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Characterizing microclimates as potential thermal buffers for reptiles, birds, and mammals in an arid-zone environment

Warner, Grace M.

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Characterizing microclimates as potential thermal buffers for reptiles, birds, and mammals in an arid-zone environment

by

Grace M. Warner

2525563

Thesis

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Supervisors

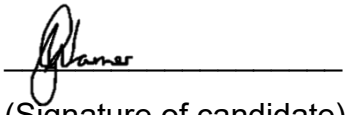
Professor Andrea Fuller and

Professor Graham J. Alexander

July 2023

DECLARATION

I declare that this dissertation is my own, unaided work. It is being submitted for the Degree of Master of Science at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other University.



(Signature of candidate)

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ABSTRACT

Aridification, increases in air temperatures and frequency of extreme weather events, such as heat waves, are predicted to intensify under climate change, suggesting dire consequences for dryland animals. Microhabitats may buffer dryland animals against the changing climate, yet microclimatic data remains scarce from Africa and arid regions. The distribution, abundance, and thermal buffering capacity of five microhabitat types (burrows, nests, rock crevices, tree hollows and vegetation) were investigated across three habitat types (dunes, plains, and mountains) in the Kalahari. The distribution and abundance of microhabitats were assessed via strip transects, while thermal buffering capacity was evaluated by comparing miniature black globe temperatures from 70 representative sheltered microhabitats with 12 localised exposed-site microhabitats. The data generated have provided a baseline measure of the abundance and distribution of microhabitats in the Kalahari and have produced a year-long fine-resolution microclimatic thermal dataset. Microhabitat types and abundance were found to differ per habitat type and across topographic gradients. Abiotic drivers, such as soil type and fire frequency, along with drivers such as biotic community composition, were highlighted as potential causes of these microhabitat distribution patterns. Burrows were the best buffered microhabitat across all tested temporal and spatial gradients, providing an average maximum decrease of -29.5 ˚C during the day, and an average maximum increase of 20.1 ˚C during the night. Well-buffered microhabitats were rare within the field-site, whereas some of the poorest buffering microhabitats (Vegetation) were abundant and widespread. Thus, competition for well-buffered microhabitats may increase under climate change, whilst the risk of traversing large distances between microhabitats may become too great for smaller animals as exposure risk to extreme temperatures increases. Furthermore, birds and large mammals may likely be at a high risk of extreme temperature exposure, as their size and structural adaptations may restrict them from access to well-buffered microhabitats. Therefore,

the need for the concurrent assessments of microhabitat distribution, abundance and buffering capacity in future species vulnerability assessments is highlighted, as it is the combination of these factors that are likely to impact population viability under climate change.

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LIST OF ACRONYMS

GCM: Global Climate Models

GHG: Greenhouse Gas

SDM: Species Distribution Models

SB: Small burrow

MB: Medium burrow

LB: Large burrow

TR: Tree

SH: Shrub

GC: Ground cover (grasses)

SRC: Small rock crevice

MRC: Medium rock crevice

LRC: Large rock crevice

AH: Abiotic hollow

BH: Biotic hollow

WB: White-browed sparrow-weaver nest

SW: Sociable weaver nest

- W: West
- E: East
- B: Base
- M: Middle
- C: Canopy

Chapter 1: Introduction

1.1. Climate change

Global change is a multifaceted threat to the biodiversity and stability of natural ecosystems worldwide (Dawson *et al.*, 2011; Convention on Biological Diversity, 2020). Human-induced climate change exacerbates the many facets of global change and has led to approximately one million species being considered at risk of extinction in the next few decades (Díaz *et al.*, 2019). Global temperatures have increased more rapidly in the last 50 years than in any other 50-year period within the last 2000 years (Masson-Delmotte *et al.*, 2021). Moreover, hot extremes and heatwaves have become more common over the last five decades, while the frequency of cold extremes has decreased (Masson-Delmotte *et al.*, 2021). Long-term projections suggest that, even under the lowest possible Green House Gas (GHG) emission scenario (SSP1–1.9), average global warming of a further 1.4 ˚C can be expected by the year 2100 (Masson-Delmotte *et al.*, 2021). These human-induced increases in GHG and consequent rises in global temperatures have had many cascading effects. Shifts in rainfall patterns, ocean acidification, retreating glaciers and rising sea levels are all seen as likely consequences of human-induced warming on our global ecosystems (Masson-Delmotte *et al.*, 2021).

1.1.1 Climate change effects across Africa

Africa — one of the most climatically exposed and socio-economically vulnerable continents to climate change (Field *et al.*, 2014; Russo *et al.*, 2016; Van Der Walt and Fitchett, 2021) — is experiencing a rate of surface temperature increase higher than the global average (Engelbrecht *et al.*, 2015; Masson-Delmotte *et al.*, 2021). The frequency of heatwave events has increased across the continent over the last few decades, and events that were historically classified as ‘unusual heatwaves’ are projected to begin occurring across all seasons by 2045 under low mitigation scenarios (Russo *et al.*, 2016). Additionally, north-western parts of the southern African subregion (Botswana, Namibia and north-western

South Africa) are projected to experience high warming rates, while mean land surface warming for the entire continent is likely to exceed the global mean temperature increase across all seasons (Niang *et al.*, 2014).

Over the last six decades, southern Africa has been warming at more than 3.2 ˚C per century, which is projected to continue at an increasing rate (Engelbrecht *et al.*, 2015; Trisos *et al.*, 2022). Concurrent with temperature increases, decreasing rainfall trends have been observed across Botswana, Zimbabwe, and western southern Africa over the last few decades. Additionally, drier winters and delayed seasonal rains have been observed, and are projected to continue for the summer rainfall regions of South Africa under low mitigation scenarios (Niang *et al.*, 2014; Davis-Reddy and Vincent, 2017). Thus, temperature increases are likely to further exacerbate dry conditions as evapotranspiration rates will be increased (Niang *et al.*, 2014; Masson-Delmotte *et al.*, 2021), which, along with delayed rainfall onset, may result in prolonged droughts and shortened productive periods (Engelbrecht *et al.*, 2015). High windspeeds and fire weather conditions are also projected to increase in the coming decades (Engelbrecht *et al.*, 2015; Masson-Delmotte *et al.*, 2021; Trisos *et al.*, 2022), which may further promote soil desiccation and ecosystem shifts in southern African.

1.1.2 Climate effects on South African drylands and the Kalahari

South Africa has been identified as having an increasing trend in desertification due to a mixture of human-induced dryland degradation (Andela *et al.*, 2013) and climate change effects (Masson-Delmotte *et al.*, 2021). Specifically, it has been highlighted that the hot desert biome in the northern area of South Africa is likely to expand southwards, leading to an approximate 40–50% potential coverage of the country by hot desert under a 3 °C global temperature increase (Engelbrecht and Engelbrecht, 2016). Furthermore, the dune fields of the Kalahari Desert, which extend into the northern parts of South Africa, have been predicted to be

reactivated (significant exposure of sand with concurrent dune movement), as a combined product of climate warming (Thomas *et al.*, 2005), and land degradation (Mayaud *et al*., 2017). In addition, the frequency of fire weather conditions are projected to increase across the subregion (Masson-Delmotte *et al.*, 2021), and the intensity and duration of heat waves are projected to increase in South Africa (Mbokodo *et al.*, 2020). Thus, considering the compounded effects of the above, it is likely that climate-induced conditions will radically impact the Kalahari ecosystem.

1.2 Biological responses to climate change

1.2.1 Ecosystem-level effects

Large scale climatic changes will not only affect animals directly through rises in ambient temperatures and climatic extremes, but also indirectly through ecosystem level changes (Fuller *et al.*, 2021). Shifts in climatic zones across South Africa have been predicted to occur due to anthropogenic climate change (Engelbrecht and Engelbrecht, 2016). These shifts will cause subsequent shifts in biome, vegetation productivity (Engelbrecht and Engelbrecht, 2016; Nzabarinda *et al.*, 2021), and modification of plant species composition (Mirzabaev *et al.*, 2019) across multiple communities. Consequently, there may be further decreases in food resources for dryland herbivores, which may lead to knock-on effects for species higher up the trophic chain (Mirzabaev *et al.*, 2019). Therefore, although most dryland animals have developed adaptations to buffer current extremes, further climatic change may impinge on their physiological welfare and population fitness (Fuller *et al.*, 2016), having cascading effects on ecosystem function.

1.2.2 Species-level effects

The negative effects of climate-induced food and water reductions in some dryland endotherms have already been documented (Iknayan and Beissinger, 2018; Weyer *et al.*, 2020). Birds and mammals are less able to buffer extreme heat by employing euhydration-dependent physiological

mechanisms such as evaporative cooling without reaching lethal dehydration (Iknayan and Beissinger, 2018). Furthermore, they may not be able to forage efficiently for enough hours (Du-Plessis *et al.*, 2012) or at the appropriate time of day (Weyer *et al.*, 2020), and thus cannot buffer extreme temperatures via physiological processes if energy resources are low (Fuller *et al.*, 2016; Weyer *et al.*, 2020). Consequently, climate effects have been recorded to have a cumulative effect on some endotherms at a population level, as concurrent decreases in food and water, along with increasing temperatures over long periods can massively decrease breeding success and population viability over time (Conradie *et al.*, 2019; Pattinson *et al.*, 2022).

Dryland ectotherms may also have a decreased ability to buffer the predicted temperature extremes (Barrows *et al.*, 2010). Recent work has shown that heat stress, and consequent heat mortality rates in terrestrial ectotherms, are likely to increase markedly with each rising degree of climate warming (Jørgensen *et al.,* 2022). Specifically, reptiles limited mobility over large distances, ectothermic physiology (Barrows *et al.*, 2010; Sinervo *et al.*, 2010; Rezende *et al.*, 2020), and constrained physiological thermoregulation (Hertz *et al.*, 1993) provide them with little opportunity for thermal buffering. Additionally, within dryland landscapes, there are commonly large distances between sunny and shady microhabitats, which increases the energetic costs of behavioural shuttling and further intensifies the exposure risk to extreme temperatures (Huey *et al.*, 2009). Consequently, local habitat structure can shape both the diversity of thermoregulatory options available to reptiles (Neel *et al.,* 2021), as well as the abundance of prey items (van der Westhuizen *et al*., 2021). Thus, drought conditions and increasing temperatures are likely to have negative effects on habitat suitability, resource distribution and consequent survival rates of dryland reptiles (Barrows *et al.*, 2010).

1.2.3 Exposure risk

For both ectotherms and endotherms, there is no single ambient temperature limit that will cause immediate death, but rather a sustained exposure to high heat loads that may lead to death over time (Mitchell *et al.*, 2018). Thus, physiological sensitivity to extreme temperatures can be buffered by reducing climatic exposure (Riddell *et al.*, 2021), and by making a compromise between the intensity and the duration of the high heat exposure (Mitchell *et al.*, 2018). Seeking cooler microclimates remains one of the primary responses of species to high environmental temperatures (Fuller *et al*., 2016), with many species observed to selectively move between microclimates as a way to prevent excessive rises in body temperature in arid environments (Hetem *et al.*, 2007; Fick *et al.*, 2009; Sinervo *et al.*, 2010; Blank, 2020). However, the number of hours that animals can remain in thermal refuges is restricted by how long they can afford to persist without foraging (Sinervo *et al.*, 2010), drinking, socialising or reproducing. Nonetheless, if continuous high heat exposure is experienced as a cumulative stressor (Rezende *et al.*, 2020), escaping the ambient temperatures even temporarily in microclimates may allow animals to persist in unfavourable conditions (Varner and Dearing, 2014; Riddell *et al.*, 2021).

1.3 Microclimates and microhabitats

Microclimates are spatially and temporally restricted climates where the thermal environment and water balance is defined by the local microhabitat, being formed either by abiotic structures or by biotic interactions within the environment (Woods *et al*., 2015). Microclimates are considered as existing in areas or microhabitats between 0.001–100 m in width and less than 10 m in vertical height (Bramer *et al.*, 2018). However, for the purposes of limiting the scope of this thesis, I will be focusing only on microclimates that are within a size range frequently utilised by birds, mammals, and reptiles (i.e., approximately 0.01 – 5 m). Microclimates can be split into two groups, namely abiotic and biotic. Abiotic microclimates

reflect environmental heterogeneity created by abiotic structures, such as rocks or soil type, and biotic microclimates reflect environmental filtering or shaping by living organisms, such as animal burrows or leaves in a canopy (Woods *et al.*, 2015). Microclimatic variance across temporal dimensions is generally accepted to exist on a timescale of hours or minutes (Bramer *et al.*, 2018).

1.3.1 Buffering potential and importance of microclimates

Microhabitats can alter the climate that sheltering species experience by providing a thermally buffered microclimate (Keppel *et al*., 2017; Lowney, Bolopo *et al.*, 2020; O'Connell & Keppel, 2016; Scheffers, Edwards *et al.*, 2014; Scheffers, Evans *et al.*, 2014; Varner & Dearing, 2014; Whittington-Jones *et al*., 2011). This thermal buffering is a dampening of macroclimatic temperature variability over time, so that temporal fluctuations within the microclimate exist, but are far less variable and less pronounced than those in the macroclimate (De Frenne *et al.*, 2021). Thermal buffering occurs on a spectrum, from weak buffering to complete thermal decoupling. Weak buffering occurs when the thermal profile of the microclimate is similar to the macroclimate, and there is a positive correlation between the macro- and microclimatic temperatures. On the opposite end of the spectrum, if the positive correlation between macro- and microclimatic temperatures is completely lost, the relationship is described as thermal decoupling (De Frenne *et al.*, 2021). In circumstances where the microclimate is buffered to the greatest possible extent, the thermal profile of the microclimate is decoupled from the macroclimate (Dobrowski, 2011; De Frenne *et al.*, 2021).

Heat loss or heat gain in microclimates and animal body temperatures are driven largely by radiative heat exchange, latent heat exchange, heat convection and heat conduction (Bramer *et al.*, 2018; Mitchell *et al.*, 2018). Hence, microclimate buffering occurs in microhabitats due to reductions in exposure to radiation (Chu *et al*., 2021; Scheffers, Evans *et al.*, 2014),

reductions in soil water evaporation rates (Breshears *et al.*, 1998), reductions in wind exposure or increases in localized humidity (O'Connell & Keppel, 2016; Whittington-Jones *et al.*, 2011). Consequently, animals can regulate their heat exchange with their environment by moving into a thermally buffered microhabitat. Microclimatic thermal buffering can reduce ambient temperature by more than 20 ˚C in extreme cases (Scheffers, Evans *et al.*, 2014), and thus can substantially reduce species' risk of exposure to lethal temperatures (Scheffers, Edwards *et al.*, 2014). It is in this way that microhabitats can function as microrefugia — small portions of the landscape that provide favourable microclimatic conditions, which allow the persistence of local species during periods of extreme environmental temperatures (Keppel *et al.*, 2012; Greiser *et al.*, 2020).

1.3.2 Landscape and topographic associations with the microclimate

Localised landscape and topography affect microclimatic temperatures (Dobrowski, 2011; De Frenne *et al.*, 2021), microhabitat prevalence (Suggitt *et al.*, 2018), and microclimatic buffering capacity (Macyk *et al.*, 1978; Suggitt *et al.*, 2011; Egli *et al.*, 2015). The direct effects of topography on microclimatic variation are attributed to the pooling of cool air or water in depressions, elevational gradients and differences in exposure to solar radiation and wind due to slope and aspect (Macyk *et al.*, 1978; Ashcroft *et al.*, 2008; Dobrowski, 2011; Egli *et al.*, 2015; Aalto *et al.*, 2017; Davis *et al.*, 2019; Massimino *et al.*, 2020; De Frenne *et al.*, 2021). Slope and aspect are suggested to be two of the most important topographic factors to shape microclimates specifically in arid regions, as they influence radiation and wind exposure, and thus affect both water balance and temperature (Dobrowski, 2011). Yet, the effects of topography on microhabitat distribution remain largely undocumented (Ward *et al.*, 2018; Massimino *et al.*, 2020). Nonetheless, it is generally accepted that topographically complex or heterogenous areas provide greater numbers of microhabitats (Dobrowski, 2011; Suggitt *et al.*, 2018),

while vegetation-based microhabitats still provide some level of thermal refuge in topographically homogenous landscapes (Milling *et al.*, 2018).

1.3.3 Microhabitat accessibility

The way in which an individual animal experiences macroclimatic temperatures in an environment will be shaped according to its' species-specific physiology, morphology, and size (Potter *et al*., 2013; Woods *et al*., 2015). Body size in particular not only has an impact on the thermal requirements of species (Mitchell *et al*., 2018) but also distinctly limits which microhabitats are accessible to them (Potter *et al*., 2013). Therefore, some species may be at higher risk of climate exposure if microhabitats are not uniformly accessible. A recent study that modelled species persistence in a desert environment found that access to microhabitats can be used to predict subsequent survival or collapse of populations, as microhabitats filter the levels of heat exposure that animals experience (Riddell *et al*., 2021). Thus, animals that rely heavily on one type of microhabitat, such as arboreal species, may be more affected by climate change than others such as terrestrial small mammals that can access a multitude of microhabitat types (Riddell *et al*., 2021).

1.4 Species vulnerability and habitat suitability

1.4.1 Historical and current methodology

Although microclimates are becoming more commonly considered in the literature, most bioclimate studies have not included any microclimatic information (Suggitt *et al.*, 2011). Climate change exposure risk and species vulnerability have historically been assessed using correlative species distribution models (SDMs) that are interpreted from coarse-resolution global data or Global Climate Models (GCMs) (Dawson *et al.*, 2011; Dobrowski, 2011; Jones *et al.*, 2016; Lembrechts *et al.*, 2019). Yet, on average, SDM climatic grids are up to 10 000-fold larger than the animals presented in the SDM (Potter *et al.*, 2013), which suggests that animals are experiencing their environments at much finer and more

heterogenous resolutions than what is present at the level of GCMs (Suggitt *et al.*, 2011; Potter *et al.*, 2013; Varner and Dearing, 2014). Even thermal data grids that are of relatively high resolution may not encompass the true thermal variation of an area, as temperatures are shown to vary at even finer resolutions than <1 km when the landscape is complex (Fridley, 2009; Dobrowski, 2011). Further, it should be noted that exclusively GCM-based projections may potentially be overly pessimistic (Gillingham *et al.*, 2012) or erroneous in that they may highlight inappropriate or reduced areas for conservation (Varner and Dearing, 2014; Lembrechts and Lenoir, 2020) if used without ground-truthing.

1.4.2 Mechanistic models

Recently there has been a trend towards using mechanistic models that incorporate variables that are relevant to microclimatic conditions, such as wind speed, solar radiation, sky radiation, relative humidity and substrate temperatures (Kearney *et al.*, 2014). Although positive in that they provide far greater detail than most SDMs, the resolution of these datasets remains around 15 km (Kearney *et al.*, 2014), which is unlikely to encompass variation that exists on a localised scale. Further work by authors such as Maclean (2020), is improving these data by modelling fine-scale (100 m resolution), hourly, climatic data, which was made possible through validation and calibration of the models with *in-situ* microclimatic data (Lembrechts and Lenoir, 2020; Lembrechts *et al.*, 2020; Maclean, 2020). These studies highlight the need for *in-situ* microclimatic measurements, not only for localised studies but also as ground-truthing for far broader mechanistic models on a global scale (Lembrechts and Lenoir, 2020). Efforts have been made to add microclimatic data to a globally distributed and freely available database (Lembrechts *et al.*, 2020). Yet data for mechanistic modelling, from extreme and remote environments, such as arid areas on the African continent, remain heavily underrepresented (Lembrechts *et al.*, 2020).

1.4.3 The need for microclimatic data

Many vulnerability assessments treat species across a large area as uniformly vulnerable, even though more recent studies suggest that localised habitat structure may be the principal causal factor for variations in vulnerability (Neel *et al.*, 2021). Habitat structure influences opportunities for behavioural thermoregulation (Neel *et al.*, 2021) and is tightly linked to exposure risk (Riddell *et al.*, 2021). Thus, biotic responses to habitat structure and resultant microclimates, such as vegetation clumping in areas where cool air and water pool, also influence species interactions within the community and thus may cause unexpected responses to macroscale climate changes (Hannah *et al.*, 2014). Therefore, ignorance of topoclimatic or microhabitat details in vulnerability assessments can lead to confounding results, as areas that host multiple microclimates will give inaccurate trends of how other areas may fair under climate change (Dobrowski, 2011).

Microhabitats and microclimates, as key regulators of ecosystem function (De Frenne *et al.*, 2021), should be considered vitally important to include in conservation and vulnerability assessments under climate change. Although microhabitats are known to be used by many species in sheltering against current climatic extremes (Hetem *et al.*, 2007; Varner and Dearing, 2014; Blank, 2020; García *et al.*, 2020; Boyers *et al.*, 2021), and there is evidence that adding additional microhabitats has beneficial effects on the reproductive capacity of natural populations (Bellrose *et al.*, 1964; Strange *et al.*, 1971), there are still no known assessments on the effectivity of preserving microhabitat refuges for conservation (Smith *et al.*, 2020). Given that one of the fundamental aims of conservation planning is to identify and preserve areas that can act as refugia under climate change conditions (Keppel and Wardell-Johnson, 2012; Varner and Dearing, 2014; Petford and Alexander, 2021), characterizing which microhabitats may be most valuable in terms of buffering potential, as well

as assessing the prevalence and distribution of such microhabitats, is key in managing African arid areas under future climate change conditions.

1.5 Aims, objectives, and hypotheses

The ultimate aim of this study was to provide an overview of the prevalence of microhabitats and their potential to provide thermal buffering to animals living in an arid landscape. Identifyication of the diversity and distribution of microhabitats, as well as information on their respective thermal buffering capacities, can provide critical information on which habitats will be available as potential thermal refugia for dryland animals under climate change. This aim was achieved through meeting the following objectives and assessing the following hypotheses:

1) Assess microhabitat distribution within three Kalahari habitat types, across various topographic gradients, and identify which specific topographic or habitat elements may be prognostic in predicting microhabitat distribution and density.
    - Hypothesis 1: The distribution and density of microhabitats vary due to habitat type.
    - Hypothesis 2: Each habitat type has a specific suite of microhabitats that characterize that habitat. For example, burrows have the highest densities in the dune habitat, rock crevices are most common in the mountain habitat and vegetation and vegetation-dependant microhabitats are most prevalent in the plains habitat.
    - Hypothesis 3: Shrub-vegetation is the most common and widely distributed microhabitat type across all habitats.
    - Hypothesis 4: Vegetation-based microhabitats are more prevalent around shared water and soil-nutrient resources.
    - Hypothesis 5: Based on topoclimatic literature, which suggests that south-facing slopes retain more moisture in the Southern Hemisphere (Dobrowski, 2011), I hypothesise that

southern mountain slopes will have greater vegetation cover, but fewer rock crevices.

- Hypothesis 6: Given the prevailing wind direction of the area (east to west), bird nests and burrows are more commonly found on the sheltered west faces of the dunes.
- Overarching hypothesis: Aspect, slope, and habitat type are significant predictors of the density and type of microhabitats available in the area.

2) Quantify several microhabitat types' buffering capacity across a landscape gradient by evaluating their individual thermal profiles in comparison to those of exposed-sites across three habitat types.
    - Hypothesis 1: Based on previous studies (Downs and Perrin, 1989; Kinlaw, 1999; Anderson and Richardson, 2005; Whittington-Jones, Bernard and Parker, 2011; García et al., 2020; van der Westhuizen et al., 2021), I hypothesize that burrows of all sizes are the most thermally buffered microhabitat available, and that rock crevices, particularly of small size, provide the second most optimum thermal buffering.

3) Evaluate the relationships between microhabitat buffering capacity and microhabitat type, microhabitat position, habitat type, season, and topography.
    - Hypothesis 1: Microhabitat buffering capacity differs between the day and night-time periods, and across seasons.
    - Hypothesis 2: All biotic microhabitats are more buffered during rainy seasons, as a consequence of vegetation greening, and increased soil water content.
    - Hypothesis 3: There are significant differences in overall buffering capacity per habitat primarily as a result of distinctive microhabitat compositions.

- Hypothesis 4: Microhabitats on or below ground level are more buffered than those above the ground.
- Hypothesis 5: The effect of aspect on microhabitat buffering varies per season.

1.6. Thesis structure

Chapter 1: Introduction

This is an introductory chapter that gives insight into the background of the study and reviews the current academic literature related to the study's main concepts. In addition, this chapter indicates where this study seeks to fill the gaps in the literature and outlines the aim, objectives and hypotheses.

Chapter 2: Microhabitat prevalence and distribution in a South African dryland

This is the first data chapter that explores objective one. An assessment of the results of microhabitat distribution across various topographic gradients is provided, along with a discussion of the implications of the findings.

Chapter 3: Variance in Kalahari microhabitats' thermal buffering across temporal and spatial scales

This is the second data chapter that elaborates on objectives two and three, which details the quantification of microhabitat buffering capacity and the evaluation of buffering capacity as a function of season, topography, position and habitat type. It also provides a discussion on the relevance and conservation implications of the results.

Chapter 4: Synthesis and conclusion

In this chapter, I provide a complete summary of the distribution patterns and buffering capacity of microhabitats in the Kalahari, the potential drivers of these effects, and discuss the possible responses of Kalahari

birds, mammals, and reptiles to climate change via the lens of microhabitat accessibility.

Chapter 2 : Microhabitat prevalence and distribution in a South African dryland

2.1 Introduction:

Habitat heterogeneity can be used as a proxy predictor of species vulnerability (Neel *et al.*, 2021) as it provides opportunities for behavioural thermoregulation (Woods *et al*., 2015; Neel *et al.*, 2021) and allows animals to select their level of exposure to climatic extremes (Riddell *et al.*, 2021). Additionally, habitat structure affects the presence of food and water in the system (Jankju, 2013; Kelvin *et al.*, 2017; Richard *et al.*, 2022), and thus has cascading effects on the physiological condition of animals (Fuller *et al.*, 2021). Similarly, the effects of climate change that animals will experience will depend on the exposure risk (Rezende *et al.*, 2020; Riddell *et al.*, 2021), compounded ecosystem effects such as reductions in water or food they experience (Fuller *et al.*, 2016, 2021; Mirzabaev *et al.*, 2019) and the interaction of these two variables with physiological limits of animals (Mitchell *et al.*, 2018; Anderson *et al.*, 2021). Local habitat structure has therefore been suggested to be the primary cause of differences in species vulnerability between distinct habitats (Neel *et al.*, 2021). To better understand the effects of anthropogenic climate change on animals, it is necessary to consider the local habitat structure that is available to them (Lenoir *et al*., 2017; Lembrechts *et al.*, 2020; Anderson *et al.*, 2021; Neel *et al.*, 2021).

