also directly impacted by the thermal consequences of rising temperatures. Population declines among butterflies in response to aspects of climate and habitat changes has been well documented (Beirão & Cardoso 2020; Hufnagel & Kocsis 2011; Mattila et al. 2011; Wilson & Maclean 2011). There is considerable variability among sympatric butterfly species in terms of thermal tolerances, which leads to different predictions regarding their responses to warming or other climate changes (Beirão & Cardoso 2020). Yet, the effects of rising temperatures on butterfly (or other) species could be altered by variation in microclimatic conditions within habitats (Hufnagel & Kocsis 2011; Bladon et al. 2020). The extent to which extreme weather associated with climate change affects butterfly populations and persistence is likely to be a strong determinant of their future conservation prospects.

Using new field observations of butterflies within a network of habitats in a protected area, I test for links between thermal conditions (relative to individual species' tolerances; Ednie & Kerr 2022) and butterfly species diversity, abundances, and persistence. This protected area includes globally rare alvar habitats with distinctive flora and particularly pronounced thermal extremes. These features may make alvars especially valuable as indicators of conservation risk consequent to climate change. While measures of thermal quality are well known predictors of individual species' behaviour and can affect their abundances, this study presents the first test of thermal position as a predictor of species' distributions and abundances within individual habitats. I predicted that butterfly species in study habitats would be more abundant if thermal position index indicated that the habitat provided thermal conditions that impinged less frequently on individual species' thermal limits. This test employs a high resolution thermal remote sensing platform, supported by intensive *in situ* sensors to calibrate remote observations. Butterfly observations included both new field collections and observations from the past 120 years across North America that enable approximate measurements of realized niche boundaries for every butterfly species detected in this rare ecosystem.

## Methods

### STUDY SITE

The study was performed at Burnt Lands Provincial Park, 30km west of Ottawa, ON, between May 17 and August 26, 2021. The park hosts an alvar ecosystem characterized by open or barren areas with limited soil and exposed limestone interspersed by mixed and primarily coniferous tree stands (NCC 2020). Its landscape heterogeneity holds potential for highly localized temperature extremes and general thermal heterogeneity. Alvars are also characterized by diverse and rare plant species enabling increased butterfly diversity (Gordon & Kerr 2022). All study patches within the park consisted of open fields to facilitate thermal mapping and transect-based butterfly surveys. Open field are also the preferred habitat of most butterfly species found in the region. We selected 15 patches varying between 0.005 and 0.026 km$^2$ (Fig. 2.1). Each patch was separated by a minimum of 20 m of forest (Gordon & Kerr 2022) and was surveyed twice with at least one month between surveys.

## BUTTERFLY SURVEY

A transect-based butterfly survey was performed at each study patch in parallel to UAV mapping. Each patch had one to three transects of either 25 m or 50 m in length. The number of transects depended on the size of the patches, the smallest having one 50 m transect and the largest having one 25 m transect and two 50 m transects. Transect locations were selected through stratified random sampling. Surveys were completed between 10:45am and 3:45pm on days exceeding 13˚C by two individuals using butterfly nets and walking at approximately 0.5 m/s (Pollard 1977). We alternated the order of UAV mapping and butterfly surveys at each site to account for potential confounding effects of UAV noise disturbance on butterfly populations.

## THERMAL TOLERANCES

Once butterfly surveys were completed, realized thermal niche boundaries of each butterfly species detected were approximated as in Soroye et al. (2020). The five hottest and coldest locations in each species' range were extracted based on historical air temperature data. Data was obtained from the Climate Research Unit dataset (Harris et al. 2014), which relies on meteorological data. Thermal tolerances were established from a baseline period (1901-1975) as climate change has accelerated rapidly thereafter. Only butterfly occurrences in that same period were used to estimate each species' upper and lower thermal limits. Butterfly occurrence information was extracted from the eButterfly citizen science program (Prudic et al. 2017) and from longer term butterfly observations assembled through the activities of systematists and biological surveyors (Soroye et al. 2018). Each submitted species observation has been verified by lepidopteran experts or can be traced to a curated museum specimen. A month-location combination was implemented to ensure only months where species observations occurred were used to extract monthly maximum and minimum temperatures. As a result, winter months of breeding sites were excluded from calculations. Although ideal for localized studies, lack of historical daily temperature prohibited the use of location-day combinations. Nevertheless, location-month combinations have proven informative of species vulnerability to climate extremes in past studies (Outhwaite et al. 2022; Soroye et al. 2020; Williams & Newbold 2021). Recently developed techniques rely on temperature modelling to produce datasets of hourly air temperature estimates at high-resolutions (30m compared to 55km for the Harris et al. dataset used; Harris et al. 2014; Kearney et al. 2020). The resolution of this dataset more closely resembles data captured with our UAV-based method. However, such techniques can only produce temperature data starting in 1957 and often underestimate thermal extremes (Kearney et al. 2020). Thus, they were considered unsuitable for the present study. However, further research comparing the accuracy of thermal limits estimated from both data sources would be beneficial. Furthermore, similarly to our study sites, meteorological stations are placed in open spaces. Thus, data included in the Harris et al. dataset is expected to be representative of conditions at our study site (Harris et al. 2014).

## THERMAL MAPPING

Remotely sensed thermal imagery was captured at each study patch in parallel to each butterfly survey. The thermal imagery was captured by a Zenmuse XT2 dual sensor with thermal (13mm focal length; 640x512 image capture) and visual (8mm focal length, 12 megapixel resolution) imaging capabilities (DJI Inc., Shenzhen, China). The sensor was carried by a DJI Matrice 300 quadcopter UAV with real-time kinetic (RTK) positioning supported by a RTK base station deployed in the field. The base station improved positioning accuracy significantly and eliminated the need for ground control points. Images were captured in the thermal infrared (TIR; radiometric-jpeg format) and red, green, and blue (RGB) spectral bands simultaneously at

1 second intervals while mapping the survey patches with 90% image overlap on all sides. These parameters followed the guidelines provided by the mapping software (Pix4DMapper; Pix4D SA, Lausanne, Switzerland) for optimal mapping accuracy. Each UAV survey was pre-programmed in the DJI pilot app to run at 2.5 m/s speed and 37 m altitude to minimize motion blur and achieve 5 cm TIR and 1 cm RGB image resolutions. Surveys were only performed on days that met the butterfly survey protocol criteria and had <50% cloud cover, as clouds affect TIR-based temperature measurements (Dai et al. 1999). Surveys were paused during cloudy periods and were either resumed or aborted if conditions persisted.

Orthomosaics (maps) were created from the collected imagery in RGB, TIR, digital surface map (DSM), and digital terrain map (DTM) formats using the Pix4DMapper software. One survey was discarded due to a RTK positioning malfunction, which caused georeferencing discrepancies. As such, 29 orthomosaics were produced for each format. DSMs represent ground topography, while surface maps represent elevation of both natural and artificial features in addition to ground topography. By subtracting the DSMs from the DTMs, we were able to produce canopy height maps representing the height of each patch's natural and artificial features. RGB maps were classified by surface type using ground truth data in the ArcGIS Pro software (Esri, Redlands, CA, USA) and each surface type was assigned an emissivity value from the literature (Ednie & Kerr 2022). The resulting maps were used to correct the TIR maps (assumed to be ground surface temperature) for emissivity. At the start of the field season, 39 iButtons (DS1922L-F5#, Maxim, Dallas, USA; accuracy: ±0.5˚C) were deployed in the field to measure air temperature at each patch (*sensu* Ednie & Kerr 2022). The data was retrieved after the last survey and compared to measurements captured in the emissivity-corrected TIR maps. The measured relationship was used to calibrate the emissivity-corrected surface temperature maps into air temperature maps (*sensu* Ednie & Kerr 2022). As the TPI relies on air temperature measurements to approximate realized thermal niche boundaries, our data was required to be in the same format.

The thermal positioning index estimates a species' proximity to its thermal limits. Values were estimated as

$$P = \frac{N_m - N_{Smin}}{N_{Smax} - N_{Smin}},$$

developed by Soroye, Newbold, and Kerr (2020), where P is the species' TPI. $N_m$ is the air temperature of a given area, $N_{Smax}$ is the species' upper thermal limit, and $N_{Smin}$ is the species' lower thermal limit. A value of 1 represents a temperature value equal to the upper thermal limit. Values exceeding 1 represent temperature readings greater than the upper thermal limit of the species. These values were estimated for every pixel of every air temperature map using the thermal tolerance of each species, thus creating a TPI map for every species for every patch survey (957 maps). The average TPI from each map was extracted to create a patch TPI value. The same value was extracted from a 4 m buffer area surrounding each butterfly transect to create a transect TPI. A relative heat indicator (the overheating index; OI), calculated as the proportion of the patch with TPI values ≥1, was also extracted from each TPI map and for each butterfly transect. The OI was a proxy for localized temperature extremes. For species richness calculations, the TPI and OI for every species was averaged into a single value per survey at both the patch and transect level.

## ENVIRONMENTAL FACTORS

Environmental data were gathered in addition to all four relative thermal indices. Time, patch size, foliage height index, floral richness, and patch isolation are all environmental factors which were included in our statistical models.

Time was measured as the number of days since the start of our surveys. Patch size was extracted from the thermal maps produced from the TIR imagery. The foliage height index represents the canopy height diversity and is a landscape heterogeneity index (MacArthur & MacArthur 1961). We classified the canopy height maps to the nearest 0.5 m interval and calculated the inverse Simpson index to obtain the foliage height index of each survey. At least one month separated surveys of the same patch. As such, the foliage height diversity of each patch was assumed to be different. Patch isolation was calculated for each patch as the sum of all least cost paths to other survey patches. The analysis was completed for each species according to their ranked habitat preference between grassland, forest, wetland, dirt path, and paved road.