The heterogeneity of habitat structure causes ecosystems to be thermally heterogeneous across space and time, especially at a fine resolution (Klinges and Scheffers, 2021), and when the landscape is complex (Fridley, 2009; Dobrowski, 2011). Microclimates, which are small climatic variations that are at least partially or temporarily decoupled from the large-scale climate, are created by fine-scale habitat structuring known as microhabitats (Bramer *et al.*, 2018). Abiotic microhabitats reflect environmental heterogeneity created by abiotic factors, such as topographic features on a broad scale, or rock formations on a fine scale (Woods *et al*., 2015; Keppel *et al.*, 2017). Whereas biotic microhabitats reflect environmental structuring by living organisms, such as animal

burrows, nests and tree cavities (Woods *et al*., 2015). Thus, although it is generally accepted that the climate experienced in an area is simply the outcome of advective and topographic influences (Pepin and Lundquist, 2008; Daly *et al.*, 2010), this idea largely excludes the impact of biotic microhabitats or abiotic influences such as soil characteristics in topographically flat areas (Lenoir *et al.*, 2017). The actuality for many animals is that the experienced climate is shaped by multiple abiotic influences as well as the composition of ecosystem engineering plants and animals that form the surrounding biotic community.

Predicting the prevalence of microhabitats and the consequent availability of high-quality thermal refugia in an environment is reliant on identifying the topographic and ecosystem processes that produce them (Dobrowski, 2011). From a topographic perspective, elevational gradients are well-known predictors of temperature (Ashcroft *et al*., 2008, 2009; Lenoir *et al*., 2017), while slope and aspect have also been recorded to have a significant effect on the climate as they alter the level of incoming of solar radiation and wind exposure (Daly *et al*., 2010; Dobrowski, 2011; De Frenne *et al.*, 2021). Similarly, depressions pool cooler air or water and lead to localised increases in soil moisture (Aalto *et al.*, 2017; De Frenne *et al.*, 2021). Even higher water saturation in soil or air due to proximity to water bodies can produce a buffered microclimate, with wind directionality playing a significant role in the level of buffering provided across time (Ashcroft *et al*., 2009; Keppel *et al*., 2017). These topographic changes may also relate to ecological changes *(Daly et al*., 2010; Keppel *et al.*, 2017; Anderson *et al.*, 2021). For example, where there is water pooling, there may be more plant life, more shrubs to create shade or more grass for birds to build nests – and these resources provide microhabitats. Yet topographic indices are rarely associated with the prevalence of particular abiotic or biotic microhabitats.

There is an agreement in the literature about the value of thermally buffered microhabitats in both historic and future climatic shifts, but there is little knowledge of the biogeographical or ecological basis on which they rely (Rull, 2009; Dobrowski, 2011). Although data indicate that vegetation and other biotic microhabitats impact the environmental conditions experienced by animals (Isaac *et al*., 2008; Whittington-Jones *et al*., 2011; Scheffers, Edwards, *et al.*, 2014; Scheffers, Evans, *et al.*, 2014; Varner and Dearing, 2014; O'Connell and Keppel, 2016; Maziarz, 2019; Lowney *et al.*, 2020; Chu *et al*., 2021), biotic microhabitats are rarely considered for the role they play in buffering future climatic changes (Keppel *et al.*, 2017). Efforts have been increased to gain more microclimatic data globally (Lembrechts *et al.*, 2020), but most microclimate research focuses on the thermal buffering capacity of microhabitats rather than the availability or distribution of microhabitats in an environment. There remains a dearth of microclimatic data from the southern hemisphere, with data lacking specifically from environments that experience extreme temperature (Lembrechts *et al.*, 2020). Thus, considering that arid ecosystems, which are characterised by extreme temperatures, are likely to be intensely threatened under climate change scenarios (Niang *et al.*, 2014; Mirzabaev *et al.*, 2019), identifying the driving factors of microhabitat prevalence may be crucial to support arid-region conservation strategies in the future.

By assessing the density and distribution patterns of microhabitats in an arid ecosystem, I aimed to provide information on which environmental factors may shape the availability of microclimates in an area that is likely to be heavily impacted by climate change. In this chapter, I quantify the density of five specific microhabitats (rock crevices, bird nests, burrows, tree cavities and vegetation cover) of varying sizes across three different habitats within the South African Kalahari landscape, and assessed their prevalence based on the factors of aspect, slope, and habitat type. Specifically, I assessed how specific microhabitat densities differ across

three distinct habitats within the same biome, quantified how slope and aspect affect the distribution of microhabitats in topographically heterogeneous environments, and assessed any patterns of co-occurrence that may exist between microhabitat types. I predicted 1) that shrubs will be the most abundant microhabitat type across all habitat types, that vegetation and vegetation-based microhabitat types would be more abundant in the plains, that burrow-based microhabitats would be most abundant in dunes, and that all rock-based microhabitats would only exist in the mountains; 2) that aspect and slope will be significant predictors of the density and type of microhabitats available in the dunes and mountains, that southern mountain slopes will have greater vegetation cover and fewer rock crevices, and that bird nests and burrows will be more commonly found on the sheltered West faces of the dunes; 3) that vegetation-based microhabitats will co-occur given shared water and soil-nutrient resources.

2.2 Materials and methods

2.2.1 Study area

The study region is located within the 114 000-ha Tswalu Kalahari Reserve in the Northern Cape Province, which exists on the south-eastern edge of the Kalahari. The reserve is divided into two fenced sections, Lekgaba and Korannaberg, where the Lekgaba section contains an ecosystem with lions, and the Korranaberg contains all other Kalahari indigenous carnivores (van Rooyen and van Rooyen, 2017). For safety reasons (lion presence), this study was conducted in the Korannaberg section only (Fig. 2.1). The notable large topographic features of the reserve are the quartzitic Korannaberg mountains on the eastern side of the reserve, and dunes in the western portion, both of which run in an approximate north-south direction. The area ranges in elevation from approximately 1020 m on the lowest point in the plains to 1586 m on the highest mountain peak (Davis *et al*., 2010).

The reserve contains five vegetation types, defined by Mucina and Rutherford (2006), and mapped more recently by Tokura *et al*. (2018). Three vegetation types, namely Gordonia Duneveld (‘dunes’), Koranna-Langeberg Mountain Bushveld (‘mountains’) and a mix of Olifantshoek Plains Thornveld and Kathu Bushveld are the most readily accessible areas to the Tswalu research centre (Tokura *et al*., 2018), and were therefore selected to be used as habitat types for this study. Since Olifantshoek Plains Thornveld and Kathu Bushveld form a mosaic where they have a patchy, interdigitated distribution, they were merged to form a ‘plains’ habitat for this study. The dune habitat is formed by parallel sand banks rising roughly 3–8 m above the plains area, where vegetation in the dunes differs from dune crests to interdunes. The combination of dunes and interdunes consists mostly of grasses, shrubs, and a few small tree species. The mountain habitat is typified by shallow, rocky soils, open shrubland, minimal trees and moderate grass cover. The plains habitat occurs on deep aeolian sand with patches of surface calcrete. The vegetation is a mix of areas that have mostly woody growth with an abundance of large tree species and sparse grasses, and open bushveld that consists of shrubs, grasses and only a few larger tree species (van Rooyen and van Rooyen, 2017).

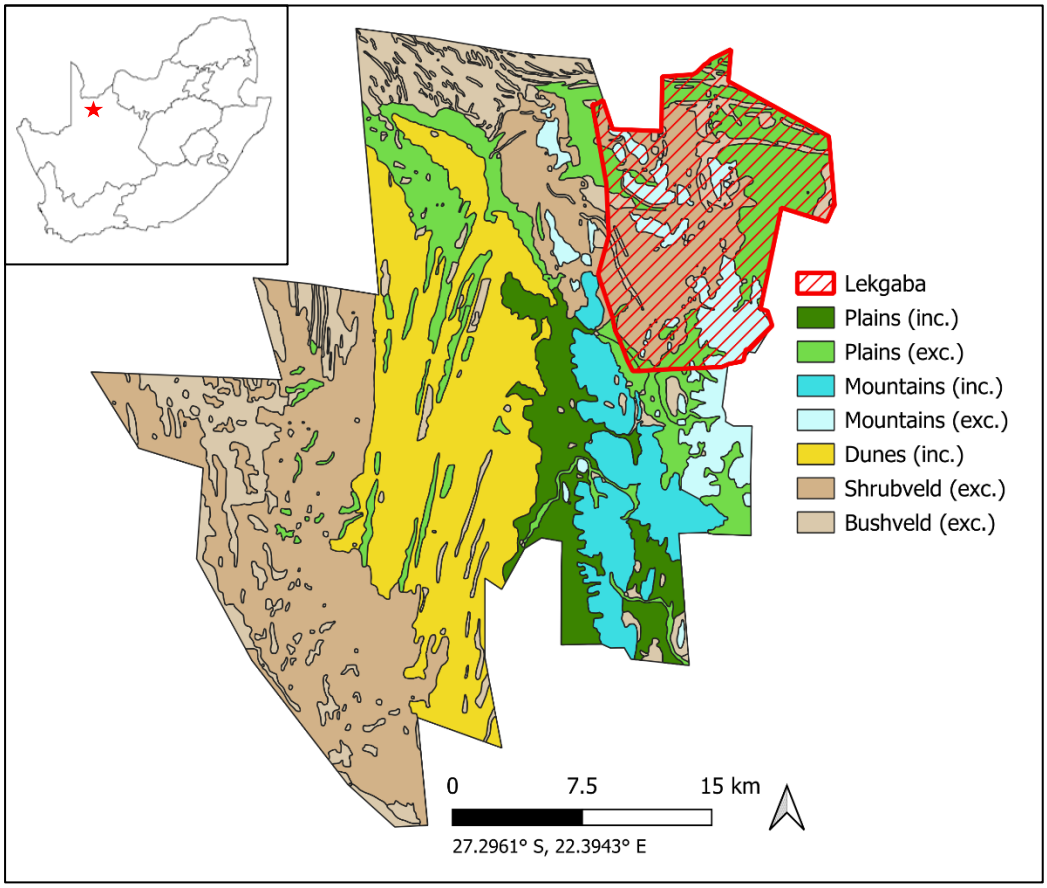

Figure 2.1: Map of the Tswalu Kalahari Reserve, with inset map indicating the reserves' position in South Africa. Brown areas indicate areas that were not used for this study. Darker colours indicate areas that were included in the study and lighter colours are areas that were excluded due to lack of ease of access. The map is redrawn from vegetation maps owned by Tswalu Kalahari Reserve and the maps produced by van Rooyen and van Rooyen (2017).

2.2.2 Transect design

A combination of 'gradsect' (gradient-directed transect) and line transects was employed to assess the distribution and density of microhabitats across the reserve. Line transects provide the benefit of covering larger stretches of land than do quadrat techniques (Buckland *et al.*, 2007), while 'gradsects' are specifically designed to provide a representative sample across highly variable topographies via the purposeful placement of surveys on the strongest environmental gradients present in a study area (Gillison and Brewer, 1985; Austin and Heyligers, 1989). The predicted

clumped distribution of some biotic microhabitats was accounted for by using multiple short-line transects that were arranged systematically along gradients, to optimize the precision and accuracy of density estimates (Nomani *et al.*, 2012), and to strengthen the effect of topography on samples.

Maps of 'habitat types' (Fig. 2.1) were based on vegetation maps of the Tswalu Kalahari Reserve (van Rooyen and van Rooyen, 2017). The vegetation map was converted from a geographic coordinate system to a projected coordinate reference system (EPSG:32734, WGS 84/UTM zone 34S) in QGIS (Version 3.18.3), with each vegetation type made into a separate shapefile of the accessible areas. The resultant maps were imported individually into Distance software, version 7.3, release 2 (Thomas *et al*., 2010), where a 1-km^2 grid was overlayed onto each habitat type. A sampling design of simple random points, under minus sampling constraints, was selected for a total of five points for plains, and 10 points for the mountain and dune shapefiles. The generated point coordinates were then transformed back into a geographic coordinate system for ease of GPS use, using an online transformation platform. Each one of these randomly generated points demarcated a randomly selected survey site.

Given that road access was limited, the closest possible road to each randomly selected site was driven, whereafter the topographically steepest area closest to the point was demarcated, and the surveyors walked 100 m off the road towards it. A waypoint was then created for this new point, which marked the starting point for each transect site (All waypoints and elevation measurements were taken using a Garmin Etrex 10). At the dunes and plains sites, ten and five 'common microhabitat' transect lines were completed in each site respectively, where the lines were made smaller to accommodate for the high numbers of specific microhabitats (common microhabitats were small burrows and shrubs, and rare microhabitats were all others). At each dune site, one line ran along the

ridge of the dune, and two lines ran on either aspect of the slope, with a minimum of 150 m between parallel lines. In the plains, the same five-line pattern was imitated, except that the direction of the midline and perpendicular lines was selected to best avoid transect lines crossing any roads.

Each ‘common microhabitat’ line was 500 m x 1 m and consisted of ten 20-m sections of effort and ten 30-m sections of no effort in between. In each 20-m section, the type and size of individual microhabitats, elevation and aspect were recorded. Elevation was recorded at each end of the 20-m lines and was used to calculate the angle of slope. The difference between elevation readings revealed the height of the slope, from which the angle of the slope was derived using trigonometric equations. The aspect was measured facing the angle of the slope, although if there was no difference seen in elevation, then it was marked as ‘valley’ for dunes, or ‘flat’ for plains areas. Five and ten more ‘rare microhabitat’ transects were walked along the same lines for both the dunes and plains, but these lines were 500 m x 10 m, and only ‘rare’ microhabitats were counted within the transect strip. Elevation and aspect were recorded every 50 m along the transect strips.

In the mountains the transect design was adjusted to accommodate for the high number of crevices and the extreme rarity of all other noted microhabitats. Thus, a similar gradsect approach was employed, except both the rare and common microhabitats were sampled simultaneously, and only one aspect of the mountain was sampled per site. At each site, two surveyors walked 5 m apart for the duration of the transect. For the first 20 m of elevation, the first surveyor counted common microhabitats in a 1 m wide strip, whilst the second surveyor counted rare microhabitats between themself and the first surveyor. After 20 m of elevation had been reached, surveyors continued to search only for rare microhabitats in the 5 m wide strip in a straight line, up to the crest of the mountain. The number

of meters walked for each line was noted along with elevation to calculate the slope. A similar approach was taken along the crest, where surveyor one counted common microhabitats for the first 50 m, and both surveyors counted rare microhabitats for a further 50 m. Again, the same pattern was repeated with common microhabitats accounted for in the first 20 m decline in elevation during the descent, and rare microhabitats accounted for in a 5-m strip transect from the crest to the base of the mountain.

2.2.3 Microhabitat categorization

Sampled microhabitats were limited to the most common microhabitats likely to affect the persistence of birds, reptiles, and mammals in the Kalahari, namely, burrows, nests, rock crevices, vegetation cover and tree hollows. Each microhabitat type was categorized into broad size classes that represented sheltered thermal environments available to animals of a specific size range.

Burrows were categorized by entrance size only, into three broad categories, small (diameter of 30–100 mm), medium (diameter of 100–200 mm) and large (diameter of 300–1000 mm). Although internal burrow diameter and depth also affect the thermal environment within burrow microclimates (Whittington-Jones *et al.*, 2011), these variables are not feasible to measure on such a large scale as it would require burrow excavation or specialized imaging equipment (Strandburg-Peshkin *et al.*, 2019), and can rather be implied given the species of each burrow engineer. Small burrows were constructed by small rodents, medium burrows were constructed by Cape ground squirrels (*Xerus inauris*), springhares (*Pedetes capensis*) or meerkats (*Suricata suricatta*). Large burrows were classified as burrows constructed by aardvarks (*Orycteropus afer*), or existing burrows that had been enlarged by aardwolves (*Proteles cristatus*) or Cape porcupine (*Hystrix africaeaustralis*).

Vegetation-based microhabitats were categorized broadly into shrubs or trees. Low-growing plants, such as grasses or creepers were excluded from transect counts due to their abundant and wide-spreading growth forms, which would make the distinction of individual plants irrelevant. Shrubs were considered woody stemmed vegetation that had lateral growth beginning at a height of less than 1 m from the ground, that was more than 1 m wide at its widest point of lateral growth, and taller than 1 m in height from the ground. Trees were defined as any single-stemmed woody growth that had lateral foliage growth more than 1 m above the ground.

Crevice sizes were split into three broad categories based on entrance size and crevice depth that would be necessary to accommodate common crevice-using species. Small crevices were those utilized by skinks, and that had an entrance of approximately 10–40 mm wide and a depth of 100–150 mm. Medium crevices that could shelter slightly larger animals such as rock agama (*Agama atra*) or small mammals, such as Namaqua rock rats (*Aethomys namaquensis*), were classified as having an entrance width of 50–100 mm and depth of 150–300 mm. Large rock crevices were those that could be used by much larger animals, such as the red rock rabbits (*Pronolagus rupestris*) or ground pangolins (*Smutsia temminckii*), with an entrance diameter larger or equal to 200 mm, and depth larger than or equal to 400 mm.

Nest categories were limited to the most common bird species present at the study site that provide long-lasting nest structures made primarily from grasses, namely sociable weavers (*Philetairus socius*) and white-browed sparrow-weavers *(Plocepasser mahali*). Whereas tree hollows were split into two categories based on whether they were excavated for a nesting function or not, namely, biotic, or abiotic hollows. Abiotic tree hollows were considered as those that had been created by abiotic influences such as tree ageing or tree damage by weather conditions, as well as by the

incidental biotic influence of herbivory. Thus, the defining feature of an abiotic hollow was that it was not pre-emptively created for a sheltering or nesting function. Biotic tree hollows were those that had been created for nesting purposes by hollow–forming animals. Both abiotic and biotic hollows, as well as nests, had to have an entrance diameter larger than 3 cm, and a depth of more than 10 cm, to be counted.

2.2.4 Data analysis

For all habitat types, microhabitat count data were converted to density data by dividing the number of microhabitats found by the total area for each designated section along the transect line. How the aspects were divided differed per habitat type (see below). All data were analyzed and visualized via R (version 4.1.1) and R studio (R Core Team, 2021) software using the following packages: ggpubr (version 0.4.0; Kassambara, 2020), rstatix (version 0.7.0; Kassambara, 2021), DescTools (version 0.99.43; Signorell et al., 2021), gridExtra (version 2.3; Auguie, 2017), vcd (version 1.4.9; Meyer et al., 2021), Matrix (version 1.3.4; Bates and Maechler, 2021), lme4 (version 1.1.27.1; Bates et al., 2015), DHARMa (version 0.4.5; Hartig, 2022), ggplot2 (version 3.3.5; Wickham. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York, 2016.), stringr (version 1.4.0; Wickham, 2019), forcats (version 0.5.1; Wickham, 2021), tidyr (version 1.1.4; Wickham, 2021), readr (version 2.0.2; Wickham and Hester, 2021), dplyr (version 1.0.7; Wickham et al., 2021), car (version 3.0.11; Fox and Weisberg, 2019), carData (version 3.0.4; Fox, Weisberg and Price, 2020), MuMIn (version 1.43.17; Barton, 2020), tibble (version 3.1.5; Müller and Wickham, 2021), purrr (version 0.3.4; Henry and Wickham, 2020), performance (version 0.9.0; Lüdecke et al., 2021), report (version 0.5.1; Makowski et al., 2020), glmmTMB (version 1.1.3; Brooks et al., 2017), ggstatsplot (version 0.9.3; Patil, 2021), psych (version 2.2.5; Revelle, 2022), rcompanion (version 2.4.15; Mangiafico, 2022) and tidyverse (version 1.3.1; Wickham et al., 2019).

2.2.4.1 Dunes

Considering that the dunes run in a relative north-south direction, transect data were reduced to four simplified aspects, top, east, west, and valley. The top was considered as any flat region at the top of the dune between east or west descents, or any line walked along the dune crest. Valleys were considered as any area of lowest elevation along the transect line where multiple uninterrupted points were taken at the same elevation. East and west were any lines walked on an east-facing or west-facing dune, respectively. To reduce zero inflation in count data, for each 500 m transect line, each aspect group was clustered into one section, where the average elevation and maximum slope were calculated. The count data of microhabitats found per each of these sections were then converted to density data by dividing them by the total area of the 'aspect section'. This density was used to calculate the maximum and average densities of specific microhabitat types. Density differences were calculated using Kruskal Wallis and Dunn post hoc tests and Wilcoxon rank sum comparison tests.

To assess the relationship between specific microhabitat densities and slope or aspect, I used zero-inflated Poisson mixed models (estimated using ML and nlminb optimizer) on the original count data with transect area included as the offset term. Standardized parameters were estimated by fitting all models on a standardized version of the dataset. 95% Confidence Intervals (CIs) and p-values were computed using the Wald approximation. The likelihood of co-occurrence was assessed using Woolf and Cochran–Mantel–Haenszel (CMH) Tests, where microhabitats were compared in a pairwise fashion, with site used as a stratifying factor. Post-hoc analysis was performed using the groupwiseCMH function. Co-occurrence was only considered to be significant overall if co-occurrence was significant at 50% or more of the tested sites. Abiotic hollows and bird nests were excluded from both topographic association and co-occurrence analysis as their occurrences were too rare to infer any correlations.

2.2.4.2 Plains

Microhabitat density was calculated as the total number of microhabitats found along each 500 m line, which was then used to calculate the maximum and average densities of specific microhabitats within the plains. Density differences were calculated using Kruskal Wallis and Dunn post hoc tests and Wilcoxon rank sum comparison tests. There were minimal levels of slope in the plains area, and thus the plains area was not tested for associations between aspect, slope, and microhabitat density. The likelihood of co-occurrence was assessed using the same method as was done for the dune habitat. Biotic hollows were excluded from the co-occurrence analysis as their occurrences were too rare to infer any correlations.

2.2.4.3 Mountains

Aspects were categorized into the four cardinal points and the top ridges of the mountains were classified as ‘top’. The density of microhabitats per each aspect-based line was calculated by dividing the count data by the total area covered by the line. Significant differences in density were detected using Kruskal Wallis and Dunn post hoc tests. To evaluate the relationship between microhabitat density and aspect or slope, a combination of linear mixed effect and linear models were run for each microhabitat type, where slope and aspect were used as potential predictors (fixed effects), and site was classed as a random effect. Elevation was found to be correlated to site and thus was excluded from the models. All microhabitat types co-occurred at all sites within the mountain bushveld and thus co-occurrence could not be statistically tested.

2.3 Results

2.3.1 Microhabitat densities across an environmental gradient

Apart from small burrows and shrubs, estimates of all biotic microhabitats had the highest maximum and highest average densities in the plains.

Rock crevices were found only in the mountains, with medium crevices being the most common, followed by small crevices and then large crevices. Medium rock crevices also had the highest average density of all microhabitat types. Shrubs were most common in the mountains and were also the most abundant microhabitat with the highest average density across all habitat types. Tree hollows and bird nests were exceptionally rare and were widely dispersed within the dune and plain habitats. Biotic hollows were found to only exist in the plains, whereas abiotic hollows, sociable weaver nests and white-browed sparrow-weaver nests were found both in the plains and dunes (Table 2.1, Table 2.2). For those microhabitats that were found in the dunes and the plains, but were absent in the mountains, the density of all microhabitats, except small burrows, was significantly greater in the plains than in the dunes (Table 2.3). Shrub density was greater in the mountains than in the dunes (Fig.2.2; $p < 0.001$), and there was no difference in shrub density between the mountains and plains ($p > 0.05$). Tree density was greater in the dunes (Fig. 2.3; $p < 0.001$) and plains ($p < 0.001$) than in the mountains, and tree density was greater in the plains than in the dunes (Fig. 2.3; $p < 0.001$).

Table 2.1: The maximum densities of each microhabitat type per 100 m^2, across all habitat types.

Microhabitat:	SB	MB	LB	TR	SH	WB
Dunes	25.00	0.40	0.40	1.20	38.33	0.33
Plains	23.50	1.00	1.00	3.50	23.00	1.50
Mountain	NA	NA	NA	0.36	46.00	NA
Microhabitat:	**SW**	**AH**	**BH**	**SRC**	**MRC**	**LRC**
Dunes	0.10	0.30	NA	NA	NA	NA
Plains	0.50	1.50	0.02	NA	NA	NA
Mountain	NA	0.18	NA	40.00	70.15	22.39

Key: SB: Small burrow, MB: Medium burrow, LB: Large burrow, TR: Trees, SH: Shrubs, WB: White-browed sparrow-weaver nests, SW: Sociable weaver nests, AH: Abiotic Hollows, BH: Biotic hollows, SRC: Small rock crevice, MRC: Medium rock crevice, LRC: Large rock crevice, NA; Non-applicable (The microhabitat type did not exist in the specified habitat)

Table 2.2: Average density of each microhabitat type per 100m^2, across all habitat types.

Microhabitat:	SB	MB	LB	TR	SH	WB
Dunes	5.82	0.03	0.02	0.11	5.64	0.004
Plains	6.88	0.19	0.07	0.68	11.76	0.07
Mountain	NA	NA	NA	0.05	20.19	NA
Microhabitat:	**SW**	**AH**	**BH**	**SRC**	**MRC**	**LRC**
Dunes	0.002	0.01	NA	NA	NA	NA
Plains	0.04	0.08	0.003	NA	NA	NA
Mountain	NA	0.01	NA	14.24	24.46	4.95

Key: SB: Small burrow, MB: Medium burrow, LB: Large burrow, TR: Trees, SH: Shrubs, WB: White-browed sparrow-weaver nests, SW: Sociable weaver nests, AH: Abiotic Hollows, BH: Biotic hollows, SRC: Small rock crevice, MRC: Medium rock crevice, LRC: Large rock crevice, NA: Non-applicable (The microhabitat type did not exist in the specified habitat)

Table 2.3: Comparisons of microhabitat density between plain and dune habitats using Wilcoxon Rank sum tests.

Microhabitat	W	n	p
Small burrows	1447.5	168	>0.05
Medium burrows	2354	194	<0.001
Large burrows	3054	194	<0.05
Sociable weaver nests	3121	194	<0.001
Sparrow-weaver nests	3170.5	194	<0.05
Abiotic hollows	2082	194	<0.001

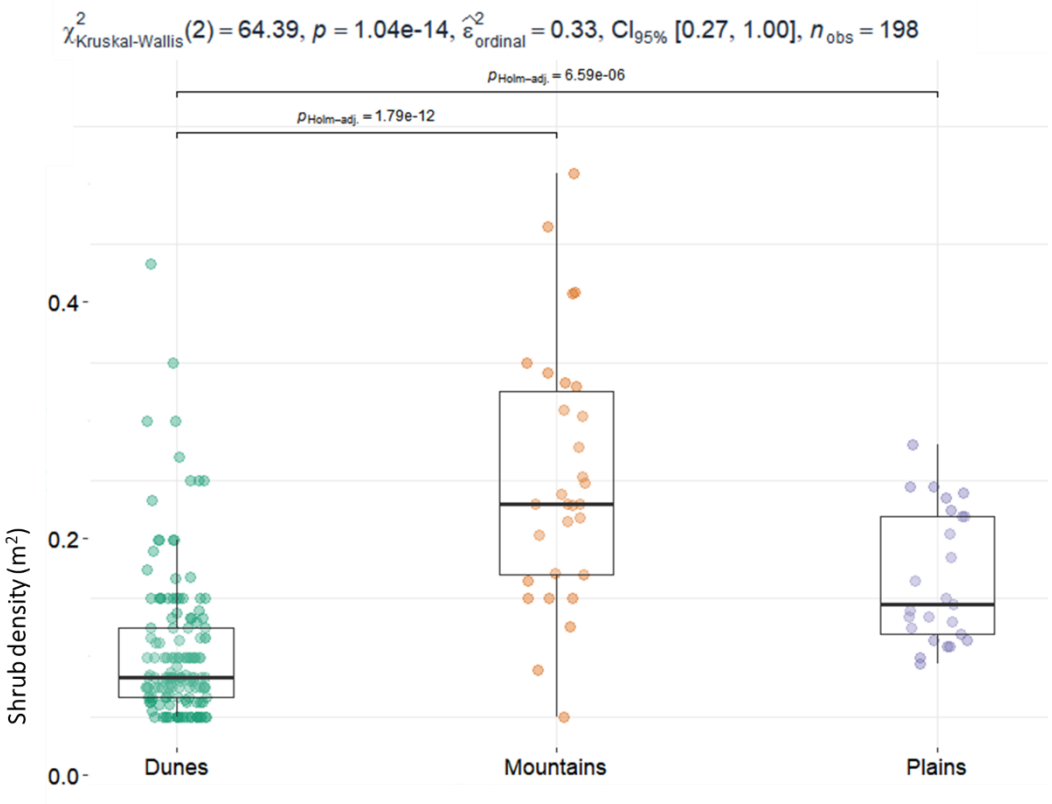

Figure 2.2 : Comparisons of shrub density between dune, mountain, and plain habitats. Coloured circles indicate the distribution of data points, and bars between boxes indicate a significant result in the Dunn post hoc test.

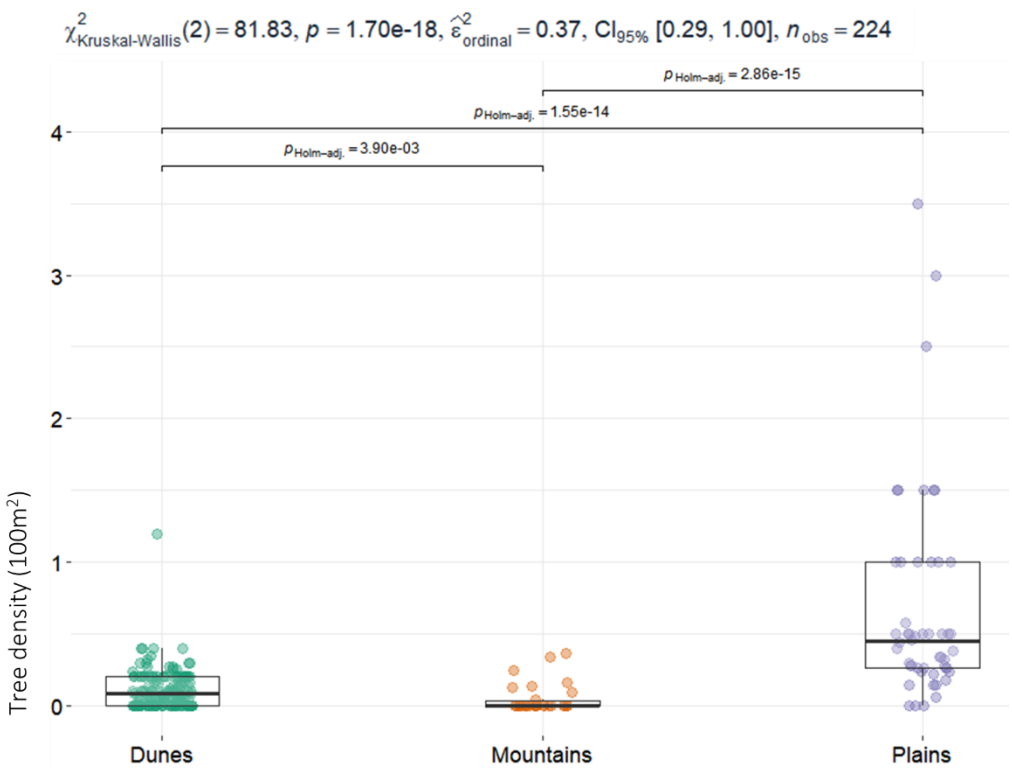

Figure 2.3 : Comparisons of tree density between plains, mountains, and dune habitats. Coloured circles indicate the distribution of data points, and bars between boxes indicate a significant result in the Dunn post hoc test.

2.3.2 Topographic influences on microhabitat densities in the dune and mountain habitats

Only shrubs and rock crevices within the mountains showed a significant association with topographic influences (Figs 2.4a, b and c, Appendix Table A2.1). Slope was significantly and positively associated with shrub density, where every one degree increase in slope was associated with a 0.006 increase in shrub density per m^{-2} ($p < 0.05$). Both slope and the northern aspect were significantly associated with an increase in large rock crevices. An increase in one degree slope was associated with a 0.005 increase in large crevice density per m^{-2} ($p < 0.05$), while a one-unit increase in northern aspect points was associated with a 0.07 increase in large rock crevice density per m^{-2} ($p < 0.05$). Medium rock crevices were also significantly associated with slope, where a one degree increase in slope was associated with an 0.009 increase in medium rock crevice

density per m^{-2} ($p < 0.05$). Small rock crevices showed no significant association with topographic factors. Furthermore, within the dune habitat, no microhabitats demonstrated a significant association with topographic factors (Table A2.2).

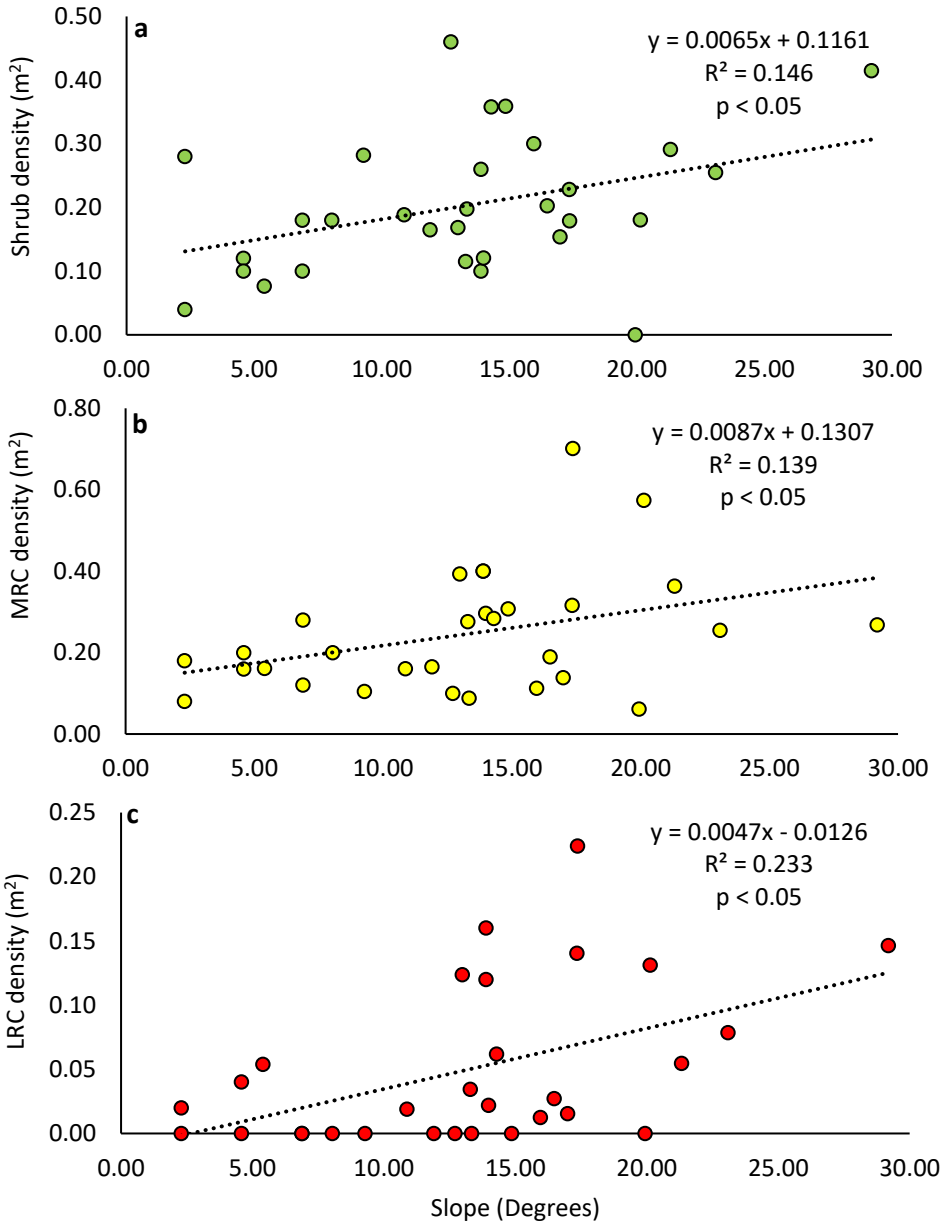

Figure 2.4 (a–c): Linear relationships between mountain microhabitats and slope (a. Shrubs, b. Large rock crevices (LRC), c. Medium rock crevices (MRC)). The dotted lines indicate the linear regression, with the line formula, coefficient of determination and p-value provided.

2.3.2 Likelihood of microhabitat co-occurrence in the dunes and plains habitats

Large burrows showed patterns of co-occurrence with trees, shrubs, and small burrows in the dune habitat (Table 2.4). Whereas, within the plains, trees showed significant patterns of co-occurrence with both forms of bird nests and large burrows, and medium burrows were significantly more likely to co-occur with sociable weaver nests (Table 2.5).

Table 2.4: Co-occurrence between dune microhabitats, assessed using Cochran–Mantel–Haenszel (CMH) tests. Highlighted rows are 'environmentally significant associations' if microhabitats were found to have significant co-occurrence in more than 50% of all tested sites.

Microhabitat co-occurrence	χ2	n	p	Number of sites of significant co-occurrence
SB–SH	0.08	573	>0.05	0
SB–MB	33.83	574	<0.001	2
SB–-LB	83.38	574	<0.001	8
SB–-TR	1.87	575	>0.05	0
MB–-SH	38.30	574	<0.001	1
MB–-LB	13.01	575	<0.001	2
MB–-TR	19.66	575	<0.001	1
LB–-SH	89.53	574	<0.001	8
LB–-TR	62.03	575	<0.001	7
SH–-TR	3.03	574	>0.05	0

Key: SB: Small burrow, MB: Medium burrow, LB: Large burrow, TR: Trees, SH: Shrubs

Table 2.5: Co-occurrence between plains microhabitats, assessed using Cochran-Mantel-Haenszel (CMH) tests. Highlighted rows are 'environmentally significant associations' if microhabitats were found to have significant co-occurrence in more than 50% of all tested sites.

Microhabitat co-occurrence	χ^2	n	p	Number of sites of significant co-occurrence
SB–-SH	0	101	>0.05	0
SB–-MB	2.50	101	>0.05	0
SB–-LB	2.02	101	>0.05	0
SB–-TR	22.48	101	<0.001	2
SB–-WB	11.55	101	<0.001	2
SB–-SW	10.08	101	<0.05	2
SB–-AH	0	101	>0.05	0
MB–-LB	10.20	101	<0.05	1
MB–-SH	1.92	101	>0.05	0
MB–-TR	10.29	101	<0.05	0
MB–-WB	25.82	101	<0.001	2
MB–-SW	23.54	101	<0.001	3
MB–-AH	3.14	101	>0.05	0
LB–-SH	2.62	101	>0.05	0
LB–-TR	39.68	101	<0.001	4
LB–-SW	2.82	101	>0.05	0
LB–-WB	3.69	101	>0.05	0
LB–-AH	1.50	101	>0.05	0
TR–-WB	60.46	101	<0.001	5
TR–-SH	20.95	101	<0.001	2
TR–-SW	58.50	101	<0.001	5
TR–-AH	24.28	101	<0.001	2
SW–-WB	0	101	>0.05	0
SW–-AH	9.24	101	<0.05	0
WB–-AH	10.58	101	<0.05	1
SH–-AH	0.038	101	>0.05	0
SH–-SW	11.45	101	<0.001	1
SH–-WB	12.95	101	<0.001	1

Key: SB: Small burrow, MB: Medium burrow, LB: Large burrow, TR: Trees, SH: Shrubs, WB: White-browed sparrow-weaver nests, SW: Sociable Weaver nests, AH: Abiotic Hollows.

2.4 Discussion

Habitat type influenced the distribution and prevalence of different microhabitats. All biotic microhabitats were more abundant in the plains than in the dune habitat, although bird nests and tree hollows were relatively rare across both. The plains had a relatively even distribution of vegetation microhabitats, with far greater densities of trees and shrubs found in the plains than in the dunes. The high density of trees in the plains is likely to have led to the higher densities of tree-associated microhabitats (nests and hollows) found in the plains than in the other tested habitats. Large burrows and trees were the only two microhabitat types with significant levels of co-occurrence across both the plain and dune habitats. Microhabitats within the dunes had a highly patchy distribution making density estimates far more difficult to quantify. Most dune crests and interdunes had more grass cover and small shrubs than the dune faces, although some sites were rich in large shrubby vegetation, potentially due to bush encroachment in disturbed soils. Nevertheless, the dune habitat had the lowest average densities of all microhabitat types, which could be due to the patchiness of resources in the habitat.

The mountain habitat had fewer microhabitat types than the plains or dunes, yet shrubs and rock crevices existed at far greater densities in the mountain than any of the other microhabitat types within the dunes or plains. Shrubs were found to be the most abundant microhabitat across all three habitats and existed at all mountain sites along with rock crevices. Trees were found only within a few isolated sites in the mountains. However, regardless of microhabitat prevalence, all microhabitat types in the mountains were found to co-occur together within the same sites. Slope was found to affect the density of all shrubs and crevices, and aspect affected large crevice prevalence. Thus, the mountain habitat was the only habitat in which topographic factors significantly affected microhabitat densities.

2.4.1 Microhabitat abundance across an environmental gradient

Biotic microhabitat occurrence increased from the dunes to the plains but decreased in the mountain habitat. Shrubs are a characteristic part of the vegetation types on the reserve, thus I hypothesized that they would be the most abundant microhabitat type found across all habitats. This prediction was in line with my findings, with a similarly high density of shrubs found in both the mountain and plains areas. Such high levels of shrub density could be suggestive of expanding bush encroachment, which was noted as a potential problem in only the mountainous areas of the reserve in a 2017 ecological evaluation (van Rooyen and van Rooyen, 2017). Further, I predicted that only vegetation-based microhabitats (vegetation, bird nests and tree hollows) would be the most prevalent in the plains, yet apart from small burrows, all biotic microhabitats had significantly higher densities in the plains than in the dunes. However, this proliferation of biotic microhabitats in the plains may be due to existing gradients in vegetation types.

There is a gradient in the abundance of woody plants from west to east in the reserve where the dune vegetation is typified by grasses and low shrubs, and the more deeply rooted vegetation such as trees and large shrubs are associated with the mountain and plains areas (Tokura *et al.*, 2018). Thus, since grasses were not counted in microhabitat transects, areas with more woody growth would appear to have a greater abundance of microhabitats. Burrows may also be more likely to be found in the plains area due to the prevailing soil types, which affect the longevity of the burrows. The plains area consists of clayey, deep soils (van Rooyen and van Rooyen, 2017), which allows burrows to remain intact for longer than those dug in the dune sand, making them more likely to be found in transects (W. Panaino, pers comm). The shallow soils of the mountain areas (van Rooyen and van Rooyen, 2017) may prevent inhabitation by woody vegetation and burrowing animals, thus excluding the majority of the biotic microhabitats from occurring within these areas. There is also

more permanent water found within the plains and mountain-valley areas than in the dunes of the reserve. Thus, animals such as birds and burrow-digging species may be more likely to colonize areas within the plains. Therefore, the gradient of biotic microhabitats in the reserve appears to potentially be based on water resources and soil properties.

2.4.2 Topographic influences

Gradients in soil nutrients and water levels are both affected by topography, and topography has been found to be an important driver of microclimatic abundance (Pepin and Lundquist, 2008; Daly *et al*., 2010; Dobrowski, 2011; Aalto *et al.*, 2017; Massimino *et al.*, 2020). I predicted that topography would have a significant effect on the density of all microhabitats in the dunes and mountains. However, only mountain microhabitats were significantly predicted by topographical factors. Dune microhabitats were on less steep inclines and showed no significant association with topography, which may suggest that the impact of topographic factors on microhabitat abundance depends on the steepness or overall height of the structure. This result is in agreement with Dobrowski (2011), who suggested that the effects of slope or aspect on microclimates may be influenced by the level of elevation. Thus, gradual slopes at low elevations may not experience extreme enough differences at different altitudes or aspects for the effect on microhabitats to be statistically visible.

Within the mountain habitat I anticipated that the southern mountain slopes would have a greater abundance of shrubs and lower densities of rock crevices, as south-facing slopes should remain cooler and retain more moisture than the northern slopes if in the southern hemisphere (Macyk *et al.*, 1978; Aalto *et al.*, 2017). Yet only the north-facing aspects were significantly associated with higher densities of large rock crevices and higher levels of slope were associated with increased densities of large and medium rock crevices and shrubs. Given that both slope and

aspect play a crucial role in water balance due to their effects on radiation, wind exposure (McVicar *et al.*, 2007; Dobrowski, 2011) and water run-off, the steeper and more exposed to radiation the slope is, the drier it may be. Thus, on drier slopes, it could be probable that rock piles accumulate, as wetter slopes would cause the rocks to slide more readily (Crosta *et al.*, 2017). Where rocks accumulate, shrubs may have more area or soil in which to settle, as rocks have been shown to provide localised increases in soil moisture and protection from strong winds (García *et al.*, 2020; van der Westhuizen *et al*., 2021). Nevertheless, there are likely limits to this effect, as steeper slopes may also deter the settlement of soil, vegetation, or rocks.

2.4.3 Interactions between biotic and abiotic influence

Tree hollow densities may be determined by complex interactions between abiotic and biotic influences. Tree hollows in savanna ecosystems are generally formed by fire (Woolley *et al.*, 2018), termites (N'Dri *et al.*, 2011) or cavity forming birds, such as woodpeckers (Kotowska *et al.*, 2020; Piechnik *et al.*, 2022). Higher densities of abiotic hollows were found in the plains than in the dunes, and biotic hollows were only found in the plains. This clumped distribution of hollows could either be following the gradient of woody growth, fire prevalence or termite and cavity-nesting bird populations. Abiotic microhabitats in this study were considered 'abiotic' if they were the result of weathering, fire, or herbivory, as opposed to specifically selected for nest cavity creation. Thus, although labelled 'abiotic', their origin still has a potential biotic influence. The wood-eating termites on the reserve have not been studied for the plains area, and fires are rare within the reserve (Tokura *et al.*, 2018), but have occurred across all habitat types (D. Smith, pers. comm.). Thus, the higher abundance of larger, and potentially older trees in the plains may have led to a greater likelihood of all hollows, regardless of potential fire, bird, or termite activity.

Biotic hollows are formed primarily by birds and are thus the result of biotic community interactions. There are two species of woodpeckers on the reserve, the golden-tailed woodpecker (*Campethera abingoni*), and the cardinal woodpecker (*Dendropicos fuscescens*), both of which rely on woodland habitat and are strictly arboreal (Chittenden *et al.*, 2018). Given the small number of species available to make biotic hollows, their isolated existence in the plains seems plausible, as woodpecker species may rely on the abundance of woody growth in the plains area (Tokura *et al.*, 2018) and may remain deterred from the dunes given the rarity of trees. Thus, I suggest that hollows of both kinds are likely to be associated with woody growth, which is associated with deep soils and abundant water sources. The split between abiotic and biotic hollows is determined by either the presence of wood-boring animals or fire. Therefore, tree hollow abundance is based on a concomitant combination of abiotic and biotic influences.

2.4.4 Implications of microhabitat co-occurrence

Shared resources may blur the division between abiotic and biotic associations as biotic microhabitat 'hotspots' will exist due to shared resources rather than a direct ecological or topographic association. The abundance of certain biotic microhabitats appeared to be correlated in several instances. Trees were found to co-occur with both kinds of bird nests, which is plausible given that white-browed sparrow-weaver and sociable weaver nests could not exist without the presence of trees. However, less clearly associated, large burrows were found to co-occur with trees in the plains and all types of vegetation (trees and shrubs) in the dunes. It is unlikely that there is a causal link for this association between burrows and woody growth forms, and thus it may be explained by soil type, as the prevalence of woody growth is associated with clay-based soils, where burrows are also more likely to persist over time. Nevertheless, this co-occurrence of burrows and trees based on soil type,

exemplifies how shared abiotic resources may also affect the distribution of biotic microhabitats.

Furthermore, although the lack of a direct and positive ecological association between burrows and vegetation is supported by a recent study (Louw *et al*., 2019), there is no known literature on the associations between burrows and other animal-engineered biotic microhabitats. In my study, medium burrows were also found to co-occur with sociable weaver nests in the plains area. Sociable weaver nests have been shown to increase terrestrial species richness locally around their host trees (Lowney and Thomson, 2021), which, while not yet documented, could potentially also relate to burrowing species. There is a documented increase in invertebrates within (Rymer *et al*., 2014; Harvey *et al.*, 2015) and around the nests, which may benefit species such as mongoose and meerkats through an increase in prey resources. Thus, more research should potentially be aimed at assessing common resource hotspots for ecosystem engineers, which could lead to 'hotspot' areas with increased biotic microhabitat abundance.

2.4.5 Considerations for conservation management

I found that most biotic microhabitats occurred at lower densities than abiotic microhabitats and may even have occurred at lower densities than I originally predicted. Misestimation of population density is likely to occur if populations have a clumped distribution, and if individuals are rare (Nomani *et al*., 2012). Biotic microhabitats, by nature, are likely to have a clumped distribution, either because they are clumped around a specific area, such as vegetation around water, or because the engineering species exist only in specific areas due to food availability. Thus, although I attempted to account for this effect by using multiple short transects (Nomani *et al.*, 2012), given the rarity of certain types of microhabitats such as hollows or bird nests, the already low densities of biotic

microhabitats found in this study may still be a misrepresentation of their true abundance.

Randomly distributed populations where individuals are common, such as the abiotic rock crevices in the mountains, are far more likely to be accurately estimated (Nomani *et al.*, 2012). Therefore, while the plains area had a greater variety of types of microhabitat present, mountainous areas in this region may represent a larger and more stable population of microhabitats in the future. Rock crevices have been shown to act as microrefugia to relict plant species in the past (García *et al.*, 2020), whereas biotic microhabitats tend to be less predictable and more variable over short spatial and temporal scales, due to their reliance on interactions between the abiotic and biotic environment (Woods, Dillon and Pincebourde, 2015). Therefore, although the microrefugia potential of biotic microhabitats should not be ignored, as even rare microhabitats can still be thermally highly valuable (Chapter 3), considering that the Kalahari is likely to experience further aridification in the future (Engelbrecht *et al.*, 2015; Mirzabaev *et al.*, 2019), abiotic microhabitats, such as rock crevices, should be highlighted as a potential microrefugial resource to explore.

Climatic microrefugia are shelters that provide uniquely buffered microclimates over generational time scales (Dobrowski, 2011; Hannah *et al.*, 2014), which are thought to have potential in reducing the impact of climate change associated loss of species (Rull, 2009; Keppel and Wardell-Johnson, 2012; Keppel *et al.*, 2012; Lenoir *et al.*, 2017). Yet, the characterization of potential refugia and their ecological drivers has only recently been assessed in an empirical rather than theoretical manner (Greiser *et al.*, 2020). The lack of empirical data on the subject may be due to the complexity of identifying and characterising microrefugia *in situ*, as this requires collecting a combination of species occurrence data, microclimatic data, and topographic data over inordinately extended periods. Therefore, studies such as mine may provide a more practical

way of assessing the potential drivers of microrefugia by using microhabitats as a proxy. Without a long-term assessment of thermal buffering capacity, we could still assume if similar drivers are repeatedly found for diverse microhabitat types, that those same drivers will likely be important in identifying microrefugia.