Data on flowering plant richness was collected at our study patches during summer 2019 (Gordon & Kerr 2022). As most species found were perennials, suggesting stable floral communities, the data was incorporated into the present study. Floral richness was the estimated number of species in bloom at each patch for a given sample day. Floral richness was measured through 1 x 1 m quadrats with the number of quadrats in relative proportion to the size of each patch. Gordon and Kerr (2022) sampled five times throughout the summer. Data from the nearest sample date to our surveys was incorporated into our study. Gordon and Kerr (2022) began sampling in mid-June, while our surveys began in mid-May. Nearest survey dates differed from 1 day to 1 month. Two of our study patches were significantly smaller subsets of larger patches surveyed in Gordon and Kerr (2022). However, as butterflies are highly mobile and tend to occupy entire patches, they were assumed to have access to the resources of the entire patch. Floral richness data may not accurately portray the conditions present during our surveys. However, the approximate data may give insight into the role of floral richness in butterfly occurrence, abundance, and richness, and provide direction for future studies.

### STATISTICS

Our data detailed potential butterfly sightings (i.e. all observed species for every transect survey) with corresponding abundance and environmental conditions. The data was tested for zero inflation. The extracted TPI and OI values at both the patch and transect level were individually verified as predictors of butterfly abundance, richness, and presence in simple linear regressions. Each relative thermal index was also modelled in generalized linear mixed effects models (GLMM) including environmental factors to find the best model fit. Model fit was determined using AIC scores. Mixed models were first run with every environmental factor. Non-significant factors were removed individually until either the simplest model with a comparable AIC score or the lowest AIC score was obtained. TPI and OI values were modelled against abundance and presence in simple regressions using negative binomial and logistic regression models respectively. A GLMM with negative binomial distribution was used to model species abundance and a GLMM with normal distribution was used to model species richness. Species presence was modelled using a logistic regression model.

## Results

Butterfly observations included thirty-three species and 411 individuals across 29 patch surveys. Observations were only included if the individual could be identified to the species level. Relative thermal indices contributed to the best model fit for species abundance, presence, and richness. The patch level OI contributed to the best model fit for both species abundance and presence and significantly predicted species abundance and presence in simple linear regressions. Patch use by butterfly species decreased overall as a function of patch OI. The average patch TPI contributed to the best fit model for species richness. Species richness models had the highest $R^2$ values but were not species specific.

### *Abundance*

The simplest GLMM model for species abundance used a negative binomial distribution and included OI ($p < 10^{-4}$), patch isolation ($p < 10^{-4}$), and time ($p < 10^{-4}$; $R^2 = 0.15$; AIC = 1594). Species abundance decreased with increasing OI but increased slightly with patch isolation and more noticeably with time. A marginally better model fit was achieved using OI, floral richness, patch size, patch isolation, foliage height index, and time as factors ($R^2 = 0.16$, AIC = 1593.2). Only OI ($p < 10^{-4}$), patch isolation ($p < 10^{-4}$), and time ($p < 10^{-4}$) significantly contributed to the model. Negative binomial distributions accounted for zero-inflation (i.e. many species that were present in the landscape were absent from individual transect surveys). Expected numbers of zero values using the negative binomial distribution more closely resembled the true amount than the poisson distribution model. Patch TPI, transect TPI, patch OI, and transect TPI were modelled separately as independent variables of species abundance using a generalized linear model with a negative binomial distribution. Patch ($p < 10^{-4}$) and transect ($p = 0.0372$) OI values, respectively, related to species abundances. Patch OI produced the best model fit ($R^2 = 0.045$; AIC = 1641.7; Fig. 2.2).

### *Presence*

The best GLMM model for species presence was achieved using a logistic regression with OI ($p = 0.0013$), floral richness ($p = 0.0032$), foliage height index ($p = 0.0056$), patch isolation ($p = 0.026$), and time ($p = 0.001$; $R^2 = 0.069$; AIC = 969.8) as factors and species and transect ID as random effects. Presence decreased with increasing OI. All other factors had positive relationships with species presence. A more complex model with similar fit was achieved with OI, floral richness, patch size, patch isolation, foliage height index, and time as factors and species and transect ID as random factors ($R^2 = 0.069$; AIC = 971.8). The model summary revealed only OI ($p = 0.0013$), floral richness ($p = 0.0056$), patch isolation ($p = 0.04$), foliage height index ($p = 0.029$), and time ($p = 0.0012$) significantly contributed to the model. Patch TPI, transect TPI, patch OI, and transect TPI were modelled separately as independent variables of species presence using a generalized linear model with logistic regression. Patch TPI ($p = 0.0053$; $R^2 = 0.0073$; AIC = 1101.8), transect TPI ($p = 0.0098$; $R^2 = 0.0064$; AIC = 1102.8), patch OI ($p < 10^{-4}$; $R^2 = 0.024$; AIC = 1083.7), and transect OI ($p = 0.00097$; $R^2 = 0.01$; AIC = 1098.3) were all individually significantly associated with species presence. However, patch OI maintained the best model fit (Fig. 2.3).

### ***Richness***

The best GLMM model for species richness using normal distribution included patch averaged TPI, time, floral richness, and patch size ($R^2 = 0.45$; AIC = 140.71; Fig. 2.4). Patch averaged TPI ($p = 0.027$) and time ($p = 0.0013$) significantly contributed to the model, while floral richness and patch size did not. Species richness decreased with increasing patch TPI but increased with time, floral richness, and patch size. A more complex model with similar fit was achieved with average patch TPI as a thermal factor and time, foliage height index, floral richness, patch size, and patch isolation as environmental factors ($R^2 = 0.50$; AIC 141.99). The model summary revealed only time ($p = 0.015$) significantly contributed to the model. Patch TPI, transect TPI, patch OI, and transect TPI were modelled separately as independent variables of species richness using a generalized linear model with normal distribution. None was significantly associated with species richness.

## Discussion

This study presents the first evidence that models linking incidence and severity of extreme weather to species extinction risks at broad scales and long time periods can be translated directly to predict distributions and abundances among individual habitats over short time periods. Such extreme events, which result from human-caused climate change, contribute to the decline of many insect and vertebrate populations globally (Outhwaite et al. 2022; Soroye et al. 2020). A key to translating this work from broad-scale models employing coarse resolution climatic data to informative local-scale predictions of species distributions is high resolution thermal remote sensing that measures microclimatic variation within individual habitats. The thermal position index integrates short term weather fluctuations relative to species' realized niche limits, as estimates from their geographical distributions. It allows those thermal tolerances to fluctuate over time, reflecting variation in individual vulnerabilities to extreme weather conditions that depend on species' life history stages.

This research was conducted in a protected area with few anthropogenic barriers to dispersal or within-habitat disturbance, but thermal conditions nevertheless affected the diversity of butterfly species, individual species' abundances, and species distributions within the landscape. Patch-level measurements of the extent of thermally-tolerable area (i.e. overheating index) were consistently better predictors of richness, abundance, and presence than transect-based measurements. The Pollard Walk (Pollard 1977) transects employed here were created to sample species numbers and abundances from the broader habitat. Butterflies' high mobility allows them to circulate within and between patches easily. Well-placed transects that are sampled repeatedly should detect most or all species present within the habitat. Transect locations were primarily situated in areas prone to thermal extremes (i.e. open spaces with few vegetative obstacles). During extreme climate events, species persisting through exploitation of microclimatic refuges (e.g. forest edges and shrubs) would not be observable in most transect locations, thus introducing uncertainty into our models. Nevertheless, statistical relationships between butterfly diversity and abundance and environmental conditions should depend on conditions across the habitat, not just those found along individual transects. When using this methodology, patch use patterns of the study species should always be considered, and alterations to the survey methods made where appropriate.

I found that thermal conditions within these protected habitat patches nevertheless exceeded species' apparent tolerances during hot periods in the summer, which would reduce usable habitat area and create a hidden area effect that acts seasonally to alter the conservation value of these areas. I anticipate that this effect would likely be more pronounced in habitats that were strongly affected by human disturbances. If so, habitat fragmentation and loss that pervade agricultural and urban areas should impose stronger seasonal effects on butterfly species. The broad-scale interaction between extreme weather and human land use contributes to population declines among many species (Outhwaite et al. 2022; Williams & Newbold 2021). The results I observe here suggest a particular mechanism that could govern that relationship, namely that seasonal extreme heat limits species capacities to use some areas but also that broad-scale measurements of butterfly realized thermal niche limits are relevant to their diversity, abundance, and presence within individual habitats.

UAV-based measurements of microclimatic variation create powerful species monitoring opportunities in these and other landscapes. Temperature can vary substantially over very short distances due to topographical variation, creating critical microclimates that shelter species from temperature extremes and reduce their extinction risk (Carroll et al. 2016; Suggitt et al. 2018). While it is possible to model expected microclimatic variation within individual habitats (Kearney et al. 2020) based on high resolution topography data and moderate resolution satellite information, such methods are necessarily limited for small-bodied organisms that respond to thermal conditions at scales below the limits of detection of the satellite data sources. It would be valuable to compare results from UAV-based remote sensing metrics of microclimate with such interpolative models to test for the latter's limits of microclimate detection. A clear strength of predictive microclimate models derived from relatively broad-scale satellite sources (e.g. Operational Land Imager or Landsat Thematic Mapper) is their capacity to provide information across broad spatial extents. Given that UAV-based metrics of thermal conditions appear capable of enabling the thermal position index (Soroye et al. 2020) to predict localized species' responses to extreme heat (e.g. Fig. 2.2), further tests of these models at mesoscales would be valuable.