2.4.6 Future research

This study, assessing the underlying factors impacting the distribution and prevalence of multiple, defined, microhabitats in an arid area, is one of the first of its kind. The majority of microhabitat or microclimate focused literature tends toward emphasizing either the thermal buffering capacity of microhabitats (Whittington-Jones *et al.*, 2011; Scheffers, Edwards, *et al.*, 2014; Lowney *et al.*, 2020) or species distribution based on microhabitat use (Choi *et al.*, 2020; Rice *et al.*, 2020; Richard *et al.*, 2022). Only a few authors have assessed associations of topographic indices with specific topoclimates or microclimates (Egli *et al.*, 2015; Aalto *et al.*, 2017; Massimino *et al.*, 2020), and even fewer have attempted to disentangle the abiotic and biotic drivers of specific microclimates (Greiser *et al.*, 2020; De Frenne *et al.*, 2021). Thus, developing a novel methodology that allowed the assessment of the biotic and abiotic basis of so many microhabitats was challenging. Much of my resultant data was zero-inflated, making analysis and result interpretation difficult, especially in areas where microhabitats occurred in sparse clusters, such as in the dune habitat.

Sparsity of microhabitats is highly likely to occur in many arid areas, as water resources will be patchily distributed, making any biotically influenced microhabitats also likely to occur in clusters. Given the projections of increasing aridity for many African countries (Engelbrecht *et al.*, 2015; Mirzabaev *et al.*, 2019), this study highlights just how rare microhabitats may be in the future, and how important and challenging it may be to know where these microhabitat ‘hotspots’ are for both animals

and conservationists. As it stands, some arid-adapted animals such as Cape cobras within the reserve, are known to utilise the same specific burrow microhabitats over extended periods (T. Beck, pers. comm.), presumably due to the value of high-quality thermal shelter in an otherwise sparse environment. Therefore, the results of this study, by showing the relative densities of microhabitats, can also provide insight into how animals may choose to shuttle throughout their environment, based on what shelter is available.

The data generated in my study have provided a baseline measure of the abundance of potential microhabitats, and their abiotic and biotic drivers, that shape arid ecosystems. This type of intensive assessment provides an idealistic protocol for conservation assessments as it is intensely time-consuming and not well fitted to clustered 'populations' of microhabitats. However, this work could give future assessments a reference on which to base their search for more specified thermally valuable microhabitats. Additionally, more insightful coverage of microhabitat types and habitats may provide a better resolution on the distribution and abundance of the targeted microhabitats and clearer data signals of their underlying drivers. For example, a more intensive sampling effort around the bases of mountains could reveal how the steepness of the mountain may be associated with vegetation-dependent microhabitat prevalence in valleys. Similarly, an assessment of the associations between biotic microhabitats and abiotic gradients, such as soil type and fire prevalence in flat areas could contribute to data on the formation of microhabitats in absence of topographic heterogeneity. Although this study did not manage to disentangle clear drivers of microhabitat abundance gradients, it has provided clarification on how to better evaluate microhabitat gradients in arid areas in the future.

2.4.7 Conclusions

The results of this study have provided evidence that microhabitat abundance differs according to microhabitat type, and across environmental and topographic gradients within a localized arid area. These data support the notion that climate varies on a localized scale (Ashcroft *et al*., 2009), and reinforces the importance of improving the resolution of course-grained temperature maps used in habitat suitability assessments (Varner and Dearing, 2014; Lembrechts *et al*., 2019; Lembrechts and Lenoir, 2020; Maclean, 2020), as high microhabitat variance represents high thermal heterogeneity. Furthermore, data from the plains area validated the idea that climatic variation will still exist even in areas of flat terrain due to the abundance of vegetation-based microclimates (Lenoir *et al.*, 2013; Milling *et al.*, 2018). Thus, although potential microrefugia for future climate change are commonly associated with topographic variation (Dobrowski, 2011), these data have highlighted that microhabitat abundance within savanna areas may exist as a result of a relationship between biotic communities and abiotic forces such as lowland topography, soil characteristics and fire prevalence. These data can be used to prioritize specific areas that are likely to be rich in microhabitats, which may assist in finding microrefugia and protecting climatically buffered areas for the future.

Chapter 3 : Variance in Kalahari microhabitats' thermal buffering across temporal and spatial scales

3.1 Introduction:

The climate of a region shapes the physiological adaptations and geographical distribution of the animals that inhabit it (Scheffers, Evans, *et al.*, 2014; Bramer *et al.*, 2018). Thus, when physiological adaptation cannot match the pace of climate change, species redistribution is expected to occur (Chen *et al.*, 2011; Dawson *et al.*, 2011; Scheffers *et al.*, 2016). Yet, numerous studies are finding that many terrestrial species are shifting less than originally predicted (Forero-medina *et al.*, 2011; Sunday *et al.*, 2012; Frenne *et al.*, 2013; Scheffers, Edwards, *et al.*, 2014). The survival of populations without redistribution may arise in part from the disparity between the resolution of the climate data that is used for species distribution modelling and the scale of space use by animals (Scheffers, Evans, *et al.*, 2014). Individual animals will often select thermally buffered areas if they are present, and rarely experience the average temperatures of the area (Storlie *et al.*, 2014; Neel *et al.*, 2021). This disparity highlights the need for greater consideration of both behavioural thermoregulation and availability of microclimates, yet localised habitat or microclimatic data are rarely considered in species vulnerability or habitat suitability assessments (Suggitt *et al.*, 2011; Storlie *et al.*, 2014; Varner and Dearing, 2014).

Most species distribution assessments rely on macroclimatic data that is sourced from weather stations which provide general atmospheric conditions (Anderson *et al.*, 2021) or Global Climate Models (GCMs) which provide climatic projections (Ashcroft *et al.*, 2009; Dawson *et al.*, 2011; Dobrowski, 2011; Jones *et al.*, 2016; Lembrechts *et al.,* 2019). However, the resolution of these datasets may not be biologically relevant as they are often thousands of folds more coarse than the species' space use under question (Potter *et al.*, 2013) and the variables that are used as predictors, such as air temperature, are poor predictors of physiological responses (Mitchell *et al.*, 2018; Anderson *et al.*, 2021). Additionally, large-scale models do not take into account behavioural adjustments of

organisms (Storlie *et al.*, 2014; Neel *et al.*, 2021), or seasonal temperature variability (Ashcroft *et al.,* 2009). Most animals use behavioural thermoregulation as a primary response to adapt to novel thermal changes (Huey, Hertz and Sinervo, 2003; Fuller *et al.*, 2016; Neel *et al.*, 2021). Thus, an evaluation of the availability and thermal buffering capacity of microhabitats within their environment could provide a proxy of how much animals may be able to buffer climatic changes.

Microhabitats have been shown repeatedly to provide thermal refuge against macroclimatic extremes (Scheffers, Edwards, *et al.*, 2014; Scheffers, Evans, *et al.*, 2014; Suggitt *et al.*, 2018; Riddell *et al.*, 2021). Yet not all microhabitats provide equal levels of thermal buffering, as some microclimates track the macroclimate, whilst others become thermally decoupled from the macroclimate (De Frenne *et al.*, 2021). These differences in microclimatic qualities are thought to be impacted by topography (Ashcroft *et al.,* 2008; Daly *et al.*, 2010; Aalto *et al.*, 2017), temporal effects, and microhabitat density (De Frenne *et al.*, 2019, 2021). However, the specific relationships between season, diel differences, topographic features, level of microhabitat prevalence and the potential for thermal buffering have yet to be assessed for microclimates in dryland environments.

Projections indicate that drylands will continue to get hotter and drier in future decades (Engelbrecht *et al.*, 2015; Huang *et al.*, 2017; Mirzabaev *et al.*, 2019), which suggests that dryland animals are facing a future of reduced water and food availability (Fuller *et al.*, 2021). Consequently, such animals are likely to be heavily reliant on modifying behaviour to cope with these conditions (Fuller *et al.*, 2016). Access to suitable microhabitats is likely to improve the physiological welfare of individuals and thus may allow for the survival of populations even under harsh conditions (Fuller *et al.*, 2021; Riddell *et al.*, 2021). Therefore, it is crucial

to evaluate the drivers of microclimatic variability within dryland areas, to identify which microhabitats provide the most thermally stable conditions.

Although dryland animals exist within the same landscape, they experience it individualistically according to their specific physiology, morphology, and size (Potter *et al.*, 2013; Woods *et al.*, 2015; Mitchell *et al.*, 2018). Thus, even if many types of microhabitats are available within the environment, not all animals will be able to access all of them. Restricted access to microhabitats is associated with a higher risk of extreme climate exposure, which is likely to increase the vulnerability of some species to climate change (Fuller *et al.*, 2016; Riddell *et al.*, 2021). Thus, it is necessary to assess the thermal buffering capacity of a diversity of microhabitats across numerous habitat types to evaluate if certain animals, which can only access some of the suites of available microhabitats, may become thermally constrained.

It is frequently suggested that microclimatic data need to be included in species vulnerability assessments to predict the future impacts of climate change (Suggitt *et al.*, 2011; Gillingham *et al.*, 2012; Potter *et al.*, 2013; Varner and Dearing, 2014; Keppel *et al.*, 2017; Lembrechts and Lenoir, 2020; Neel *et al.*, 2021), yet the data needed to achieve this aim remain scarce. Thus, by evaluating the microclimatic thermal landscape, I aimed to provide insight into what thermal gradients are available to facilitate or impair heat loss, allowing animals to survive in arid conditions. In this chapter, I measured the thermal profiles of five microhabitats (rock crevices, bird nests, burrows, tree hollows and vegetation cover) across three habitat types within the Kalahari over a year-long period, to assess their thermal buffering value. I assessed the thermal buffering capacity of each type of microhabitat, and quantified temporal differences in thermal buffering capacity, over the diel cycle and across seasons. I also evaluated the impact of position, aspect, season, and habitat type on thermal buffering for each microhabitat. I predicted, 1) that, as suggested

by the literature (Anderson and Richardson, 2005; Whittington-Jones *et al.*, 2011; García *et al.*, 2020; van der Westhuizen *et al.*, 2021), burrows and rock crevices will be the most thermally buffered microhabitats in the landscape, 2) that buffering capacity differs between day and night and across seasons, but all microhabitats will be more buffered during the rainy seasons as a consequence of vegetation greening and greater soil water content, 3) that there are differences in overall buffering capacity per habitat due to differences in microhabitat composition, 4) that ground level and subsurface microhabitats are more buffered than those above ground, and 5) that the magnitude of the effect of aspect on microhabitat buffering will vary according to season.

3.2 Materials and methods

3.2.1. Study site

The study site was located at the Tswalu Kalahari Reserve (See Chapter 2, Fig. 2.1), which is a semi-arid savanna, experiencing variable rainfall which occurs primarily in the summer months (November to March) (Tokura *et al*., 2018). The wettest months of the year are December and January, with approximately 65 mm of rainfall per month (van Rooyen and van Rooyen, 2017). June and August are the driest months, with an average of only 5 mm of rainfall per month (van Rooyen and van Rooyen, 2017). The mean annual rainfall for Tswalu is 175–595 mm per year (van Rooyen and van Rooyen, 2017), although the region has experienced many years of highly variable rainfall, with multiple years of drought (Weyer, 2018). Nonetheless, heavy rainfall occurred throughout the reserve in 2020 and 2021, with a mean annual rainfall of 567 mm reported for June 2020 to June 2022 (D. Smith, pers. comm.). However, the mean potential evaporation for the region is between 2755–2875 mm per annum, which far exceeds the amount of annual precipitation, even in the wettest years (van Rooyen and van Rooyen, 2017). The average annual temperatures range from 16.8–18.2 °C, with an extreme maximum of 42.5

°C in summer, and an extreme minimum of -6.6 °C in winter (van Rooyen and van Rooyen, 2017).

3.2.2. Microhabitat categorization

The most common microhabitats likely to affect the distribution and persistence of birds, reptiles, and mammals in the Kalahari were sampled. These were burrows, bird nests, rock crevices, vegetation cover and tree hollows. Each microhabitat type was categorized into broad size classes that represented sheltered thermal environments available to animals of specific body sizes (Table 3.1; Chapter 2).

3.2.3. Microhabitat site selection

Six sites were selected, two sites in the dunes (one dune, west and east aspects), two sites in the mountains (one mountain, west and east aspects) and two sites in the plains (two separate sites). At each site, one set of temperature loggers was deployed into one representative of each size and type of microhabitat available within that habitat type (Table 3.1). Within the dunes and mountains, temperature loggers were deployed into microhabitats that were on areas of steepest slope to highlight the effects of aspect on the thermal buffering capacity of microclimates. Two loggers maximally exposed to solar radiation were placed within 500 m of the microhabitat loggers at each site as unbuffered comparisons (See ‘Macroclimate temperatures’ at 3.2.5.6). A total of 96 temperature loggers were used for the duration of the study.

Table 3.1: Microhabitat type classifications

Microhabitat	Size classes	Specifications	Habitat type
Vegetation cover	Ground cover	Low-growing grasses and creepers	All
	Shrubs	Woody stem, lateral growth below 1000 mm	All
	Trees	Woody stem, lateral growth above 1000 mm	Plains and dunes
Bird nests	White-browed sparrow-weaver	Species-specific nest	Plains and dunes
	Sociable weaver	Species-specific nest	Plains and dunes
Tree-hollows	Biotic	Formed by a cavity-nesting animal	Plains
	Abiotic	Formed by weathering (via ageing, climate, or herbivory)	Plains and dunes
Burrows	Small	Small rodent burrow (30–100 mm)	Plains and dunes
	Medium	Squirrel or Meerkat burrow (100–200 mm)	Plains and dunes
	Large	Aardvark burrow or larger (300–1000 mm)	Plains and dunes
Rock crevices	Small	10 x 100 mm to 30 x 150 mm	Mountains
	Medium	50 x 150 mm to 100 x 300 mm	Mountains
	Large	200 x 400 mm or larger	Mountains

3.2.4 Assembly of miniature black globe loggers

Miniature (30 mm diameter) black globes were used for temperature measurements to provide an integrated measure of air temperature, wind speed and radiation (Hetem *et al.*, 2007) in the selected microhabitats. Each globe consisted of an outer copper sphere (Press Spinning & Stamping Co (Pty) Ltd, Cape Town, South Africa), with a temperature data logger (Maxim ibutton - DS1922L-F5# Hi-Res, Fairbridge Technologies, Sandton, South Africa) placed in the middle. Copper hemispheres were first spray-painted matt black ('Rust-Oleum: Paint+Primer', Flat black) before a temperature logger was placed on a blob of silicon at the side of one of the hemispheres. (Fig. 3.1a). A 300 mm length of nylon fishing gut was then fixed to the opposite side of the other hemisphere, and the two hemispheres were then sealed together using black silicon (Fig. 3.1b). For burrow microhabitats, where the logger was inserted deep enough such that it would not be affected by wind or solar radiation (that is, dry-bulb temperature would be equal to black globe temperature), a miniature black globe was not used. Instead, the temperature loggers were secured in fobs (iButton fob holders, Fairbridge Technologies, Sandton, South Africa), and attached to either 1.5 m of pliable wire for small burrows, or 2.5 m of semi-rigid wire for medium and large burrows. The same thermal loggers used in burrows were also used in rock crevices, as small and medium crevices were too narrow to accommodate the miniature black globes. Although large rock crevices were spacious enough to hold miniature globes, the same loggers on fobs were used as in the rest of the crevices, to reduce confounding factors in differences between crevice temperatures.

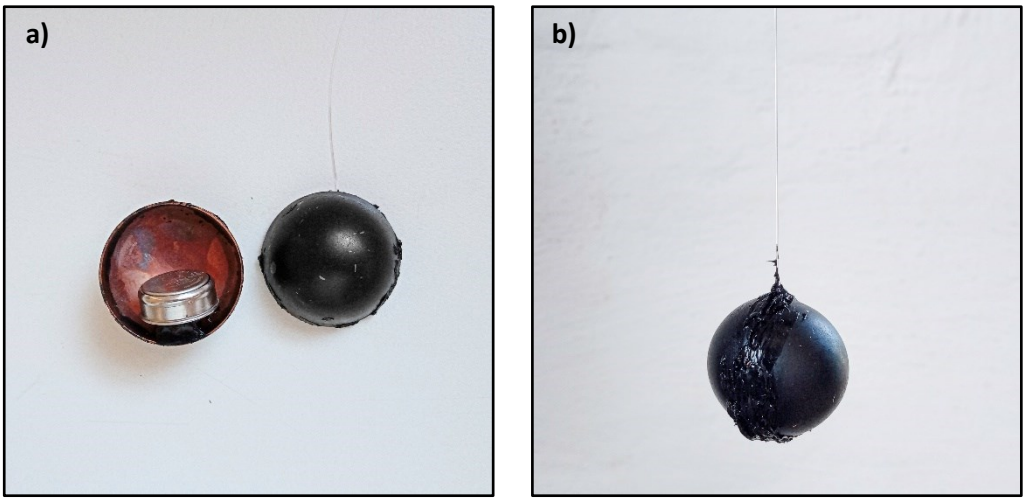

Figure 3.1: a) The inside of a mini black globe during construction, and b) The finished mini black globe once sealed with silicone.

3.2.5 Logger placement and collection

The habitat type, time, date, aspect, and GPS co-ordinate of every logger was taken each time a logger was placed in a microhabitat. Loggers were checked every ten days to ensure that they had not been removed or disturbed by wildlife. If they were found to have been adjusted or removed from the microhabitat, the adjustment was corrected, and the date and time were noted so that data collected during that period could be omitted. Loggers were collected for data download and redeployment every two months.

3.2.5.1 Vegetation

The buffering capacity of vegetation differs according to canopy density, size and height (Jankju, 2013; Scheffers, Edwards, *et al.*, 2014), and thus the thermal environments of each size category of vegetation (Table 3.1) were measured and compared. One thermal logger was used for ground-cover vegetation (low-growing grasses and creepers) at the soil/vegetation interface. Loggers were tethered with nylon fishing gut to a tent peg which was pushed into the ground under the vegetation so that the logger was touching the ground at its base while being sheltered by the vegetation

above (Figure A3.1). Two thermal loggers were placed in shrubs, one in the centre at the soil interface, and another within the densest area of foliage. Shrub base loggers were attached and placed in the same way as ground cover loggers, with the logger placed as centrally as possible at the base of the shrub. Shrub canopy loggers were tied to a branch in the central canopy of the shrub, ensuring that approximately 50% of the shrub foliage was above the logger (Figure A3.2). For trees, one thermometer was placed at the base of the trunk, one at a meter above ground (tree 'Middle' loggers), and another placed in a dense portion of the canopy (Figure A3.3). Tree base and tree middle loggers were tied to an insulated steel pole that was 1.5 m in height. The pole was sunk into the ground next to the trunk of the tree, with the tree base logger tied so that the base of the logger touched the ground, and the tree middle logger was tied at a 1 m height on the pole. Tree canopy loggers were tied to the lowest lateral branch of the tree, as centrally in the canopy as possible.

3.2.5.2 Nests

Nests were first checked for vacancy, using a flexible inspection mirror and light, before placement of temperature loggers, and subsequently blocked at their entrance using wire chicken mesh to prevent removal of the loggers. For sociable weaver nests, the globe, tied onto a flexible wire, was inserted as deep as possible into a nesting chamber and the wire was bent and pushed into the surrounding nesting material to keep the logger in place. Wire chicken mesh was placed over the entrance to the nesting chamber and fixed with two pieces of thin wire, which were also pushed into the surrounding nesting material (Figure A3.6). White-browed sparrow-weaver nest loggers were only placed in non-brood nest chambers, which are open at both ends. Nests were checked to be vacant via inspection, and the globe attached to the wire was inserted so that the globe was in the most central and sheltered point of the nest. The wire was then bent and fixed to the supporting branch. Both open ends of the

nest were sealed with wire chicken mesh and fixed to the nest and branch with wire.

3.2.5.3 Tree hollows

Biotic hollows were relatively rare in the reserve and were often occupied, thus only one biotic hollow was used for thermal measurements. Both abiotic and biotic hollows were checked for vacancy using a flexible inspection mirror and light. Once vacancy was confirmed, a miniature black globe tied onto a flexible wire was lowered into the hollow until it reached the base. The wire was then secured to the relevant tree trunk or branch, and the entrance to the hollow was covered with wire mesh, which was secured to the branch or trunk (Figures A3.4 and A3.5).

3.2.5.4 Burrows

Loggers inserted in large and medium burrows were secured to semi-rigid wire and were lowered to approximately 2.5 m into the burrow, whereas loggers for small burrows were placed at a maximum of 1.5 m from the entrance (Figures A3.7 and A3.8). A single tent peg was used to tether the wire to the ground near the burrow entrance for all burrows, and another tent peg was used to keep the wire on the side of the burrow in large burrows. This was done to decrease the likelihood of the logger being covered in sand if the burrow was modified and to decrease the likelihood of the logger or wire being pulled out of the burrow. If the burrows were found to be collapsed the loggers were removed and replaced in a new burrow.

3.2.5.5 Rock crevices

All rock crevice loggers, on flexible wire, were placed in the crevices so that the thermally sensitive portion of the logger was touching the ground or rock (Figure A3.9). In small rock crevices, the logger was always forced between two rocks, but for large and medium rock crevices, the logger was placed on the floor of the crevice with the thermal logger facing the

ground. This was done to emulate the position of an animal in the crevice. Rock crevices were only considered as a crevice and used for logger placement if the rocks forming the crevice were largely immoveable.

3.2.5.6 Macroclimate temperatures

Exposed-site temperature stations were used to gain a comparison of exposed-site temperatures (hereon referred to as 'macroclimate temperatures') to the microhabitat temperatures. Each station consisted of two miniature black globe thermometers, attached to a 1.5 m insulated steel pole, with one globe attached at ground level and another at a 1 m height (Figure A3.10).

3.2.6 Data analysis

Temperatures were recorded every 30 minutes for 10 months. Macroclimate and microclimate readings were taken over the same periods, although not necessarily simultaneously. The starting times of the thermal loggers within the globes differed per batch of miniature black globes that were assembled. Therefore, since the thermal loggers were changed out frequently, the batch start-times did not always align perfectly. Thus, to compare microhabitat temperatures as accurately as possible to macroclimate temperatures, comparative datasets were created where sheltered data from each microclimate were aligned with the relevant macroclimate data so that every two compared readings were less than 15 minutes apart.

Two consecutive months of ground-level macroclimate temperature measures were lost from the dune habitat due to loggers being removed by wildlife before the logger collection date. Thus, to have relevant comparative macroclimate measures, an interpolated dataset was created. To create this dataset, the average difference between the above-ground and ground-level macroclimate temperatures was calculated for the prior eight months. This value was subsequently deducted from the above-

ground macroclimate measures for the same time as the ground-level data was missing.

To ensure that these interpolated data were accurate, another dataset of interpolated day and night ground-level data was compared via Bland Altman plots to the original ground-level temperatures taken over the first eight months of sampling. The average difference between the interpolated and original datasets was less than 0.2 ˚C for both day and nighttime, which suggests that the method performed well. Further, there were no distinct patterns visible on the plots and the variability was consistent across the given temperature gradients. The limits of agreement were wider in the daytime data than in the nighttime data, with a maximum and minimum limit of approximately 6 ˚C and -6 ˚C respectively. However, most of the points were clustered around the average difference, with only 4% of points lying beyond the limits. The nighttime data had a maximum and minimum limit of approximately 2 ˚C and -2 ˚C respectively, again, with most of the data points clustered around the mean difference, and around 4% of points beyond the limit lines. Thus, the interpolated data were considered to be sufficiently similar to the original data to be used as macroclimate temperature data for the missing January and February portions in the dune dataset.

I predicted that thermal buffering capacity would differ during the coldest and hottest periods of the day, thus full datasets were broken up into three distinct periods, namely, ’day’, ’night’ or ’crepusculum’. Daytime was considered as being any time from eight hours before the earliest sunset of the year (09:47–17:47), and nighttime was considered as being any time from eight hours before the earliest sunrise of the year (21:35–05:35). The crepusculum period was the transitional eight-hour periods between sunrise to daytime, and sunset to nighttime, and was removed from further analysis. Each dataset was summarized as an average daily or nightly temperature for both macroclimate and sheltered microclimate data. I

created ‘offset’ datasets, where the offset is the difference between microhabitat and macroclimate temperatures at a point in time (De Frenne *et al*., 2021). For these datasets, the daily average offset was calculated for each daytime and nighttime dataset. For the descriptive and overview statistics, the daily and nightly average offsets were averaged across all sites per microhabitat type.

To evaluate the buffering capacity of each microhabitat type, I followed the methodology of De Frenne *et al.* (2021) and used simple linear regressions to measure regression coefficients (B_1) of the relationship between microhabitat and macroclimate temperature data across time, for both daytime and nighttime datasets. The regression coefficient reveals if the microclimate is either tracking, buffered or decoupled from the macroclimate temperature. If $B_1 \sim 1$, then the microclimate is tracking the macroclimate temperature, if $1 < B_1 > 0$, the microclimate is buffered, and if $B_1 = 0$, the microclimate is decoupled from the macroclimate temperatures (De Frenne *et al.*, 2021).

Pairwise *t*-tests were used to compare macroclimate temperatures during the day and night, for above-ground and ground levels. These tests were done to ensure that any significant differences seen in the microhabitat offset comparisons were not caused by differences in macroclimate temperatures. Pairwise *t*-tests and Mann-Whitney U tests were used to compare offset above ground and at ground level. To assess the differences in average microhabitat offset per habitat type one-way ANOVAs were run for nighttime and daytime offset datasets respectively. To ensure that offset was not only specific to the habitat and that the inter-habitat comparisons were relevant, the daytime and nighttime average daily macroclimate temperatures were also compared via one-way ANOVAs.

The individual and interactive effect of aspect and season were tested only for the dune and mountain datasets given that the plains area was topographically flat. Seasonal data was split as follows: Winter (June, July, August), Spring (September, October, November), Summer (December, January, February) and Autumn (March, April, May). Only vegetation, burrows, and rock crevices were tested, as these were the most abundant microhabitats found along both aspects of the dune and mountain habitats. Generalized linear models (GLM, estimated using ML) were fitted to predict offset with season and aspect, and the interaction between season and aspect.