Species abundance and occurrence models for butterfly species included time and patch isolation. Butterfly life histories are highly seasonal and depend also on the availability of host plant and nectar resources, which are also seasonal (Courtney 1981; Williams et al. 1983), so it is unsurprising that butterfly abundance and presence would vary over time. As a result, some butterfly species consistently emerge or migrate during specific and predictable periods, and most peak in summer where temperature is at its highest. As we started our surveys in May, when butterflies first emerge, and ended our surveys in August, in peak butterfly season, it was expected that time would play a significant role in predicting species presence and abundance.

Overall butterfly abundance rose with patch isolation. This effect contrasts with expectations from simple metapopulations and metacommunities, where immigration rates to habitat patches rise with proximity to other suitable habitats (Matthews et al. 2005; Van Dorp & Opdam 1987). However, dispersal capacities of butterfly species vary enormously (Burke et al. 2011), and butterfly species abundance and diversity in this protected area is known to depend on traits as well as predation (Gordon & Kerr 2022; Gordon et al. in prep.). The effects of temperatures in this landscape appear to alter the suitability of individual patches in terms of butterfly abundance and persistence, suggesting that metacommunity dynamics in this landscape cannot be fully explained without measuring how transitory, extreme weather alters the capacity of butterfly species to use key habitats.

Patch-level measurement of thermal position, in the form of the overheating index, related to butterfly abundance and presence more strongly than detailed measurements of vertical habitat complexity. We would expect this result if foliage height were an imperfect surrogate for the availability of microclimatic variation and the availability of microrefugia during the hottest measurements periods during which butterfly species were observed. Microclimate availability in study sites certainly did vary to a large degree with habitat complexity (measured as the foliage height index), but also in highly localized ways that did not reflect gross vegetation difference. If habitats provide sufficient resources in terms of host plant and nectar resource availability (which we also found: floral richness was positively related to butterfly diversity; see also Braschler & Hill 2007; Geister et al. 2008; Jain et al. 2021; Gordon & Kerr 2022), then the effects of habitat complexity on these butterfly communities is a reflection of microclimatic variation, which was measured directly through the overheating index. Increased habitat size, however, could effectively increase resource availability and diversity by reducing spatial constraints and interspecific flora competition (Goldberg & Barton 1992; Heegaard et al. 2007; Jacquemyn et al. 2001), thus supporting regionally uncommon butterfly species more effectively.

Remote sensing for microclimatic measurement is advancing rapidly. While this study demonstrates that UAV-based thermal measurements can help translate broad-scale, niche-based estimates of thermal tolerance to locality-specific predictions of butterfly presence, abundance, and richness, limitations remain. Most UAVs can sustain flight for less than an hour, making battery life a key limitation to measurements across broader extents. Such limitations illustrate that UAV measurements of microclimates or other habitat characteristics complement model-based or coarser resolution remote sensing metrics (Kearney et al. 2020; Maclean & Klinges 2021) but cannot replace them. Cross-comparison of validated UAV measurements of thermal conditions (such as those used here) with those broader-scale models that fuse remote sensing and topographical data is needed. Despite their limitations, UAV-based thermal microclimatic assessments provide distinct insights into how species respond to extreme weather, enabling realized niche mapping within habitats. Such approaches create frontiers for conservation applications that could fundamentally alter conventional approaches from measurements of habitat area to measuring the value of particular habitats for protecting vulnerable species and communities.