All data were analyzed and visualized via R (version 4.1.1), R studio (R Core Team, 2021) and Microsoft Excel. Within the R environment, the following packages were used for analysis: rstatix (version 0.7.0; Kassambara, 2021) gridExtra (version 2.3; Auguie, 2017), ggplot2 (version 3.3.5; Wickham, 2016.), car (version 3.0.11; Fox and Weisberg, 2019), carData (version 3.0.4; Fox, Weisberg and Price, 2020), MuMIn (version 1.43.17; Barton, 2020), sjPlot (version 2.8.10; Lüdecke, 2021), report (version 0.5.1; Makowski *et al*., 2020), ggstatsplot (version 0.9.3; Patil, 2021), lattice (version 0.20.44; Sarkar, 2008), viridisLite (version 0.4.0; Garnier *et al*., 2021) and viridis (version 0.6.2; Garnier et al., 2021).

3.3. Results

3.3.1 Microhabitat thermal buffering capacity

Large and small burrows had the largest daytime and nighttime maximum and average offsets amongst all tested microhabitats (Table 3.2). Large burrows had a maximum offset of -30.5 ˚C during the day and small burrows had a maximum offset of 24.1 ˚C during the night. An average offset of -17.2 ˚C was recorded for large burrows during the day, and an average offset of 10.2 ˚C was recorded for small burrows during the night. Shrub canopy and groundcover were the poorest nighttime shelters, with the lowest maximum and average offsets during the night, in comparison

to all other tested microhabitats (Table 3.2). Shrub canopy was recorded to have a maximum offset of 4.0 ˚C during the night, and groundcover had an average offset of 0.6 ˚C during the night. Shrub canopies also exhibited the smallest average daily offset, of only -5.5 ˚C. All observed microhabitats provided buffered microclimates of different extents (Fig. 3.2a-e). Burrows (daytime B_1 = 0.372, nighttime B_1 = 0.630, average B_1 = 0.501) were the best overall thermal buffers, followed by rock crevices (daytime B_1 = 0.641, nighttime B_1 = 0.875, average B_1 = 0.758) and tree hollows (daytime B_1 = 0.754, nighttime B_1 = 0.757, average B_1 = 0.755). Based on average buffering throughout the diel cycle, bird nests (daytime B_1 = 0.763, nighttime B_1 = 0.893, average B_1 = 0.828) and vegetation (daytime B_1 = 0.760, nighttime B_1 = 0.949, average B_1 = 0.854) were the least buffered microhabitats of all tested types. All microhabitats provided better buffering during the day than during the night. Buffering was shown to increase with increasing daytime temperatures across all microhabitats (Figs 3.2a-e) yet burrow (Fig. 3.2a) and tree hollow (Fig 3.2c) buffering decreased with increasing nighttime temperatures. Rock crevices, bird nests and vegetation as poor nighttime buffers, showed tracking of the macroclimate during the night.

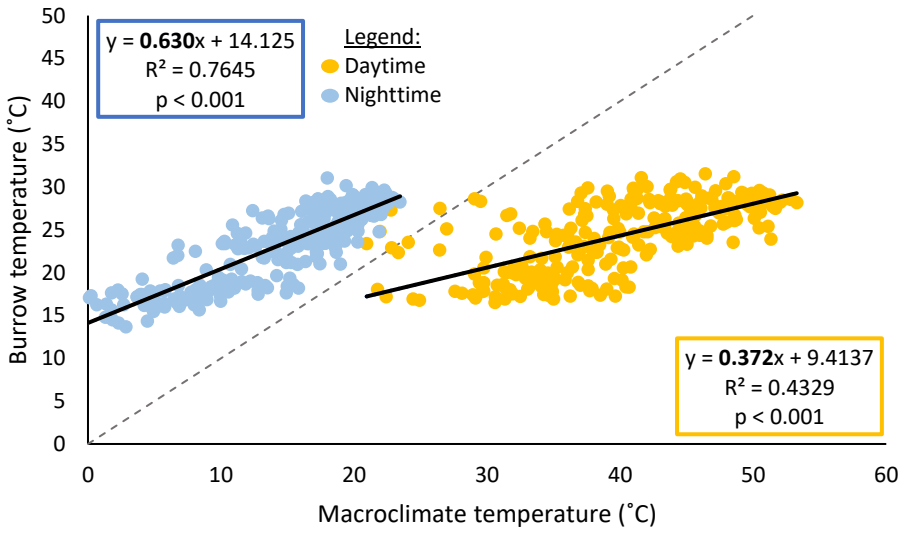

Figure 3.2a: The linear relationship between burrow and macroclimate (exposed site) temperatures.

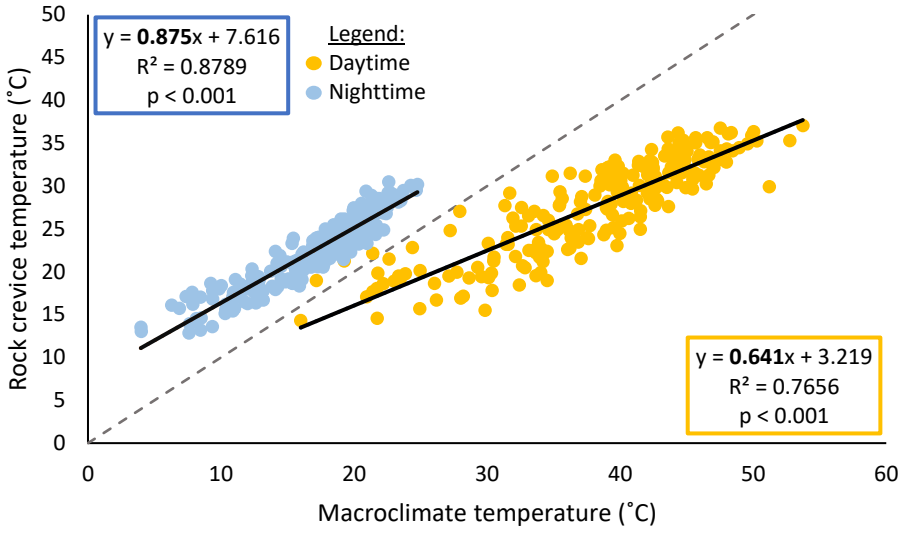

Figure 3.2b: The linear relationship between rock crevice and macroclimate (exposed site) temperatures.

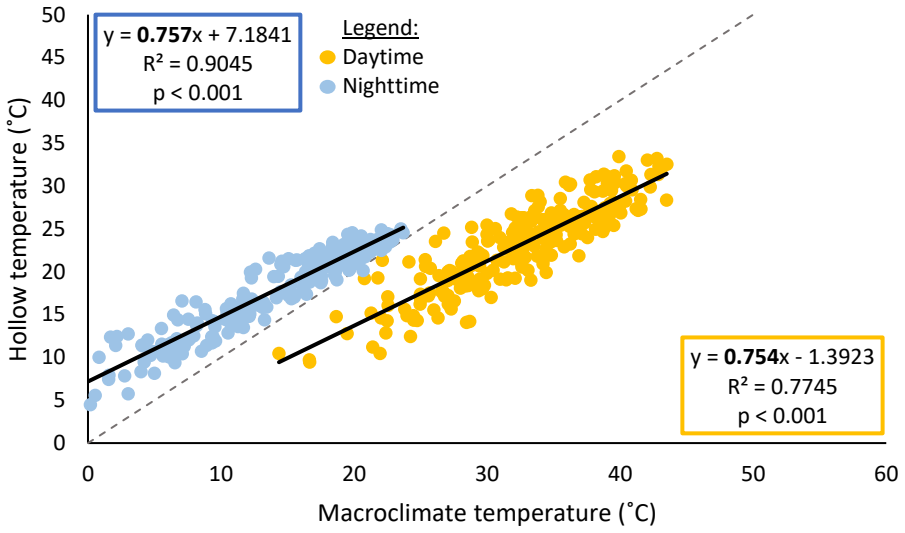

Figure 3.2c: The linear relationship between tree hollow and macroclimate (exposed site) temperatures.

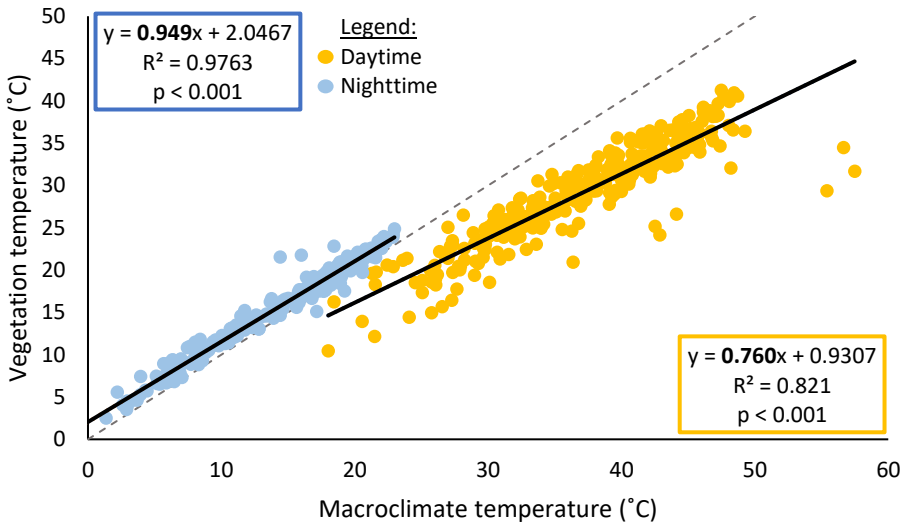

Figure 3.2d: The linear relationship between vegetation and macroclimate (exposed site) temperatures.

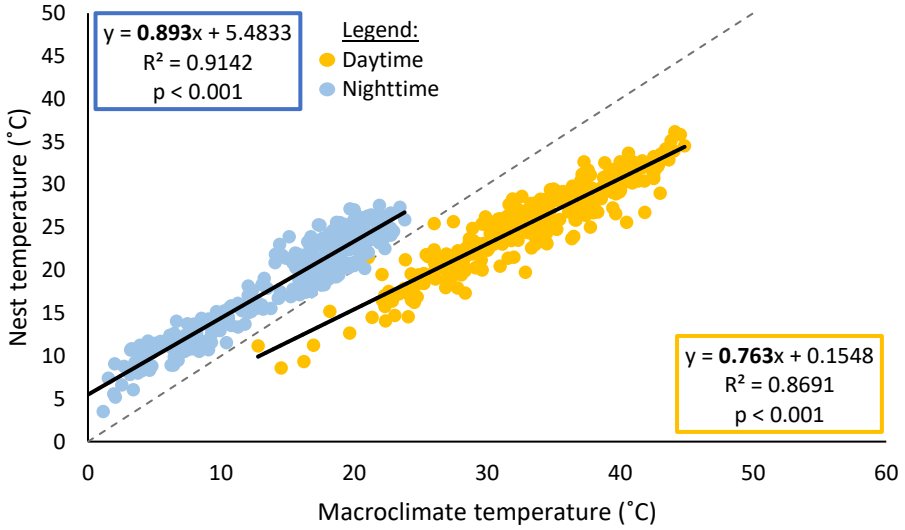

Figure 3.2e: Linear relationships between bird nest and macroclimate (exposed site) temperatures.

Table 3.2: Microhabitat maximum and average temperature offsets

Microhabitat	Position	Max. offset (˚C)	Max. offset (˚C)	Avg. offset (˚C)	Avg. offset (˚C)
AH	AG	-15.0	7.7	-8.1	3.2
BH	AG	-17.4	13.0	-11.4	5.3
SHC	AG	-16.2	4.0	-5.5	0.8
SW	AG	-17.0	11.1	-8.1	5.0
WB	AG	-14.9	5.9	-7.0	2.5
TRC	AG	-18.1	6.1	-7.0	2.2
TRM	AG	-15.4	5.0	-6.9	1.4
GC	G	-16.6	5.4	-6.1	0.6
LB	G	-30.3	16.1	-17.2	6.9
LRC	G	-29.3	10.2	-12.5	4.8
MB	G	-30.5	20.0	-17.0	7.7
MRC	G	-29.6	8.7	-9.5	4.4
SHB	G	-26.4	6.3	-11.9	1.4
SB	G	-27.9	24.1	-15.5	10.1
SRC	G	-26.4	13.7	-9.1	6.5
TRB	G	-26.0	6.3	-12.5	1.2

Key: Position refers to if the microhabitat is above ground level (AG), or on or below ground level (G). Yellow sections of the table refer to data measured during the daytime, and blue sections refer to data measured during the nighttime. Microhabitats: GC = Ground Cover, SHB/TRB = Shrub/Tree base, SHC/TRC = Shrub/Tree canopy, TRM = Tree middle, A/BH= Abiotic/Biotic hollow, S/M/LB = Small, medium, and large burrows, WB = White- browed sparrow-weaver nest, SW = Sociable weaver nest, S/M/LRC = Small, medium, and large rock crevices.

3.3.2 Thermal buffering capacity over time

Thermal buffering differed vastly between day and night and between months. The largest observable difference between day and night buffering was seen in the mountain habitat (Fig. 3.3), where almost all the microhabitats were extremely poor buffers during the night. Additionally, within the mountain habitat, vegetation-based microhabitats appeared to be poor buffers from August to December but became better buffers from January to March. Within the first two months of the year the east aspect appeared to be associated with poor day-time thermal buffering, as five of the six microhabitats were weak buffers ($B_1 > 0.5$) in January and bad

buffers ($B_1 = 1$) in February. Whereas on the west aspect, with exception of the shrub canopy microhabitat, all microhabitats were good buffers from January to March. Furthermore, in the mountain habitat, the only microhabitat that appeared to be a good buffer for most of the year, during the day and night was small rock crevices on the east aspect.

Within the dunes and plains habitats (Fig. 3.4), burrows were the best buffers overall, as they were for the majority, good buffers ($B_1 < 0.5$) during the day and night. Biotic and abiotic hollows in the plains were the second most stable buffers, with a buffering capacity of $B_1 < 0.7$ for both day and nighttimes throughout the year. During the day, all vegetation-based microhabitats in the dunes and plains were better buffers from January to March than the rest of the year, with only a few having a similarly high level of buffering from October to December in the plains. Ground cover was an overall poor buffer across time of day, month, and habitat type. Nests appeared to be good buffers during the day and night only within the plains, although their best buffering was restricted to the months of January to March. A similar monthly pattern was visible in the dunes, but nests were not a good nighttime buffer. Vegetation-based microhabitats were overall poor nighttime buffers regardless of the time of year, or habitat.

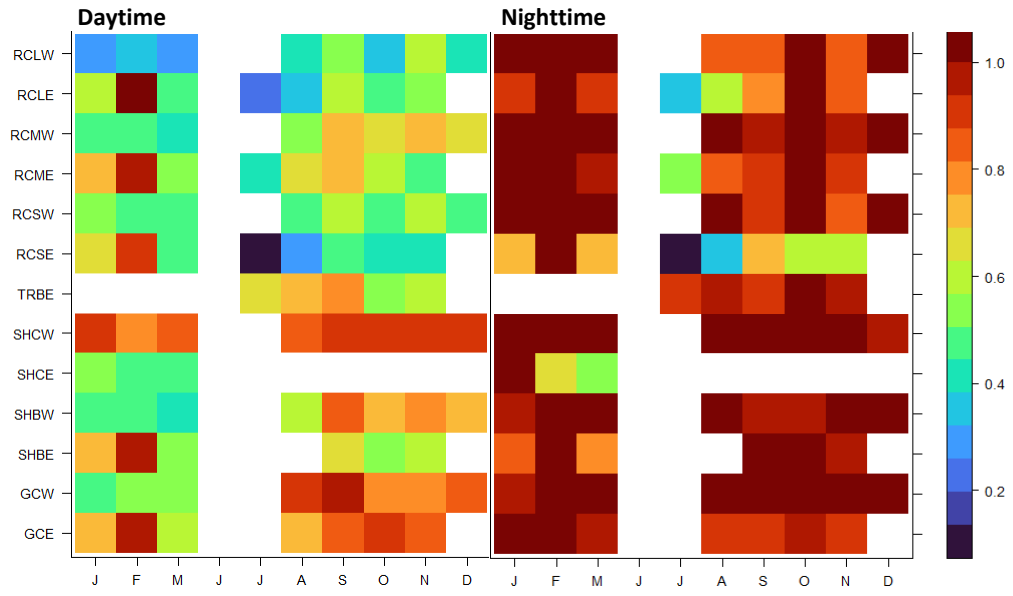

Figure 3.3a (L) and b (R): The day and night buffering capacity (B_1 on the right-hand scale of 0–1, where 0 represents a good buffer, and 1 represents a poor buffer) of mountain microhabitats over 10 months (indicated on the x-axis), where April and May are excluded. Blank squares indicate months that had too few data to run a regression analysis. Microhabitat type key, from top to bottom: RCL/M/S = Large, medium, and small rock crevices, TRB = Tree base, SHC = Shrub canopy, SHB = Shrub base, GC = Ground Cover, --W=West, --E = East

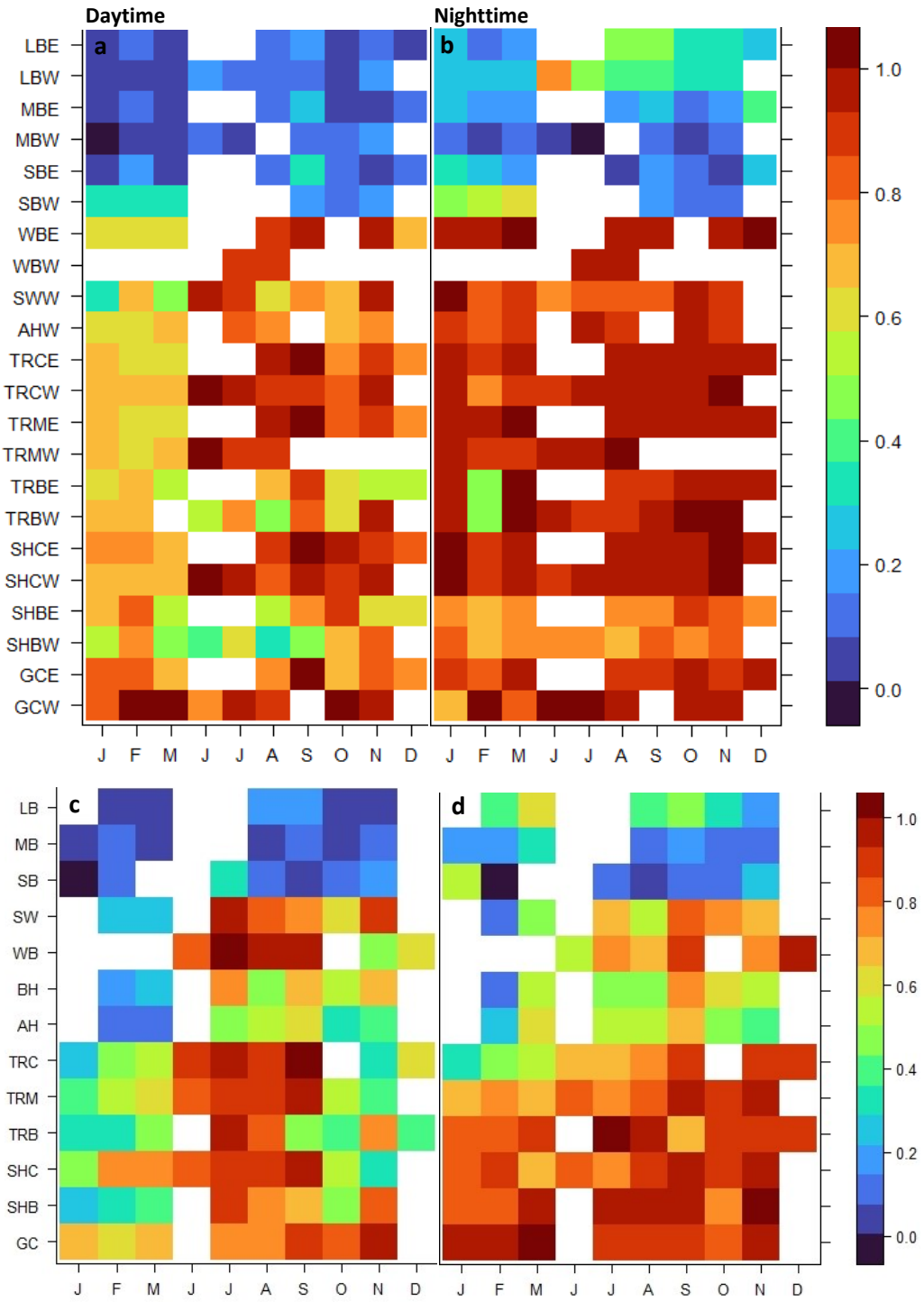

Figure 3.4 (a-d): The day and night buffering capacity (Right-hand scale of 0–1, where 0 represents a good buffer, and 1 represents a poor buffer) of dune and plains microhabitats over 10 months (indicated on the x-axis), where April and May are excluded. Figure a and b refer to dune microhabitats, and c and d refer to plain microhabitats. Blank squares indicate months that had too little data to run a regression analysis. Microhabitat type key: S/M/LB = Small, medium, and large burrows, WB = White-browed sparrow-weaver nest, SW = Sociable weaver nest, A/BH= Abiotic/Biotic hollow, SHC/TRC = Shrub/Tree canopy, TRM = Tree middle, SHB/TRB = Shrub/Tree base, GC = Ground Cover, --W=West, --E = East

3.3.3. Environmental influences on microhabitat buffering

Pairwise tests were used to assess the effect of microhabitat position on offset. Pairwise *t*-tests showed that microhabitats at ground level were significantly cooler than above-ground microhabitats during the day (t = 49.59, n = 9640, $p < 0.001$). Ground-level microhabitats experienced a daytime average offset of -12.1 ˚C, whereas above-ground microhabitats experienced a daytime average of -7.1 ˚C. Nighttime data were nonparametric, and thus a Mann-Whitney test was used. There were significant differences between ground and above-ground temperatures during the night ($U = 8.09^{-6}$, $p < 0.0001$), with the median of nightly ground temperatures at 3.2 ˚C, while the median of above-ground temperatures was 1.4 ˚C. Pairwise *t*-tests were also used to test if macroclimate above-ground and ground temperatures were different. The results showed that above-ground macroclimate temperatures were cooler than ground-level temperatures (Fig. 3.5) during the day (t = -12.72, n = 11, $p < 0.001$), whereas there was no significant difference between above-ground and ground temperatures during the night (t = 0.28, n = 11, $p > 0.05$).

One-way ANOVAs were used to assess if there were any differences in macroclimate temperatures per habitat. Significant differences were found between habitats during both the day ($F_{(2, 636)} = 4.19$, $p < 0.5$; Fig. 3.6) and night ($F_{(2, 615)} = 9.15$, $p < 0.001$; Fig. 3.6). However, Tukey's HSD *post hoc* tests revealed that during the daytime, there were only significant differences between the plain and mountain habitats ($p < 0.05$), where the plains macroclimate was significantly warmer than the mountain macroclimate. Furthermore, Tukey's HSD *post hoc* tests showed that the mountain macroclimate was significantly warmer than both the dune ($p < 0.05$) and plains ($p < 0.001$) macroclimates during the night.

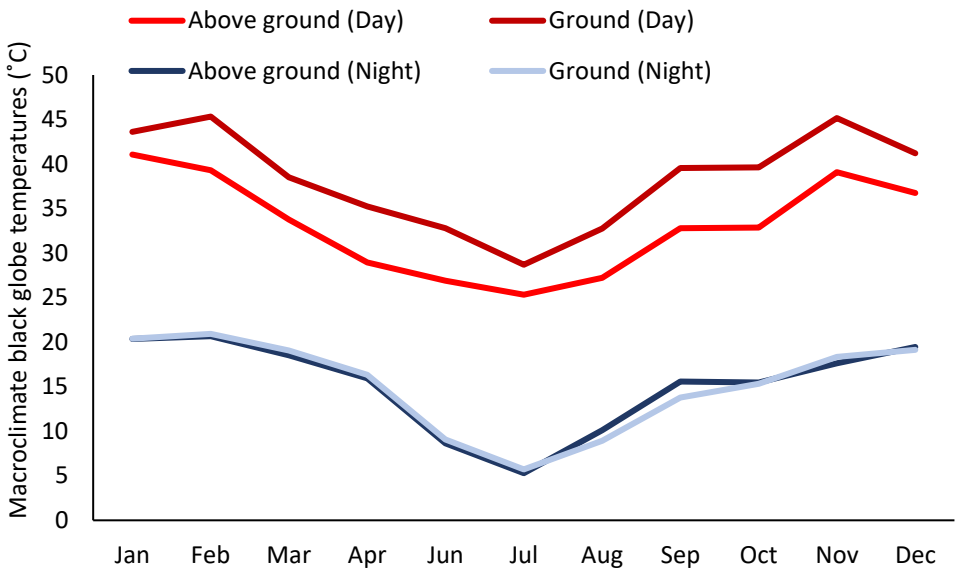

Figure 3.5: The average monthly macroclimate temperatures above-ground and on ground-level across all habitats. Daytime data are in red, and nighttime data are in blue.

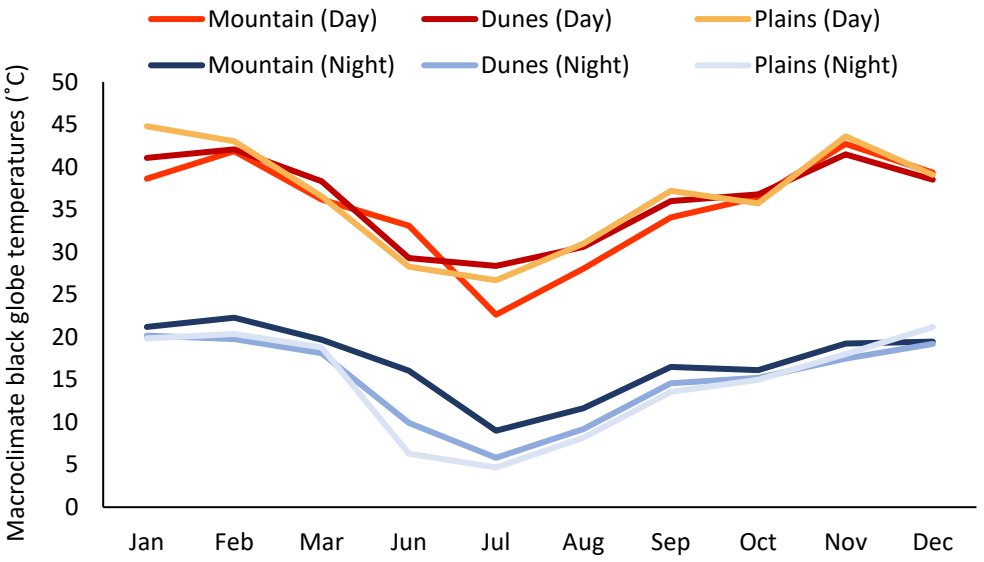

Figure 3.6: The average monthly macroclimate temperatures for each habitat. Daytime data are in red, and nighttime data are in blue.

A one-way ANOVA was used to examine the effects of habitat type on average microhabitat temperature offset. There was a statistically significant difference between the effects of the three habitats on

temperature offset ($F_{(2, 681}$ = 55.24, p < 0.001) during the day. Tukey's HSD *post hoc* tests showed that the mean daytime temperature offset in the plains was significantly more negative than in the mountains (p < 0.0001), and dunes (p < 0.0001). The mean temperature offset in the mountains was significantly more positive than in the dunes (p < 0.0001). Thus, considering the macroclimatic differences, during the day, the plains had better buffering microhabitats than the dunes, and the dunes had better buffering microhabitats than the mountains. However, the differences between the plains' and mountains' microhabitat buffering capacity is not comparable due to the significant differences between the macroclimatic temperatures.

Another one-way ANOVA was used to assess nighttime data. A significant effect of habitat on nighttime average microhabitat temperature offset ($F_{(2, 690}$ = 27.06, p < 0.001) was detected. A Tukey's HSD *post hoc* test showed that there were significant differences between average offsets in the dunes and plains (p < 0.0001) and offset in the mountains and dunes (p < 0.0001), and no significant difference was detected between the plains and mountains (p > 0.05). However, considering that the mountain macroclimate was significantly warmer than both the dunes and plains macroclimates, and that the average nighttime offsets per habitat (dunes: 3.9 ˚C, mountains: 3.3 ˚C, plains: 3.2 ˚C) were less than a degree apart, the offset differences between habitat types at night is unlikely to be biologically relevant.

Linear models were used to test the interactive effects of aspect and season on vegetation and burrows in the dunes, and vegetation and rock crevices in the mountains. Within the dunes habitat during the day, only winter and spring were found to have a significantly positive effect on vegetation offset (p < 0.001), whereas the interactive effect of the west aspect in winter was found to have a significantly negative effect on vegetation offset (p < 0.05)(Table 3.3a; Fig. 3.7a), although the model's

explanatory power was weak (R^2 = 0.09). Winter, summer and spring were all found to have significantly negative effects on burrow offset ($p < 0.05$), while the interactive effect of the west aspect during spring and winter was significantly positive ($p < 0.05$) for burrows (Table 3.3b, Fig. 3.7b). The model's explanatory power was also weak (R^2 = 0.07). Within the mountain habitat during the day, spring and the west aspect were found to have significantly negative ($p < 0.001$) effects on vegetation offset, whereas the interactive effect of the west aspect during winter and spring was found to have a positive effect on vegetation offset ($p < 0.001$). The explanatory power of this model was moderate (R^2 = 0.15) (Table 3.4a, Fig. 3.8a). Spring, winter, and the west aspect were all found to have significantly negative ($p < 0.001$) effects on rock crevice offsets, while summer had a significantly positive ($p < 0.05$) effect on rock crevice offset. The interactive effect of the west aspect during spring and winter had a significantly positive ($p < 0.001$) effect on rock crevice offset, and the models' explanatory power was substantial (R^2 = 0.43) (Table 3.4b, Fig. 3.8b). Within the dune habitat during the night, only winter had a significantly positive ($p < 0.001$) effect on vegetation offset, although the model's explanatory power was very weak (R^2 = 0.03) (Table 3.5a, Fig. 3.9a). Whereas winter and spring both had significantly negative ($p < 0.05$) effects on burrow offset, and the west aspect had a significantly positive ($p < 0.05$) effect on burrow offset. Although, again, the model's explanatory power was weak (R^2 = 0.05) (Table 3.5b, Fig. 3.9b). Within the mountain habitat during the night, spring, winter, and the west aspect had significantly positive ($p < 0.001$) effects on vegetation offset, while the interactive effect of the west aspect during spring, summer and winter had a significantly negative effect ($p < 0.05$) on vegetation offset. The model's explanatory power was also weak (R^2 = 0.12) (Table 3.6a, Fig. 3.10a). For rock crevice offset, spring, summer, winter, and the west aspect all had a significantly positive effect ($p < 0.001$). Although the interaction of the west aspect during spring, summer and winter had a significantly negative ($p <$

0.05) effect on rock crevice offset. The model's explanatory power was substantial (R^2 = 0.30) (Table 3.6b, Fig. 3.10b).

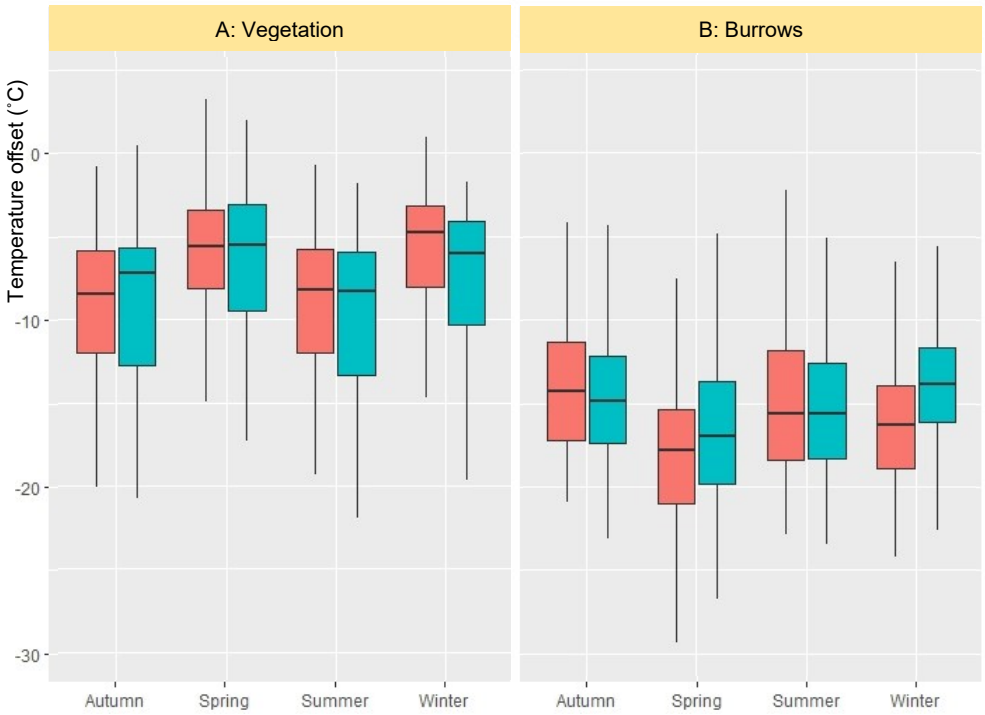

Figure 3.7a and b: Dune daytime vegetation and burrow offset plotted per season and aspect (red = east, blue = west).

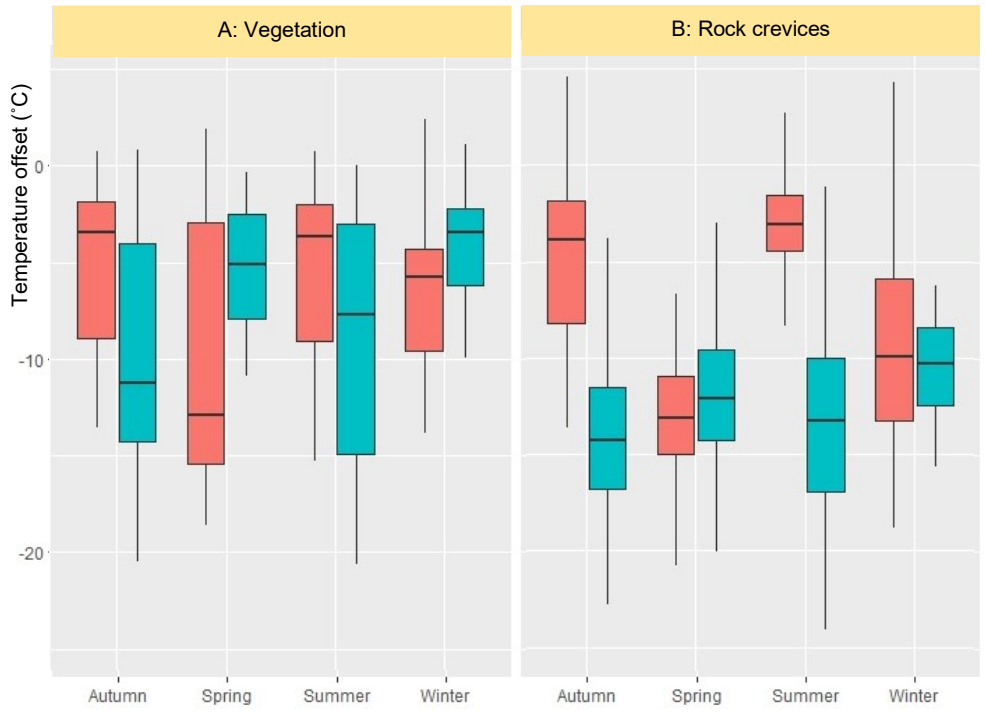

Figure 3.8a and b: Mountain daytime vegetation and crevice offset plotted per season and aspect (red = east, blue = west).

Table 3.3a and b: The effects of season and aspect on dune vegetation (a) and burrow (b) offset during the daytime. CE = Coefficient Estimate, CI = Confidence Interval.

A: Vegetation

Predictors	CE	CI	p
Intercept	-9.12	-9.83 – -8.40	**< 0.001**
Season (Spring)	2.86	2.00 – 3.71	**< 0.001**
Season (Summer)	0.14	-0.68 – 0.97	0.734
Season (Winter)	3.12	2.18 – 4.05	**< 0.001**
Aspect (West)	0.25	-0.78 – 1.27	0.635
Spring * West	-0.45	-1.67 – 0.77	0.469
Summer * West	-0.86	-2.05 – 0.33	0.157
Winter * West	-1.85	-3.11 – -0.59	**< 0.05**
Observations	2332		
R^2	0.087		

B: Burrow

Predictors	CE	CI	p
Intercept	-13.32	-14.36 – -12.29	**< 0.001**
Season (Spring)	-4.47	-5.74 – -3.20	**< 0.001**
Season (Summer)	-1.41	-2.63 – -0.19	**< 0.05**
Season (Winter)	-2.92	-4.34 – -1.50	**< 0.001**
Aspect (West)	-0.27	-1.71 – 1.17	0.715
Spring * West	1.86	0.11 – 3.62	**< 0.05**
Summer * West	-0.34	-2.12 – 1.44	0.706
Winter * West	2.23	0.28 – 4.19	**< 0.05**
Observations	1132		
R^2	0.072		

Table 3.4a and b: The effects of season and aspect on mountain vegetation (a) and crevice (b) offset during the daytime. CE = Coefficient Estimate, CI = Confidence Interval.

A: Vegetation

Predictors	CE	CI	p
Intercept	-5.31	-6.35 – -4.28	**<0.001**
Season (Spring)	-4.58	-5.83 – -3.32	**<0.001**
Season (Summer)	-0.28	-1.66 – 1.09	0.686
Season (Winter)	-1.15	-2.72 – 0.42	0.151
Aspect (West)	-4.47	-5.96 – -2.99	**<0.001**
Spring * West	9.06	7.28 – 10.84	**<0.001**
Summer * West	1.10	-0.77 – 2.98	0.249
Winter * West	6.91	4.67 – 9.14	**<0.001**
Observations	1020		
R^2	0.154		

B: Rock crevices

Predictors	CE	CI	p
Intercept	-4.72	-5.53 – -3.92	**<0.001**
Season (Spring)	-8.28	-9.28 – -7.28	**<0.001**
Season (Summer)	1.62	0.52 – 2.71	**<0.05**
Season (Winter)	-4.45	-5.57 – -3.34	**<0.001**
Aspect (West)	-8.93	-10.04 – -7.83	**<0.001**
Spring * West	10.12	8.75 – 11.50	**<0.001**
Summer * West	-1.25	-2.72 – 0.22	0.097
Winter * West	7.83	6.20 – 9.47	**<0.001**
Observations	1086		
R^2	0.432		

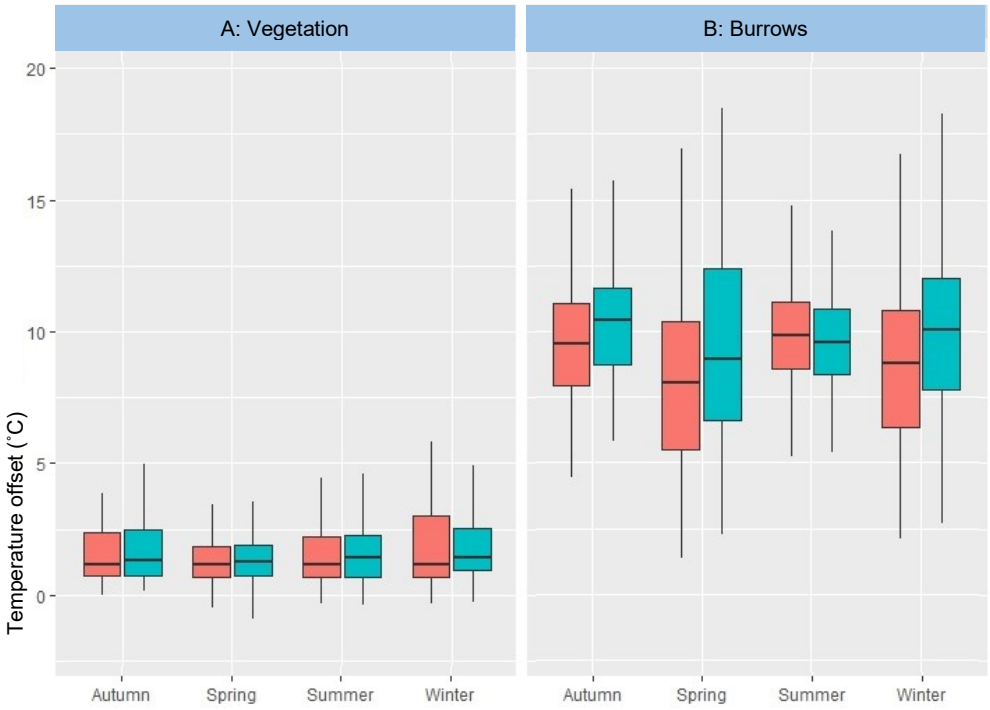

Figure 3.9a and b: Dune nighttime vegetation and burrow offset plotted per season and aspect (red = east, blue = west).

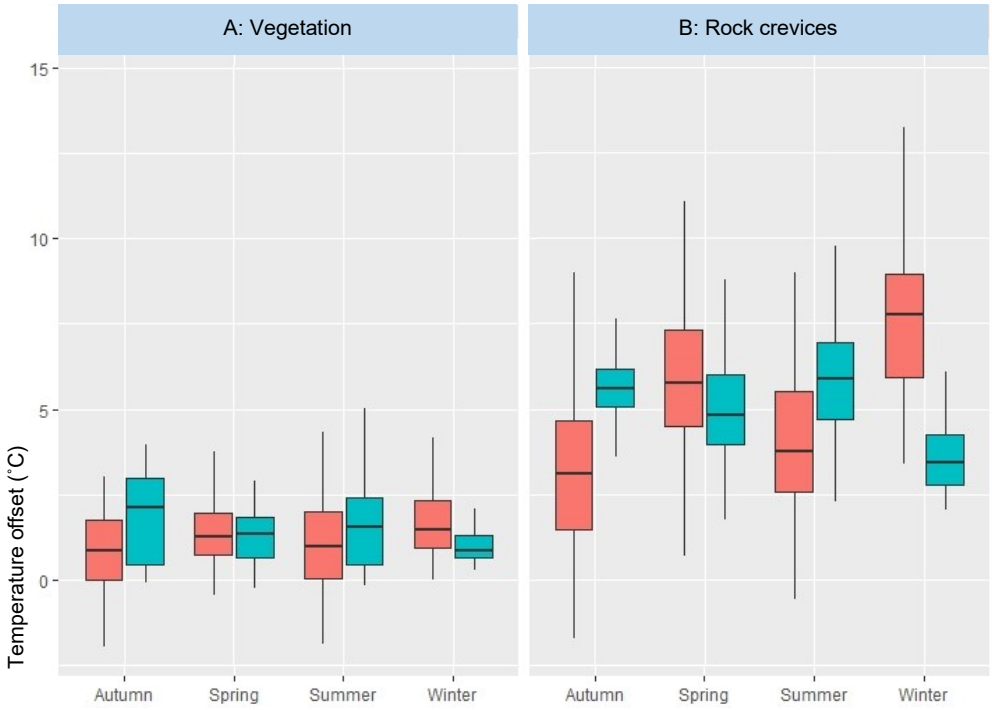

Figure 3.10a and b: Mountain nighttime vegetation and crevice offset plotted per season and aspect (red = east, blue = west).

Table 3.5a and b: The effects of season and aspect on dune vegetation (a) and burrow (b) offset during the night. CE = Coefficient Estimate, CI = Confidence Interval.

A: Vegetation

Predictors	CE	CI	p
Intercept	1.49	1.31 – 1.67	**<0.001**
Season (Spring)	-0.12	-0.34 – 0.10	0.301
Season (Summer)	-0.03	-0.24 – 0.18	0.776
Season (Winter)	0.41	0.16 – 0.65	**<0.05**
Aspect (West)	0.16	-0.11 – 0.42	0.240
Spring * West	0.06	-0.26 – 0.37	0.719
Summer * West	-0.05	-0.36 – 0.26	0.740
Winter * West	-0.13	-0.46 – 0.20	0.440
Observations	2370		
R^2	0.028		

B: Burrows

Predictors	CE	CI	p
Intercept	9.56	8.93 – 10.18	**<0.001**
Season (Spring)	-1.22	-1.98 – -0.45	**<0.05**
Season (Summer)	0.25	-0.49 – 0.99	0.512
Season (Winter)	-0.93	-1.79 – -0.06	**<0.05**
Aspect (West)	0.88	0.02 – 1.75	**<0.05**
Spring * West	0.49	-0.57 – 1.54	0.369
Summer * West	-1.05	-2.13 – 0.03	0.056
Winter * West	1.05	-0.13 – 2.24	0.082
Observations	1153		
R^2	0.051		

Table 3.6a and b: The effects of season and aspect on mountain vegetation (a) and crevice (b) offset during the night. CE = Coefficient Estimate, CI = Confidence Interval.

A: Vegetation

Predictors	CE	CI	p
Intercept	0.35	0.11 – 0.59	**<0.05**
Season (Spring)	1.03	0.74 – 1.32	**<0.001**
Season (Summer)	0.29	-0.03 – 0.61	0.074
Season (Winter)	1.46	1.09 – 1.83	**<0.001**
Aspect (West)	1.51	1.16 – 1.85	**<0.001**
Spring * West	-1.60	-2.02 – -1.19	**<0.001**
Summer * West	-0.55	-0.98 – -0.11	**<0.05**
Winter * West	-2.29	-2.81 – -1.76	**<0.001**
Observations	1040		
R^2	0.125		

B: Rock crevices

Predictors	CE	CI	p
Intercept	3.21	2.87 – 3.55	**<0.001**
Season (Spring)	2.79	2.37 – 3.22	**<0.001**
Season (Summer)	0.90	0.44 – 1.37	**<0.001**
Season (Winter)	4.32	3.84 – 4.80	**<0.001**
Aspect (West)	2.36	1.88 – 2.84	**<0.001**
Spring * West	-3.41	-4.01 – -2.82	**<0.001**
Summer * West	-0.69	-1.32 – -0.06	**<0.05**
Winter * West	-6.31	-7.05 – -5.57	**<0.001**
Observations	1113		
R^2	0.301		

3.4 Discussion

Burrows, rock crevices and tree hollows were the most thermally buffered microhabitats available to birds, reptiles, and mammals within the Kalahari. Burrows remained a good buffer throughout the day and night, and across seasons, providing a microclimate that, on average, was approximately 16 ˚C cooler during the day, and 8 ˚C warmer during the night in comparison to the surrounding ground-level conditions. Rock crevices were generally good buffers during the daytime although buffering differed per season, aspect, and individual crevice. Tree hollows only within the plains were a good buffer, during both the day and night, and had their best buffering occurring during the peak of the rainy season. Vegetation and bird nests were relatively poor buffers, although buffering capacity varied extensively between different vegetation and nest types and peaked during the wetter time of the year. Microhabitats on or below the ground showed greater thermal buffering than microhabitats above ground and thermal buffering also differed significantly per habitat type for both the day and night. The effects of aspect and season, both alone and interactively, influenced the thermal buffering provided by vegetation, rock crevice and burrow microhabitats in the dunes and mountains.

3.4.1 Microhabitat thermal buffering

As hypothesized, all burrow sizes were found to provide an exceptionally well, and consistently, buffered microclimate. Although it is considered that burrows with smaller entrances and tunnel diameters are more thermally buffered than larger ones (Bulova, 2002; Whittington-Jones *et al.,* 2011), I found no substantial seasonal differences in buffering capacity between burrows of different sizes. Nevertheless, there was a difference in buffering capacity across sizes over the diel cycle. Large and medium burrows were more buffered (cooler) than small burrows during the day, but, during the night, small burrows were more buffered (warmer) than either large or medium burrows. Thus, there may be differences in warm versus cool buffering capacity, which could be related to humidity. Longer

burrows with smaller diameters are associated with increased humidity (Bulova, 2002), where increased humidity in building structures (Wang *et al.*, 2022), and increased soil moisture content (Selker and Or, 2022), have been associated with increased thermal heat conductivity. Thus, smaller, and more humid burrows may be able to hold heat for longer during the cooler nighttime periods, whereas larger burrows may be exposed to more airflow and thus will be cooler due to evaporative heat loss during the day. Nonetheless, regardless of size or temporal scale, burrows remain the most thermally buffered microhabitat within the Kalahari.

Rocky habitats are thought to have potential as microrefugia under climate change (García *et al.*, 2020). Yet, for a microhabitat to be classified as a microrefugium, it should be a good thermal buffer across long-term or generational time scales (Rull, 2009; Dobrowski, 2011; Hannah *et al.*, 2014). Rock crevices in this study did not appear to meet these criteria. During the daytime, rock crevices were primarily good thermal buffers, however, their buffering varied extensively according to aspect, season (Table 3.4b), and individual crevice (Fig. 3.3b). However, I did not account for rock thickness when selecting crevices for our study. Both rock size and rock thickness are associated with the level of thermal buffering provided by rocks (Huey *et al.*, 1989; Kearney, 2002), where large, thick rocks are associated with more buffered microclimates (Huey *et al.*, 1989; van der Westhuizen *et al.*, 2021). Thus, the diversity seen in rock crevice buffering, across sizes, may be explained by the confounding factor of individual differences in rock thickness (Huey *et al.,* 1989). Therefore, although rock crevices showed strong daytime buffering, the ‘one-size-fits-all’ approach, that all rock crevices could be suitable microrefugia, may not hold. Nonetheless, considering the abundance of rock crevices in mountain habitats (Chapter 2), the likelihood of at least some suitable microrefugia existing per rocky patch may still be plausible.

Tree hollows are known to provide buffered microclimates to multiple animals (Isaac, De Gabriel and Goodman, 2008; Maziarz, 2019; Penton *et al.*, 2021), and as a result, cavity-forming birds are often recognised as keystone species (Kotowska *et al.*, 2020). Larger diameter tree trunks (O'Connell and Keppel, 2016) and smaller hollow entrances have been associated with increased thermal buffering (Isaac *et al.*, 2008), and it has been suggested that smaller biotic hollows may be particularly well-buffered due to purposeful selection for nesting (R.Thomson, pers. comm., 2021). Yet, I found little difference in buffering capacity between the larger abiotic, and smaller biotic, hollows. There was a visible difference in hollow buffering capacity between the plains and dunes (Figs 3.4a–d), but the hollows chosen to be tested in the dunes were limited by scarcity (Chapter 2). Thus, the poorly buffered dune hollows were in the branches of small *Boscia* species, whereas the well-buffered abiotic and biotic hollows in the plains were in the larger trunks of *Vachellia* species. Thus, apart from the differences in trunk size, the insulation properties of the wood may also differ per species (Piechnik *et al.*, 2022). Hence, it appears that, given the wood type, the girth of the host trunk, and the depth of the cavity are similar, the buffering capacity will remain analogous regardless of the hollow origin or size.

Sociable weaver nests are regarded as one of the most iconic features of the Kalahari and are heralded as an important thermal shelter for many Kalahari animals (Leighton and Echeverri, 2014; Lowney *et al.*, 2020). Yet, although my overall results (Table 3.2) of daily and nightly average offsets agree with the results presented by Lowney *et al.* (2020), in comparison to all other microhabitat types, sociable weaver nests were found to provide relatively poor thermal buffering. Thus, these results of poor thermal buffering, even in the highly insulated sociable weaver nests, reinforce the idea that dryland birds may be at a high risk of climate exposure (Conradie *et al.*, 2019; McKechnie *et al.*, 2021; Riddell *et al.*, 2021). Moreover, nesting material will likely become scarce as vegetation growth dwindles

with increasing aridity, decreasing the ability of birds to maintain their nests. Therefore, the plethora of biodiversity that is supported by bird nests in the Kalahari (Maclean, 1973; Lowney and Thomson, 2021) may potentially be unsustainable under climate change. Considering that the tested bird nests provided a relatively poor level of thermal buffering in a year with good rainfall and high vegetation productivity, under increasing aridification, they may be unlikely to shelter their host species from climatic extremes.