**Figures**

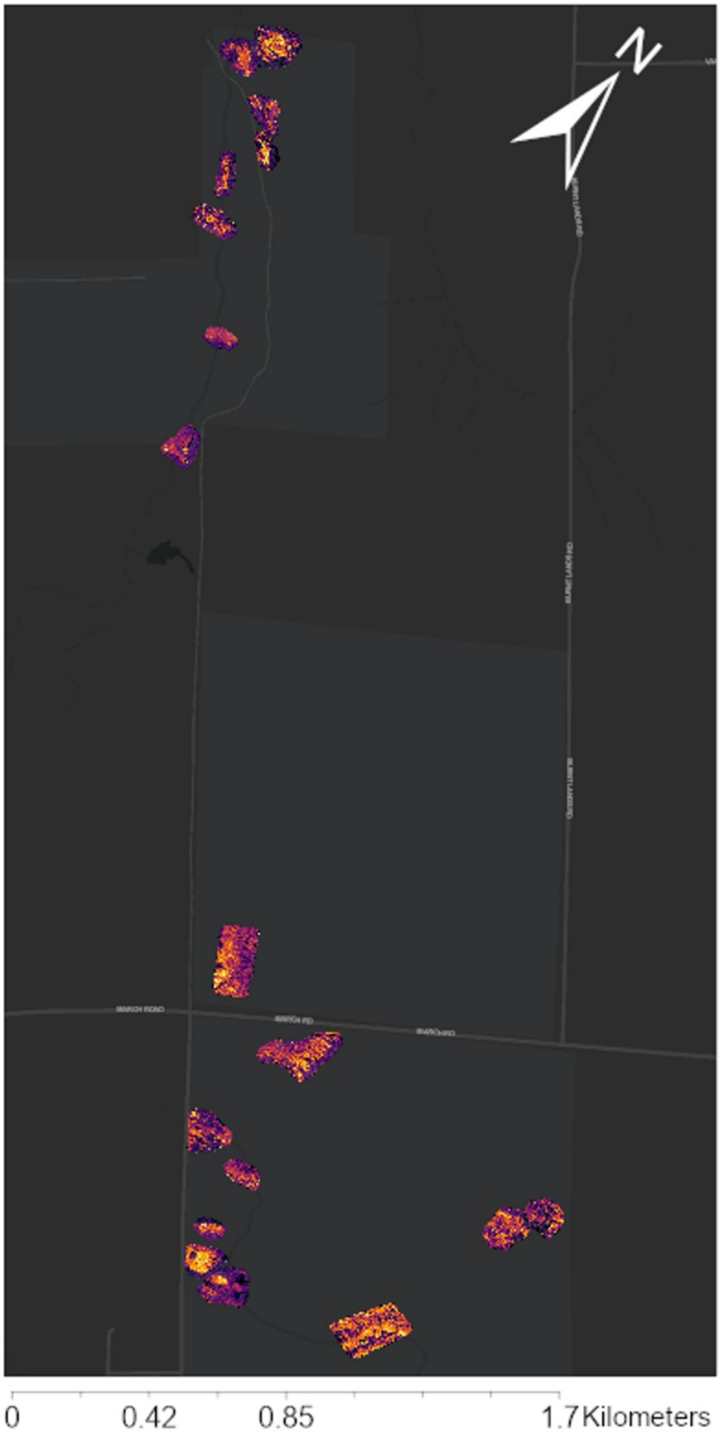


Figure 2.1. Air temperature maps of all our study patches within our study site, Burnt Lands Provincial Park.