There is ample evidence to suggest that vegetation can provide thermal buffering (D'Odorico *et al.*, 2013; Scheffers, Edwards, *et al.*, 2014; Scheffers, Evans, *et al.*, 2014; De Frenne *et al.*, 2019; Chu *et al.,* 2021; Sharpe *et al.,* 2022), and the results of my study corroborate this evidence. Yet when compared to all other tested microhabitats, vegetation was the poorest buffer available in the Kalahari. Furthermore, as it is a poor buffer, vegetation-based microclimates are highly correlated with the macroclimate, suggesting that they may be more affected by environmental indices such as topography. This effect has been reported in the literature (D'Odorico *et al.*, 2013; Sklenář *et al.*, 2016), and was confirmed in my study, as vegetation offsets were significantly affected by the aspect in the mountains. Furthermore, vegetation buffering will differ per season, or water availability, as some plants will gain and lose foliage accordingly (Davis *et al.*, 2019). That issue is evident in the daytime results of my study (Figs 3.3 and 3.4), which show that vegetation buffering improved in the months with higher rainfall (From January to March), potentially as a result of increased vegetation greening. Thus, my results reiterate that thermal buffering provided by vegetation, although relatively poor, will be highly variable according to the type and position of the vegetation (Scheffers, Edwards, *et al.*, 2014; Sklenář *et al.*, 2016; Chu *et al.,* 2021), as well as seasonality and water availability (Davis *et al.*, 2019).

3.4.2 Environmental influence on microhabitat buffering

An estimation of the overall thermal buffering capacity provided by an environment would allow conservationists to pinpoint areas that are likely to provide refuge under climate change. With this aim in mind, I predicted that microhabitat composition alone would relate proportionally to the overall buffering capacity of a habitat type. However, I found that habitats with similar microhabitat compositions had different overall microhabitat offsets, indicating that this hypothesis cannot be supported. For example, microhabitats in the plains had greater buffering capacity than those of the same kind in the dunes. This result may be due to reflected solar radiation from high albedo surfaces created by open patches of sand (Finch, 1972; Mitchell *et al.*, 2018), increasing the radiative heat gain that the microhabitats need to deflect in the dunes. Plains microhabitats are commonly surrounded by vegetation-covered ground, which will scatter or absorb some of the incoming radiation. Thus, the dense vegetation in the plains could also decrease overall heat loss at night, as the ground may not experience as much radiant heat loss to the open sky (Swinbank, 1963; D'Odorico *et al.*, 2013; Mitchell *et al.*, 2018), thereby making the ground around microhabitats warmer and decreasing their heat loss. This difference between the dunes and plains exemplifies why increasing aridification is also likely to further decrease the buffering capacity of all microhabitats, and not only affect vegetation-based microhabitats that may have less access to water. Additionally, it emphasizes that both microhabitat composition and microhabitat density will need to be assessed for an accurate evaluation of overall buffering capacity per habitat.

It is important to note that even if an environment has multiple well-buffered microhabitats, it is access to, rather than the existence of, microhabitats, that will influence what thermal buffering is available to most animals (Riddell *et al.*, 2021). Accessibility will be filtered by both the position of the microhabitat and animal size. Position (ground-level,

subsurface or above-ground microhabitats) will restrict access since microhabitat useability can be constrained by an animal's structural adaptions (fossorial, aerial, cursorial, arboreal etc.). This restriction is critical, as differences in microclimatic buffering were found to be associated with microhabitat position. I found that the most strongly buffering microhabitats were on the ground-level or subsurface, which may be linked to decreases in convective cooling, as there is likely to be more shelter from the wind lower to the ground. Furthermore, a denser cover, whether from soil or vegetation, above the ground or subsurface microhabitats, would also reduce radiative heat gain or loss during the respective days or nights (D'Odorico *et al.*, 2013). We can thus infer that birds, which are unlikely to utilize ground-level microhabitats, and large animals, which are too large to access burrows, will be at a higher risk of climate exposure. This inference supports the arguments of Hetem *et al.* (2014), Fuller *et al.* (2016), and Riddell *et al.* (2021), and highlights why the accessibility of microhabitats, and not only the presence of microhabitats, needs to be assessed.

Topography is also known to shape the availability and buffering capacity of various microhabitats (Daly *et al*., 2010; Dobrowski, 2011; Sklenář *et al.*, 2016), yet season, as an interactive effect along with topography, is infrequently considered. In my study, both the individual and interactive effects of season and aspect were found to be extremely weak as predictors of microhabitat buffering in the dunes but were moderately strong predictors for microhabitat buffering in the mountains. However, the mountains were far larger than the dunes, and thus it is plausible that the mountains' topography may have a greater effect on topoclimates. Therefore, this result highlights that aspect may be a stronger predictor if the angle of slope is greater, or if the elevation is higher, as elevation and slope both affect the level of exposure to wind and radiation (Dobrowski, 2011).

Although both the effects of season and aspect were noted as significant predictors of vegetation and crevice buffering in the mountain, these results may also have been caused by a confounding effect of differences in macroclimatic temperatures. The mountains' west-face macroclimate was warmer in the evening, and cooler in the morning, than the east-face, likely as a result of exposure to radiation at sunset, and less radiation at sunrise. Thus, this inconsistency made it difficult to disentangle the thermal value of the microhabitats from the effects of the surrounding environment. Therefore, although these results correspond with published findings in the literature that suggests that topography affects microclimates (Ashcroft *et al.*, 2009; Daly *et al.*, 2010; Sklenář *et al.*, 2016), they also highlight that the size of topographic features and localised topoclimate need to be considered if clear-cut effects are to be found.

3.4.3 Future research

Throughout all tested habitats, greater levels of thermal buffering were seen mostly during hot periods of the year and during the day, while less buffering was seen during cooler periods and during the night. Similar results were reported by De Frenne *et al*. (2019) when measuring the microclimates created by tree canopies in a tropical biome. Thus, analogous to the findings of De Frenne *et al*. (2019), this seasonal and diel buffering disparity could be a result of weak buffers only buffering ambient temperatures at a detectable level in extreme heat or extreme cold.
This effect could explain the higher offsets seen during the rainy season, as the Kalahari experiences rainfall during some of its hottest months. Therefore, although thermal buffering was predicted to increase in the rainy season due to vegetation greening and soil moisture content, this may not be the prime cause. Thus, milder temperatures experienced during temperate seasons or years should be considered a confounding effect and accounted for in future work.

The recorded poor nighttime buffering may primarily be caused by heat loss to the night sky. One of the major heat sinks in drylands is via radiative heat loss to clear night skies, which can reach temperatures as low as -30 ˚C (Fuller *et al.*, 2021). Thus it is interesting to note that only microhabitats which were substantially sheltered from the night sky (Burrows and tree hollows) maintained a relatively high level of thermal buffering throughout the night, regardless of the season. These results suggest that exposed microhabitats, such as rock crevices and tree canopies, which have had high radiative heat gain during the day, will rapidly lose their heat via long-wave radiation to the cold atmosphere during the night (D'Odorico *et al.*, 2013), thus possibly reducing their insulating properties. Therefore these results highlight the importance of assessing microclimatic buffering capacity across the diel cycle, as different times of the day impose unique thermal challenges.

Furthermore, position above ground can have a substantial impact on experienced temperature, as depending on topography and ambient conditions, the heated topsoil can warm the layer of air just above the ground during the day (Sklenář et al., 2016). In my study, macroclimate ground-level temperatures were found to be warmer than macroclimate above-ground temperatures. Thus, although ground-level microhabitats were reported as providing better thermal buffering during the day, this may simply be due to the increased macroclimatic temperatures allowing for greater offsets. Nevertheless, during the night, there was no difference in macroclimate temperatures between the two positions, and ground-level microhabitats again provided greater buffering than above-ground. Thus, overall, it is likely that within the Kalahari, the most buffered microhabitats are available on or below the ground. Yet, it is important to note for future research, that there is a large difference between macroclimate temperatures measured at ground or above ground level, and that these differences need to be accounted for when performing microclimate and macroclimate comparisons across the diel cycle.

The drivers of microclimatic heterogeneity are diverse and complex (Dobrowski, 2011), making it extremely difficult to account for each confounding factor. Yet, as for most studies, the value of long-term data and comparative analyses cannot be overstated. Nonetheless, if comparing across multiple sites or microhabitat types, topoclimates or localised macroclimates need to be considered. As seen in this study, within the mountains, all microhabitats were weak thermal buffers throughout the night (Fig. 3.3b) yet the macroclimate temperatures in the mountains were slightly warmer than in the other habitats (Fig. 3.5). Thus, it is not an equal comparison between habitats, as the mountain microhabitat offsets are restricted by the overall warmth of their nighttime habitat. Consequently, microclimates can only be practically compared when the macroclimatic temperatures are equal, which may be problematic for review papers wanting to collate microclimatic buffering results. Furthermore, if microclimates are only assessed during one or two seasons, the results may be misleading, as the lack of extreme temperatures may mask strong buffering effects. Thus, both macro- and microclimatic data should be collected for as long as possible across temporal scales, or through at least a representative period of both extreme and mild temperatures.

3.4.4. Conclusions

Differences in microhabitat buffering capacity, whether caused by topography, season, or microhabitat density, provides flexibility in thermoregulatory behaviour for resident animals. Seeking shelter in microhabitats is seen to be one of the primary responses of animals to extreme environmental temperatures (Fuller *et al*., 2016), with many animals selectively moving between microhabitats to adjust for both hot and cold environments (Bartholomew and Hudson, 1961; Kinlaw, 1999; Anderson and Richardson, 2005; Hetem *et al.*, 2007; Fick *et al.*, 2009; Blank, 2020). Therefore, although we can identify specific microhabitats as better buffers, a high buffering capacity does not necessarily imply that the

microhabitat will always provide optimal thermal quality for all animals. If there are multiple different thermal options available in proximity, being able to shift between warm and cool microclimates may be more beneficial for an animal than remaining at one buffered intermediate temperature (Johnson *et al.,* 2022). Thus, having a diversity of microhabitats across multiple topographic or positional gradients may be more important, as animals can utilise the microhabitats as necessary. Accounting for this, and in line with the findings of Hannah *et al.* (2014), climate conservation measures should potentially be more focused on identifying and preserving a diversity of microhabitats, and not only aiming to preserve microrefugia.

Numerous studies have indicated that microclimatic assessments will be crucial in assessing species vulnerability under climate change (Suggitt *et al.*, 2011; Storlie *et al.*, 2014; Varner and Dearing, 2014), and that extreme-environment microclimate data for use in predictive mechanistic models are lacking, even on a global scale (Lembrechts *et al.*, 2020). Thus, the microclimatic data produced by this study have provided fine-resolution thermal data for use in further modelling and have presented a reference of what microclimatic shelter may be available in the drylands of Africa. Additionally, my study has emphasized the importance of burrow-digging ecosystem engineers, such as aardvarks and ground squirrels, which provide invaluable shelter to many other Kalahari species. Furthermore, my results have highlighted that vegetation and bird nests, as comparatively poor thermal buffers, are likely to be affected by increasing aridification and may not be able to provide substantial shelter to large mammals and birds under climate change. In conclusion, my work has provided a basis on which to improve microclimatic data collection that is specific to drylands. These data can thus be used to improve conservation assessments for dryland ecosystems and increase awareness of the conservation value of ecosystem engineering species.

Chapter 4 : Conclusion and synthesis

My study assessed the distribution and thermal buffering capacity of five distinct microhabitats (burrows, rock crevices, tree hollows, bird nests and vegetation) in three defined habitats (plains, dunes, and mountains), across topographic and seasonal gradients for a year. The data that were generated are some of the first to provide information on the temporal and spatial impacts that affect the distribution, density, and thermal buffering capacity of multiple microhabitats in an arid area. Climatic projections suggest that aridification, extreme temperatures and frequency of extreme weather events will increase across southern Africa (Engelbrecht *et al.*, 2015; Engelbrecht and Engelbrecht, 2016; Mirzabaev *et al.*, 2019; Masson-Delmotte *et al.*, 2021), with the potential to severely affect the persistence of many dryland animals. To assess animal vulnerability to climatic changes, their exposure risk should be evaluated (Dawson *et al.*, 2011). In the absence of migration, the level of exposure risk is dependent on behavioural thermoregulation and the availability of microhabitats within their habitat (Storlie *et al.*, 2014; Pincebourde and Woods, 2020; Neel *et al.*, 2021; Riddell *et al.*, 2021). Thus, by evaluating which microhabitats are available in a semi-arid landscape, and measuring their thermal buffering potential across seasons, I have provided information that can be used to assess the climate vulnerability of Kalahari animals and have highlighted the thermal value of ecosystem engineers.

Habitat type had a major influence on both microhabitat abundance and microhabitat thermal buffering capacity. The plains habitat had the highest densities of biotic microhabitats and the greatest overall thermal buffering during the day and night. Microhabitats in the dunes had a more patchy distribution, which is potentially part of the reason for their poorer thermal buffering abilities, as there is more open ground with high albedo sand surfaces that may reflect more incoming radiation during the day, and cause greater radiant heat loss to the open sky at night (Swinbank, 1963; Finch, 1972; D'Odorico *et al.*, 2013; Mitchell *et al.*, 2018). The mountain habitat consisted mostly of rock crevices and low-growing vegetation as

the only potential microhabitats and provided particularly poor thermal buffering across all microhabitat types during the night, although rock crevices still provided strong thermal buffering during the day. Thus, microhabitat abundance, which is dictated by a combination of abiotic and biotic habitat-specific properties, may affect the presiding macroclimate of the area, which in turn will affect the buffering capacity of the local microhabitats.

Thermal buffering varied seasonally across most vegetation dependant microhabitats (vegetation, bird nests and tree hollows), with the greatest buffering seen during the high-rainfall, summer period. This occurred possibly as a consequence of both the vegetation greening and higher day-time temperatures allowing for greater thermal offsets. Burrows remained the best thermally buffered microhabitat throughout the year, with little variation in buffering capacity seen across topographic or seasonal gradients. The mountain environment showed the strongest effects of topography on both microhabitat densities as well microhabitat buffering capacity, suggesting that the effects of topography on microhabitats may be increased with increasing elevation and steepness of slope. The position of microhabitats in the environment also affected the overall buffering capacity of microhabitats. Most ground-level or underground microhabitats offer greater buffering than above-ground microhabitats, which highlights the problems associated with microhabitat accessibility to individual animals (Riddell *et al.*, 2021). Although it is uncertain if the tested microhabitats will be able to buffer dryland animals against the full extent of future climatic extremes, these data have expanded our knowledge of microhabitat occurrence and their thermal buffering capacity.

4.1 The impacts of climate change on microhabitats

Although the latest climate change projections indicate the increasing likelihood of drought for the southern African region, they also indicate that

there have been increasing frequencies of pluvial flooding events (Masson-Delmotte *et al.*, 2021). These may be partially due to the increasing severity of the impacts of the El Niño-Southern Oscillation (ENSO). The ENSO strongly affects interannual rainfall patterns in southern Africa, specifically in the summer seasons from December to February (Hulme *et al.*, 2001). Throughout the period of my fieldwork, the Kalahari experienced summers within the La Niña phase (L'Heureux *et al.*, 2021). This phase, which is associated with increased rainfall (Ropelewski and Halpert, 1989; Hulme *et al.*, 2001), is predicted to continue throughout the summer of 2022, until early 2023 (L'Heureux *et al.*, 2022). Thus, although my project aimed to assess the availability and thermal buffering capacity of microhabitats in an arid environment, the reserve in which it was conducted experienced its highest levels of annual rainfall in the last ten years (Fig. 4.1) during the period of my study.

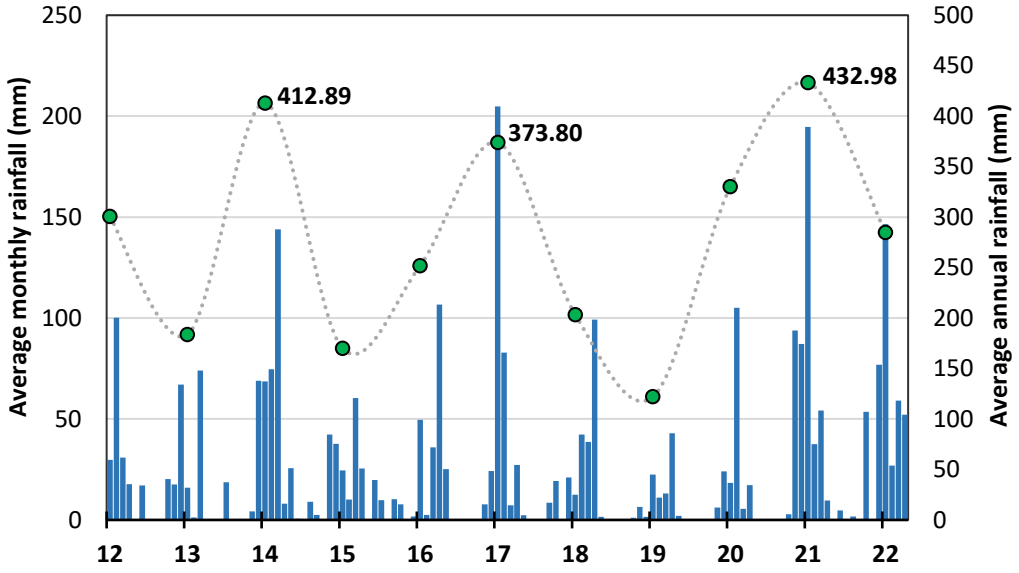

Figure 4.1. Average monthly (bars) and annual (dashed line) rainfall at Tswalu Kalahari Reserve over the last 10 years (2012–2022). The highest rainfall was recorded in 2014, 2017 and 2021 (Annual rainfall, in mm, provided in bold text).

The data presented in my study illustrates a 'best case scenario', where biotic microhabitat abundance is not restricted by drought conditions. However, it should be noted that the results, especially concerning the

abundance and thermal buffering potential of vegetation-dependent microhabitats, may differ under drier conditions. Furthermore, although the recent conditions experienced during this La Niña were not destructive within my study site, the projected pluvial flooding (Masson-Delmotte *et al.*, 2021) may not be beneficial in the future, especially in a system that is not adapted for it. Flooding can impact vegetation negatively through water-logging of roots and stems, the creation of anoxic root conditions (Parolin and Wittmann, 2010), direct damage to all above-ground plant bodies (including hosted nests and hollows), and destruction of burrow systems. Thus, except for rock crevices, it is likely that the occurrence of all microhabitats will be affected by any extreme climatic changes, whether that may be extreme droughts or flooding.

4.2 The relationships between microhabitats and exposure to extreme temperatures

Animals selectively move between microhabitats to effectively thermoregulate (Hetem *et al.*, 2007; Fick *et al.*, 2009; Sinervo *et al.*, 2010; Fuller *et al.*, 2016; Blank, 2020) but their use of microhabitats differs according to their physiological requirements and what microhabitats are available in their proximity (Woods *et al.*, 2015). My study has shown that the prevalence and thermal buffering capacity of microhabitats are affected by habitat type. Certain microhabitats, such as rock crevices, only exist in one habitat, whereas others, such as vegetation, are common across the landscape. Thus, depending on what kind of microhabitats an animal uses, and what habitat it exists in, it may be more, or less, restricted in its behavioural thermoregulatory abilities. Furthermore, habitats with greater overall densities of microhabitats showed increased thermal buffering within some of the local microhabitats. Although not necessarily a causal relationship, the enhanced buffering in individual microhabitats could be produced by increases in collective shading and consequent decreases in exposure to radiative sources or sinks. Therefore, animals that exist in habitats with fewer microhabitat options

available, or where microhabitats exist more sparsely, may be at a higher risk of climate exposure.

4.2.1 The value of thermal buffering in common and rare microhabitats

It should be considered that rare, but well-buffered microhabitats may still be extremely valuable to animals. A variety of arid-adapted animals, such as some snakes (Johnson *et al.*, 2022; T. Beck, pers. comm.), pangolins (Pietersen *et al.*, 2014) and meerkats (Strandburg-Peshkin *et al.*, 2019), will seek out and remember the location of specific microhabitats in their home range. For example, adult pangolins remember the location of their burrows and will consistently return to them for daily shelter (Pietersen *et al.*, 2014). Burrows throughout arid landscapes are also often utilised for longer-term resting, reproduction or vulnerable life stages by many animals – as seen with the facultative use of burrows by other non-fossorial animals for denning (Melton, 1976; Whittington-Jones *et al.*, 2011; Mukherjee *et al.*, 2019) and reproduction (Alexander, 2018). Therefore, microhabitats, even if rare, may be sought after if they are extremely thermally valuable to their occupants. Hence ecosystem engineering species are exceptionally important in dryland systems, as these rare and thermally valuable microhabitats are often created by them, as nesting or burrowing animals.

Nevertheless, poorer buffering microhabitats also remain important in the landscape. Some animals, such as pangolins, when unfamiliar with an area or during dispersal events, will use poorly buffered microhabitats such as rock crevices or vegetation as a temporary measure, for both shelter and predator avoidance, until they form their new home range (Pietersen *et al.*, 2014). Thus, a high density of poorly buffered microhabitats may still be valuable to animals as they can be accessed without spatial memory or any form of territoriality. Therefore, since exposure to extreme temperatures can be considered a cumulative

stressor (Rezende *et al.*, 2020), escaping ambient temperature extremes temporarily in relatively poor thermal shelters might be sufficient whilst foraging or dispersing. For longer periods, high-value thermal shelters may be necessary. Thus, the recorded diversity in my study, of rare, but well-buffered microhabitats, and common, but poorly buffered microhabitats may be an ecological factor that allows animals to balance their thermoregulatory needs with their activity.

4.2.2 The impacts of microhabitat accessibility on exposure to extreme temperatures

Individual animals will utilize different microhabitats according to their specific physiology, morphology, and size (Potter *et al.*, 2013; Woods *et al.*, 2015). Thus, it is access to, and not necessarily the availability of, microhabitats that affects population or community success under extreme environmental conditions (Riddell *et al.*, 2021). Both the size and position of a microhabitat can restrict accessibility, as its utility will vary according to the animals' size and morphological adaptations (fossorial, aerial etc.). Therefore, within the bounds of my study, the only microhabitat that would accommodate large (greater than 1 m in height) animals was vegetation, and the only microhabitats that most types of birds would be able to access were vegetation, nests, and tree hollows. Notably, vegetation was found to be a relatively poor thermal buffer year-round, and most microhabitats above ground (vegetation-canopy, bird nests and some tree hollows) were poorer buffers than those on or below the ground level. Furthermore, bird nests and tree hollows were rare across all habitats. Therefore, it is important to note that both large mammals and birds may be limited in their access to well-buffered microhabitats.

Mammals and birds have a variety of physiological mechanisms which they utilize to cope in drylands but these physiological mechanisms come at a high water and high metabolic cost (Du-Plessis *et al.*, 2012; Fuller *et al.*, 2021). With projected increasing aridity (Mirzabaev *et al.*, 2019) there

will be less food and water available in some environments to sustain these costs, resulting in animals becoming more reliant on behavioural thermoregulation (Fuller *et al.*, 2021). Arid-adapted bird populations have been seen to decline when there are insufficient numbers of thermally buffered microhabitats available (Riddell *et al.*, 2021), where exposure to consistent extreme heat conditions has led to chronic negative effects on their survival and reproductive rates (Conradie *et al.*, 2019; Pattinson *et al.*, 2022). These effects may be partially caused by the use of microhabitats reducing foraging time and increasing competition (Sinervo *et al.*, 2010; Fuller *et al.*, 2021). Therefore, for microhabitat use to be worthwhile in hot environments, the microhabitats need to be of high thermal buffering value, as this would help dissipate heat loads at a faster rate, meaning that the animal could remain in the microhabitat for shorter periods. Consequently, large mammals and birds may be at higher risk of climate exposure, not simply because they cannot access many microhabitats, but because they cannot access microhabitats that provide a sufficient level of thermal quality for their physiological requirements under climate change.

4.3 Topographic influences

Various features of topography, as drivers of topoclimatic heterogeneity, are relatively well documented (Pepin and Lundquist, 2008; Daly *et al.*, 2010; Dobrowski, 2011; Egli *et al.*, 2015; Aalto *et al.*, 2017; Massimino *et al.*, 2020), yet the relationship between the topoclimate and the abundance or buffering capacity of microhabitats is not as regularly identified. In my study, only the topographic features in the mountains were found to be associated with the density of certain microhabitats. Furthermore, topographic features in the mountains had much stronger associations with microhabitat buffering, than those tested in the dune habitat. Yet the Korannaberg mountains on the reserve are approximately 500 m at their maximum elevation above the plains (Davis *et al.*, 2010), whereas the dunes are only approximately 3–8 m above the plains (van

Rooyen and van Rooyen, 2017). Thus, the different aspects of the mountains are likely to experience more extreme differences in temperature and water accumulation than those in the dunes, as a consequence of vast differences in wind direction and radiation per aspect (McVicar *et al.*, 2007). Hence, the larger the topographic features are, the larger the differences will be in topoclimates, and the more likely the topography is to affect the distribution and buffering capacity of microhabitats.

Certain topographic features may also cause cascading effects within an ecosystem (Dobrowski, 2011). For example, the pooling of cool air or water affects the distribution of certain microhabitats, such as vegetation. Animals may consequently utilise the vegetation and shape further microhabitats, such as tree hollows or bird nests around these. Thus, both biotic and abiotic forces play a role in the distribution of microhabitats. In my study, I found that microhabitat prevalence in the dunes and plains was influenced by a combination of biotic community interactions and other non-topographic associated abiotic influences such as gradients in soil type and fire prevalence. Therefore, although the presence and buffering capacity of microhabitats may be driven by topography in highly topographically heterogeneous areas, in the absence of large topographic features, such as in savannas, other drivers should be considered. Although there is evidence in the literature that microclimates exist in the absence of topographic heterogeneity (Lenoir *et al.*, 2013; Milling *et al.*, 2018), microclimate studies are still northern-hemisphere dominated (SoilTemp, 2022), where topographic features often govern the landscape. Thus, it is important to note that the associations between topography and microhabitat prevalence or buffering may be different in African savannas.

4.4 Temporal influences

Seasonal increases in rainfall may cause vegetation greening, or increase the density of foliage (Davis *et al.*, 2019), which will have knock-on effects

on microhabitats in the surrounding areas. I found that most vegetation-based microhabitats had increased buffering during the summer rainfall period and that an increased density of surrounding vegetation increased the buffering capacity of some microhabitats within the area. However, extremes in macroclimate temperatures can be associated with an increase in the potential difference between the macro- and microclimate temperatures (De Frenne *et al.*, 2019). Thus, the recorded increase in buffering during the summer period may have been related to both an increase in vegetation greening and the increased macroclimatic temperatures. Therefore, seasonality is an important confounding factor to note in future work, as microhabitats that exist in areas that experience fewer thermal extremes may reflect as having a poorer buffering capacity than those that exist in extremely hot or cold environments. Considering that many studies are only run over one or two seasons, these assessments may not provide an accurate representation of the extent of microhabitat buffering, unless a representation of both mild and extreme weather seasons is chosen.