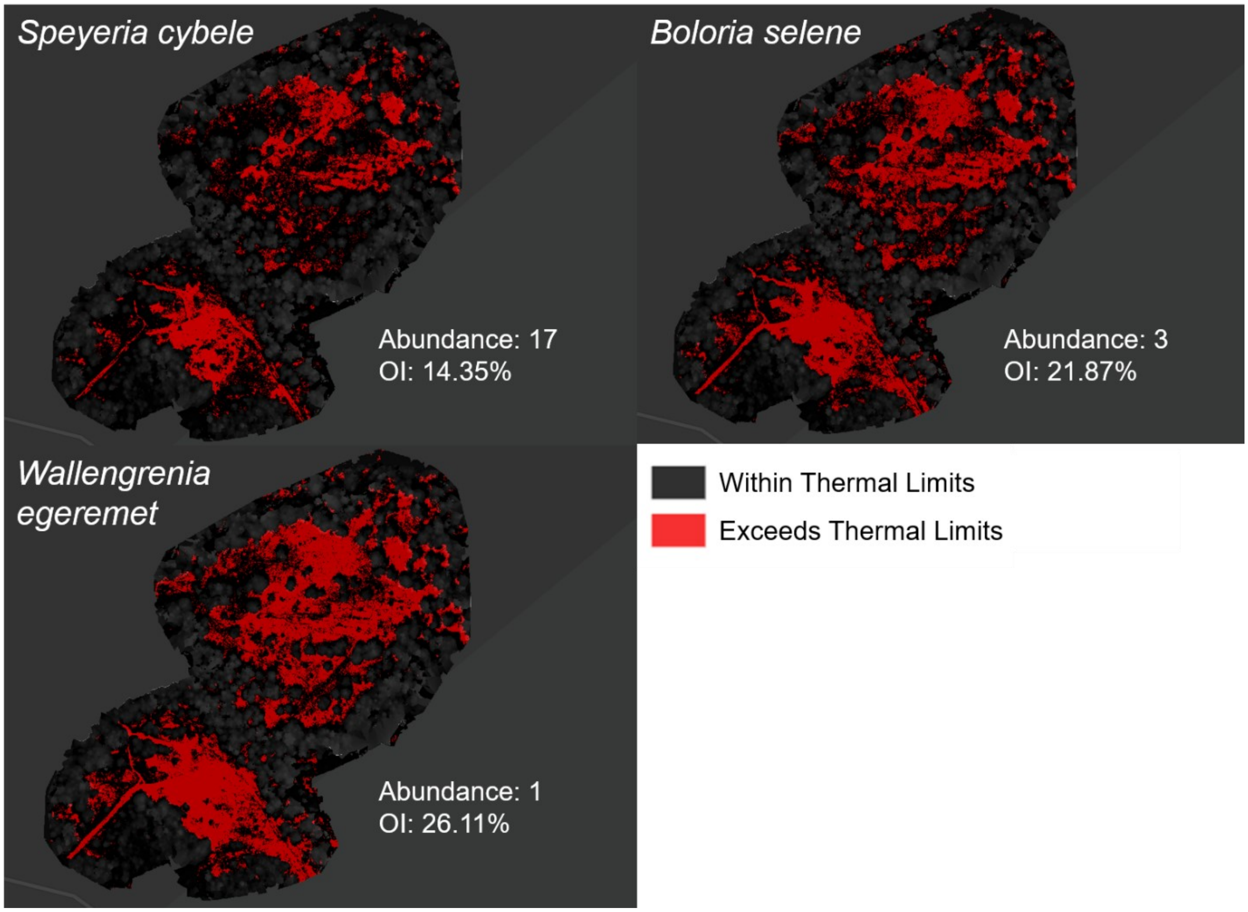


Figure 2.2. TPI maps of three butterfly species with their respective abundances and overheating indices (OI). Areas in red represent TPI values exceeding or equal to 1 (thermal extremes). The maps were rendered slightly transparent and overlaid on a shaded relief map of its canopy height map to depict topographic variation also.

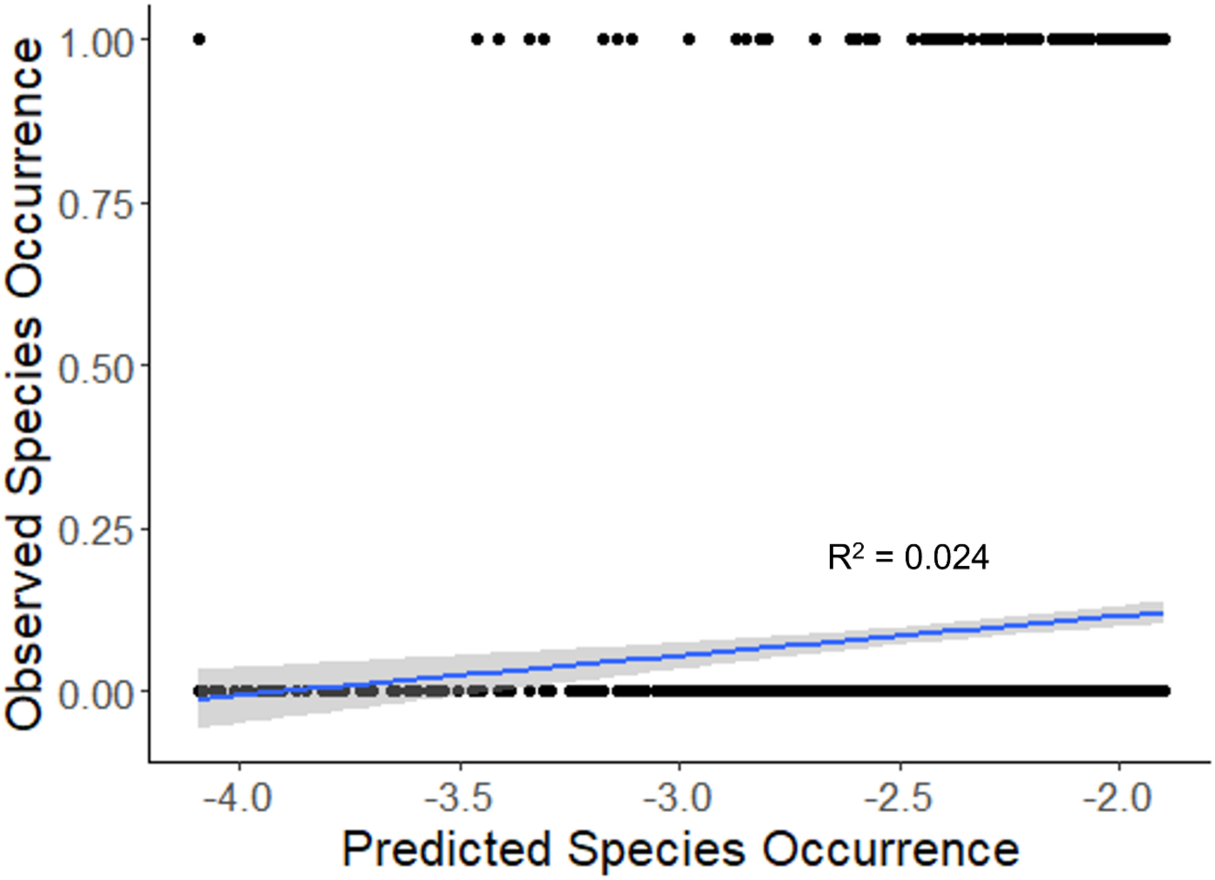


Figure 2.3. Observed species occurrence plotted against species occurrence predicted by the patch level overheating index.

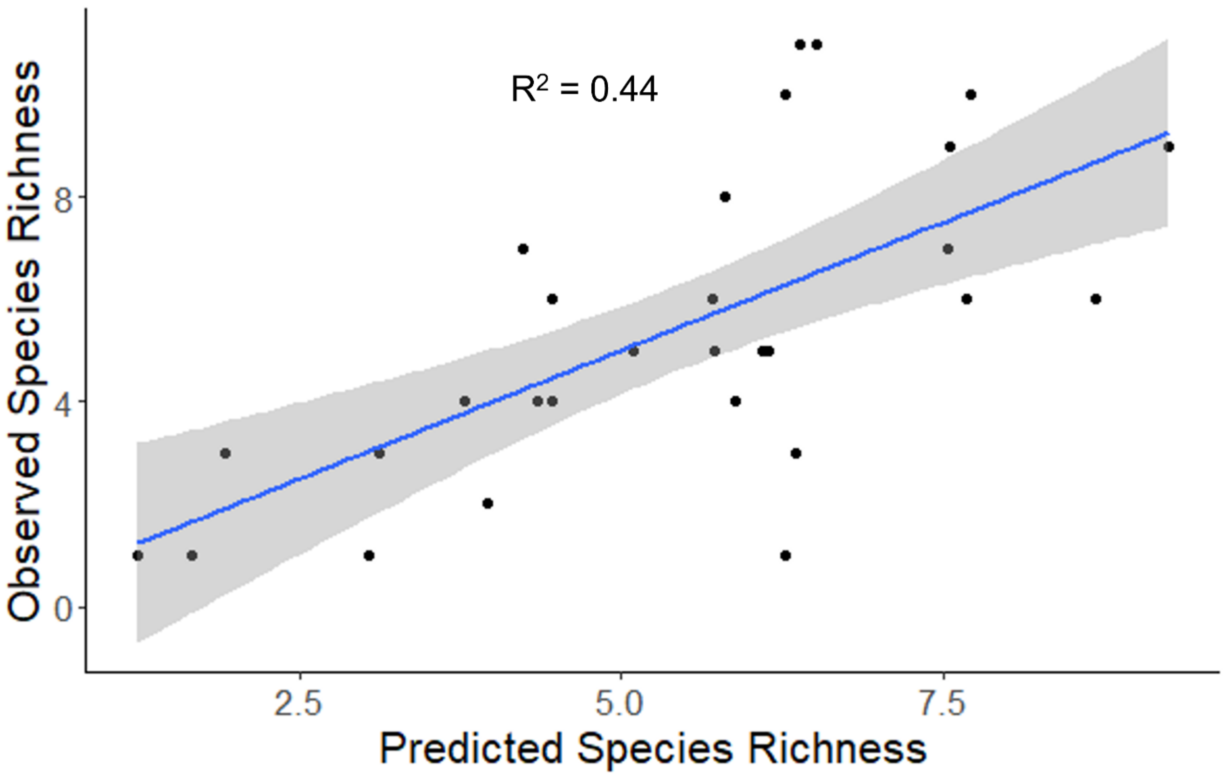


Figure 2.4. Observed species richness plotted against species richness predicted by the best model fit.

# Conclusion

UAV technology presents unique opportunities for microclimate modelling for applied ecological management purposes. My first chapter proposed a UAV-based methodology that enables direct air temperature measurements that are biologically relevant for individual butterfly species. These measurements were tested and validated using *in situ* temperature measurement and were found to be both accurate and precise. Such measurements of microclimatic conditions within habitats enabled broad-scale models using the previously-published thermal position index to be applied to predict variation in habitat suitability within individual habitats for exemplar butterfly species, namely *Coenonympha tullia* (common ringlet), *Hesperia sassacus* (indian skipper), and *Speyeria aphrodite* (Aphrodite fritillary). The thermal position index was created to measure the cumulative effects of extreme weather on species persistence and population trends, and it has been shown to do so for bumblebee, mammal species, and, in a modified form, for insect species in general at continental and global extents. This chapter was intended to provide a methodological roadmap to enable the application of such niche-based approaches to within-habitat measurements using very high resolution remote sensing platforms, such as UAVs.

In this study, I assembled observations of butterfly abundance and distributions among habitat patches in a protected area (Burnt Lands Provincial Park) and applied the methodology pilot from Chapter 1 to develop models of microclimatic suitability for observed butterfly species among study sites. Specifically, suitability was assessed using site-specific thermal position indices for species based on UAV-based measurements of temperature. Species' upper and lower thermal limits were assessed based on their distributions across North America, and these values were taken as estimates of species' realized niche boundaries. Then, areas within study sites that exceeded species' thermal limits could be identified. Patch-level measurements of thermally tolerable area, which I have named the overheating index, helped predict aspects of butterfly abundance, presence, and overall species richness, along with some conventional habitat metrics that are relevant for butterfly biology, including floral species richness, habitat area, and patch isolation. This chapter underscores that considering thermal extremes can modify understanding of butterfly distribution and abundance, even in protected habitats. Accounting for extreme weather, such as exceptionally hot temperatures relative to species tolerances, improves understanding of microclimatic variation and its importance for species and community-level understanding.

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