Similarly, within my study, thermal buffering was seen to differ across the diel cycle. Throughout the year, the weaker thermal buffering microhabitats showed greater thermal buffering during the daytime periods than during the nighttime. This trend could be due to the hot daytime temperatures being more extreme than the cold experienced during the night, allowing for greater thermal offsets during the day. However, even during the winter period when nighttime temperatures frequently dropped below 0 ˚C, nighttime buffering remained poor. The only microhabitats that remained good buffers during the nighttime, regardless of season, were burrows and tree hollows. Therefore, these results could suggest that only microhabitats that are sheltered from the night sky (within a tree trunk and underground) may be protected from extreme radiative heat loss. At night, a clear night sky acts as a massive heat sink (Swinbank, 1963; Mitchell *et al.*, 2018). Thus, microhabitats such as rock crevices or tree canopies,

which are warmed during the day by radiative heat gain, and are directly exposed to the open sky, will rapidly lose long-wave radiation to the cold atmosphere above them during the night (D'Odorico *et al.*, 2013). Consequently, it is important to assess buffering capacity both across day and night, as different times of the day impose divergent thermal restrictions on animals, especially within dryland areas.

4.5 The future of microclimate research

Predicting the vulnerability of species to climate change will require a holistic view of many aspects impacting both animals and their environment. Microhabitats, as essential forms of shelter, are directly linked to the exposure risk of animals within an environment. Yet it is often assumed if microhabitats are accessible within an environment, that all animals will be able to use these microhabitats to avoid lethal exposure (Kearney *et al.*, 2018). However, depending on the distribution or prevalence of these microhabitats, animals may still experience restricted access to thermal shelter (Kearney *et al.*, 2021; Briscoe *et al.*, 2022), as the distances between microhabitats may be too far for smaller animals whose body temperatures fluctuate rapidly in response to the macroclimate (Sears and Angilletta, 2015). Furthermore, the costs of utilising microhabitats that are spatially far apart may be too high, as foraging times may be greatly restricted (Sinervo *et al.*, 2010), and food decreases could further diminish the physiological capacity to respond to thermal extremes (Fuller *et al.*, 2016). Thus, the concurrent assessment of the distribution, abundance and buffering capacity of microhabitats should be supported in future work.

The data generated by my study have provided a representation of the abundance of microhabitats, their thermal buffering capacities over time and their abiotic and biotic drivers within the Kalahari. Yet the methodology used, due to its' time-consuming and labour-intensive nature, is unlikely to be feasible to repeat at larger scales, making it relatively

impractical for conservation measures in the future. With the rise of new drone photogrammetry and LiDAR mapping technologies used to achieve accurate, extremely high resolution, 3D maps of topography (Choi *et al.*, 2019; Duffy *et al.*, 2021), it is becoming possible to assess the thermal landscape over much larger areas of land at a more efficient pace. Therefore, especially for the identification and assessment of the distribution of microhabitats, these newer technologies should be utilised. However, studies using *in-situ* thermal loggers, as was the case in my study, are still needed to provide high-resolution and ground-truthed thermal data across long periods. These data are critical for use in biophysical and mechanistic modelling (Kearney and Porter, 2017; Briscoe *et al.*, 2022), and if combined with more comprehensive distribution data, could substantially contribute to increasing the accuracy of species vulnerability assessments.

4.6 Conclusions

Many dryland animal species face an uncertain future, where well-sheltered microhabitats may be the 'final frontier' that stands between them and considerable population declines. Drylands, at present, cover two-thirds of Africa (Mbow *et al.*, 2021), and southern Africa is projected to experience continued increases in aridity under climate change (Masson-Delmotte *et al.*, 2021). Yet microclimate research remains more common in the Northern Hemisphere, which provides results that may not be applicable in African dryland systems. My study has presented one of the first datasets on the prevalence of multiple types of microhabitats within a dryland system and has provided a fine-resolution dataset of the microclimatic thermal landscape over the course of a year. The results have revealed that abiotic drivers, such as fire and soil type, along with biotic community composition may shape microhabitat abundance in savanna areas and have highlighted which microhabitats formed by indigenous, burrowing species may be vital for ecosystem functioning under climate change. Thus, although improvements should be

implemented in future work, this study has provided a baseline on which to develop more targeted, efficient, and much-needed microclimate assessments for the drylands of southern Africa.

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Appendix

Table A2.1: Linear relationships between slope, aspect, and microhabitats in the mountain habitat

Microhabitat	R2	Predictors		beta	95% CI	p-value
Shrubs	0.62	Slope		5.26^{-3}	9.95^{-4}, 9.52^{-3}	< 0.05
Large rock crevices	0.51	Slope		5.97^{-3}	1.84^{-3}, 0.01	< 0.05
		Aspect	North	0.07	9.33^{-3}, 0.14	< 0.05
			South	-3.86^{-3}	-0.08, 0.07	> 0.05
			Top	0.04	-0.04, 0.12	> 0.05
			West	-0.02	-0.08, 0.05	> 0.05
Medium rock crevices	0.14	Slope		8.67^{-3}	6.88^{-4}, 0.02	< 0.05
Small rock crevices	1.47^{-4}	Slope		1.58^{-4}	-4.68^{-3}, 5.00^{-3}	> 0.05

Table A2.2: The linear relationships between slope, aspect, and microhabitats in the dunes.

Microhabitat	R2	Predictors		beta	95% CI	p-value
Trees	0.60	Slope		-4.87^{-3}	-0.12, 0.11	> 0.05
Shrubs	0.07	Slope		-0.06	-0.13, 0.01	>0.05
		Aspect	Top	-0.30	-0.80, 0.19	>0.05
			Valley	0.38	-0.05, 0.82	>0.05
			West	0.38	-4.41^{-3}, 0.75	0.05
Large burrow	0.36	Slope		0.14	-0.11, 0.39	>0.05
Medium burrow	0.20	Slope		0.09	-0.07, 0.24	>0.05
Small burrow	2.04^{-4}	Slope		-0.02	-0.07, 0.03	>0.05



Figure A3.1. Left: An example of a ‘groundcover’ cluster of grass. The yellow dot represents the placement of the temperature logger underneath the leaves. Right: leaves moved aside on the same cluster of grass to show the placement of the logger (encircled in yellow).

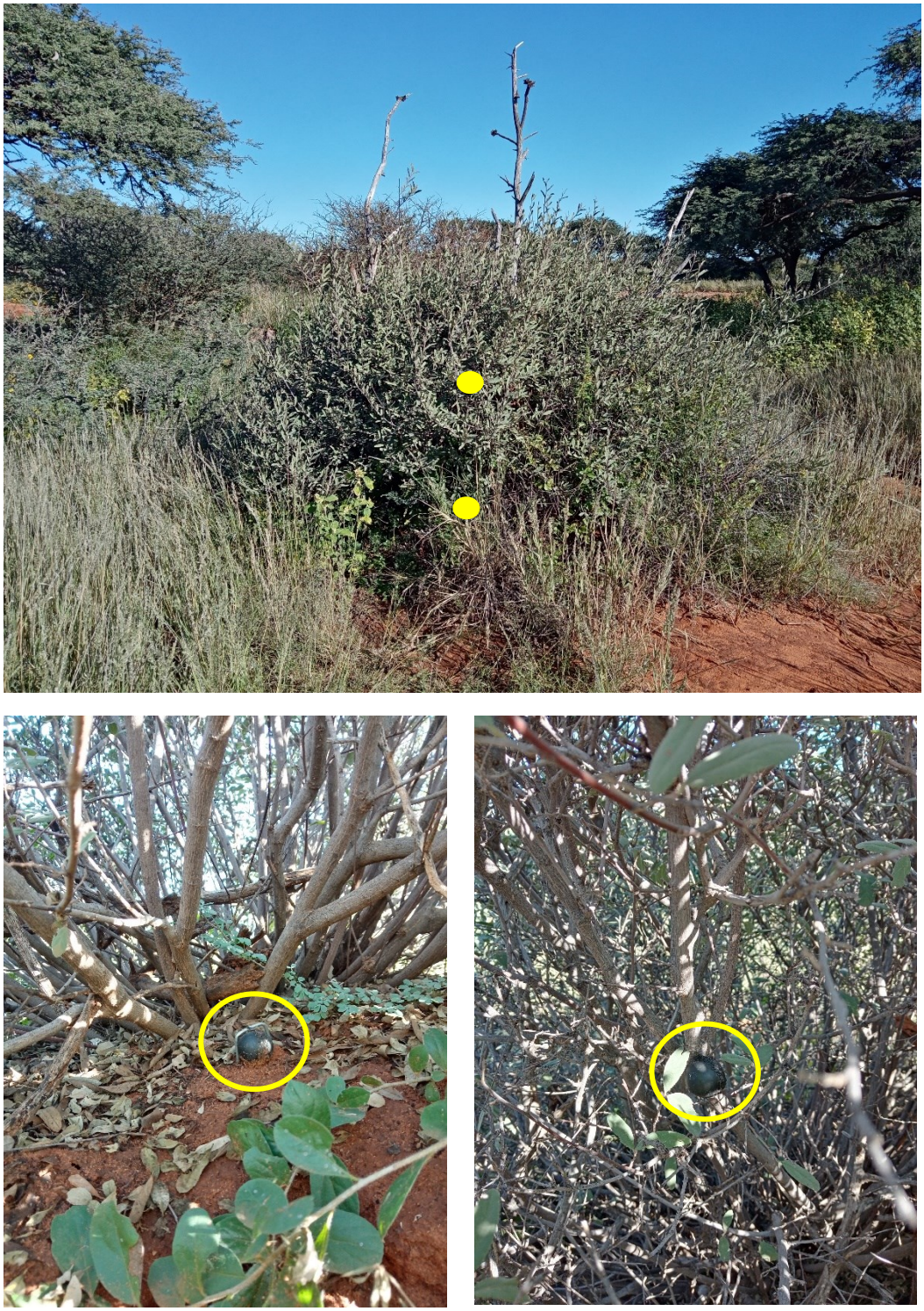

Figure A3.2. Top: A shrub, where the approximate placement of the ‘shrub base’ and ‘shrub middle’ temperature loggers were placed is highlighted in yellow. Bottom left: the ‘shrub base’ logger at the base of the shrub. Bottom right: the ‘shrub middle’ logger tied to a branch in the approximate centre of the shrub (loggers encircled in yellow).

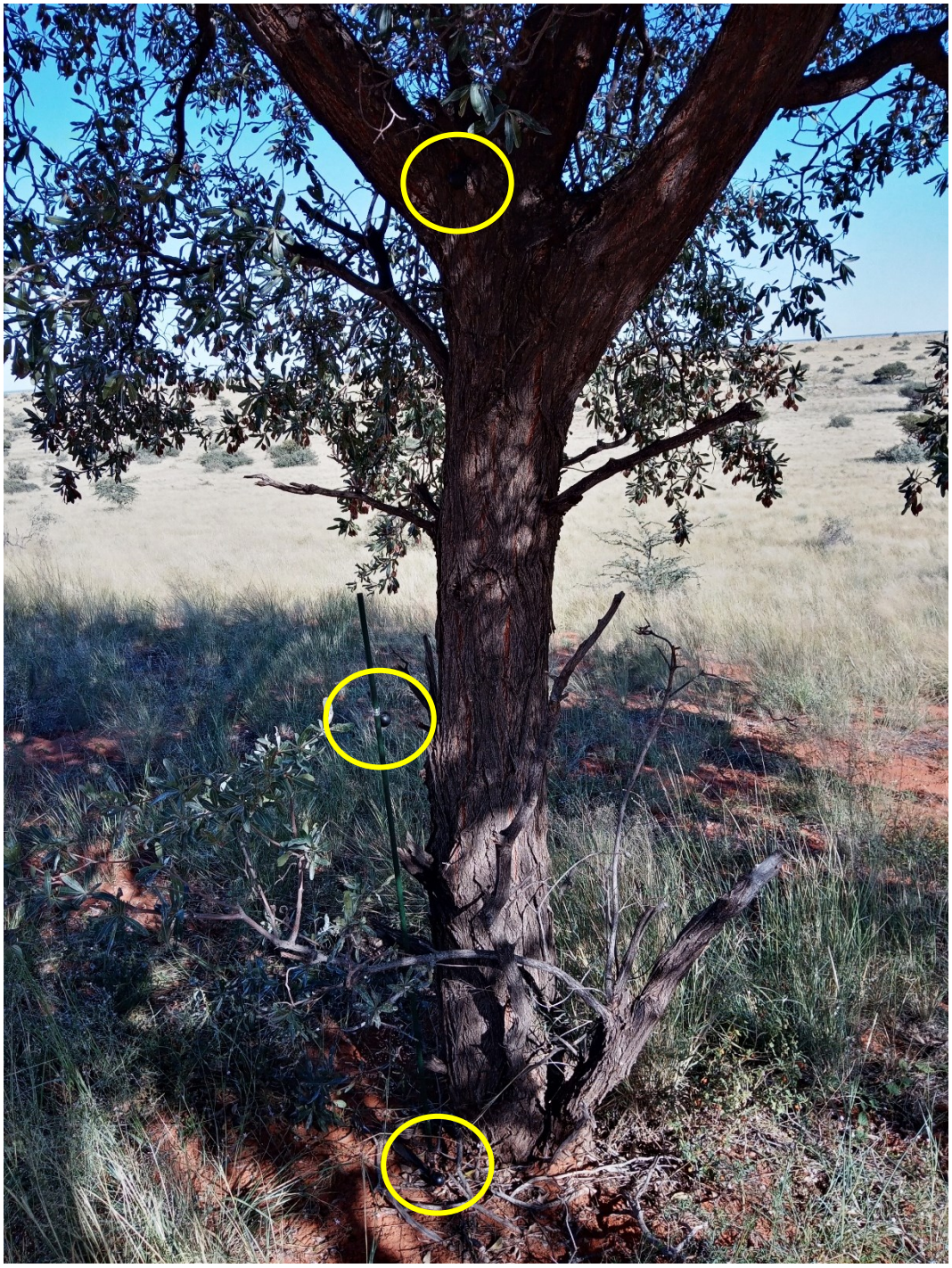

Figure A3.3. A tree showing the placement of the ‘tree base’, ‘tree middle’ and ‘tree canopy’ loggers (encircled in yellow).



Figure A3.4. A tree with an ‘abiotic hollow’ in the trunk. The yellow circle highlights the hollow which has a temperature logger placed inside of it and sealed with wire mesh to prevent disturbance from wildlife.



Figure A3.5. A tree with a ‘biotic hollow’ in its trunk. The hollow, wherein the logger is placed, is covered with wire mesh to prevent disturbance of the logger by wildlife.

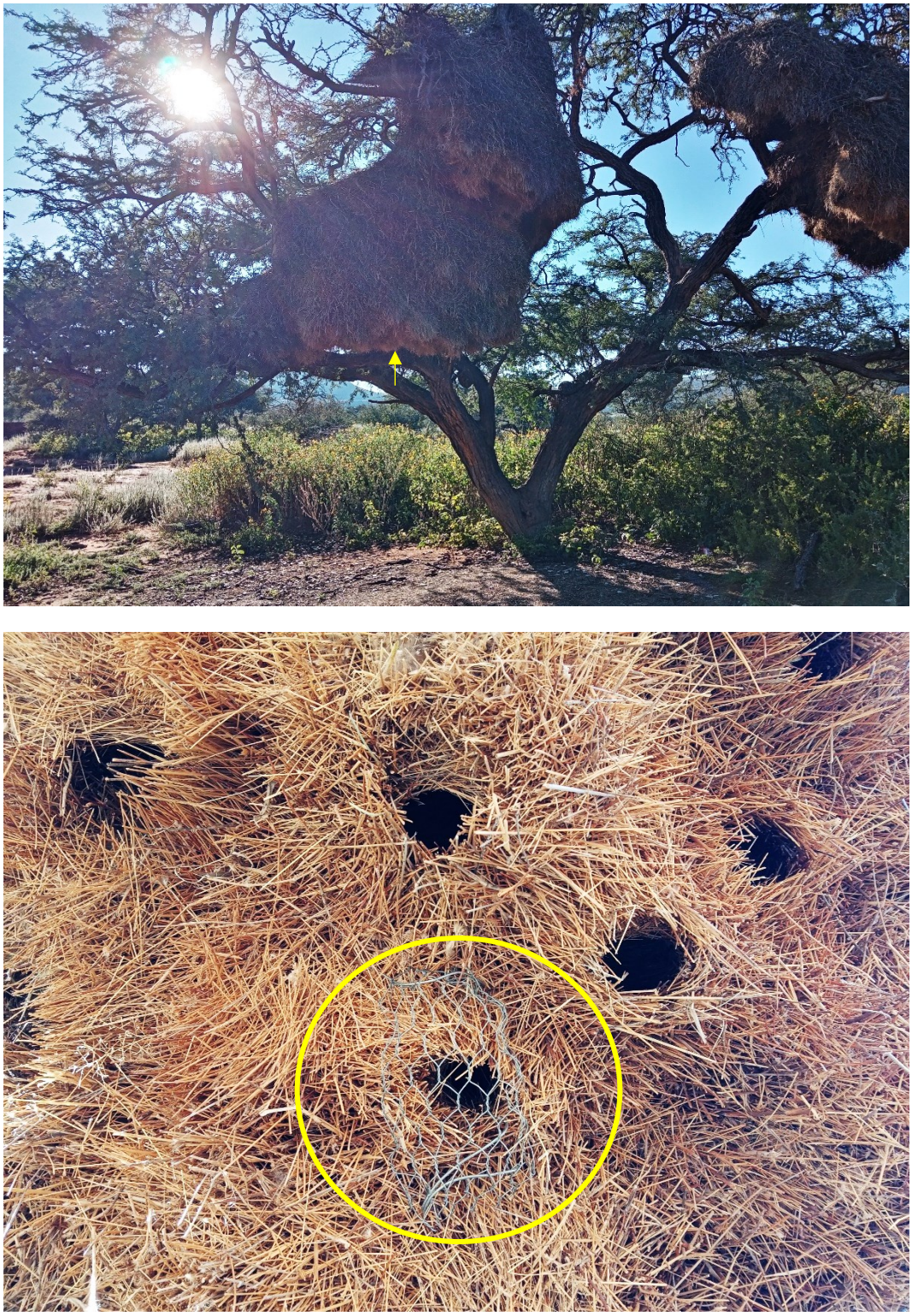

Figure A3.6. Top: A sociable weaver nest, with yellow arrow showing the placement of the temperature logger in a central chamber. Bottom: a view of the sociable weaver nest from below, showing the mesh covered nest entrance of the nesting chamber with a logger in it.



Figure A3.7. Top: A small burrow entrance, with the wire from the temperature logger exiting the burrow on the right-hand side. Bottom: A medium burrow entrance, with the wire from temperature logger visible exiting the burrow on the right-hand side.



Figure A3.8. A large burrow entrance, with the wire from the temperature logger exiting the burrow on the left-hand side.



Figure A3.9. Above: a small rock crevice. This photo was captured as the logger was being collected for data download — when placed for data collection, the coil of wire currently visible on top of the rock was fastened to the neighbouring rock and was not invasive or obviously visible in the environment. Below: a medium rock crevice with the wire connected to the temperature logger visible exiting the crevice centrally. The wire was fastened to the neighbouring rock, visible in the bottom right corner of the photo.

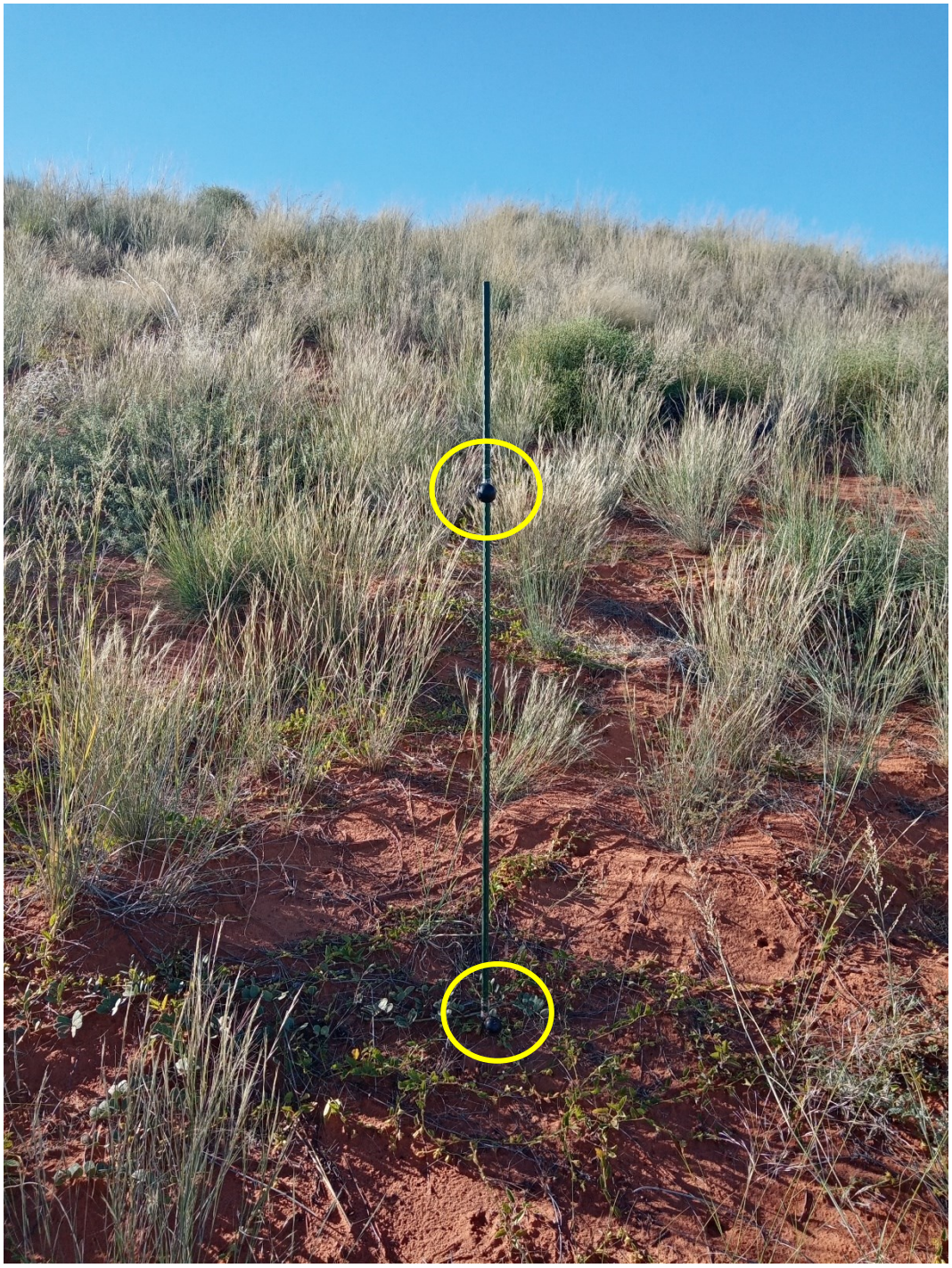

Figure A3.10. An example of one of the 'exposed site' macroclimate loggers in the dunes. Temperature loggers at ground level and above-ground level are encircled in yellow.

Table A3.1 a: Daytime buffering capacity (B_1) of vegetation microhabitats in the dune habitat

Month	GCW	GCE	SHBW	SHBE	SHCW	SHCE
Jan	0.79	0.80	0.54	0.63	0.69	0.71
Feb	1.00	0.84	0.71	0.82	0.67	0.72
Mar	1.00	0.68	0.47	0.51	0.65	0.67
Jun	0.73		0.38		1.00	
Jul	0.99		0.59		0.93	
Aug	0.85	0.75	0.32	0.52	0.81	0.91
Sept		1.00	0.47	0.76	0.93	1.00
Oct	1.00	0.67	0.66	0.92	0.85	0.95
Nov	0.99	0.81	0.84	0.59	0.96	0.88
Dec		0.77		0.58		0.79
Month	**TRBW**	**TRBE**	**TRMW**	**TRME**	**TRCW**	**TRCE**
Jan	0.63	0.56	0.66	0.65	0.67	0.65
Feb	0.63	0.66	0.62	0.56	0.65	0.61
Mar		0.55	0.63	0.61	0.65	0.59
Jun	0.52		1.00		1.00	
Jul	0.73		0.92		0.95	
Aug	0.46	0.64	0.87	0.93	0.88	0.94
Sept	0.79	0.91		1.00	0.92	1.00
Oct	0.61	0.59		0.78	0.79	0.75
Nov	0.93	0.50		0.90	0.99	0.92
Dec		0.53		0.72		0.74

Table A3.1b: Daytime buffering capacity (B_1) of hollow, nest and burrow microhabitats in the dune habitat

Month	AHW	SWW	WBW	WBE	SBW	SBE	MBW	MBE	LBW	LBE
Jan	0.56	0.25		0.58	0.30	0.00	0.06	0.02	0.01	0.01
Feb	0.61	0.64		0.598	0.28	0.10	0.02	0.04	0.04	0.06
Mar	0.63	0.44		0.56	0.30	0.03	0.04	0.03	0.02	0.00
Jun		0.96					0.05		0.13	
Jul	0.80	0.87	0.85				0.02		0.05	
Aug	0.70	0.62	0.90	0.91		0.05		0.07	0.02	0.03
Sept		0.73		0.95	0.11	0.25	0.05	0.22	0.08	0.13
Oct	0.68	0.63			0.03	0.05	0.03	0.02	0.02	0.01
Nov	0.76	0.99		0.93	0.11	0.01	0.17	0.01	0.16	0.04
Dec				0.69		0.05		0.04		0.00

Table A3.2: Daytime buffering capacity (B_1) of all microhabitats in the plains habitat

Month	GC	SHB	SHC	TRB	TRM	TRC	
Jan	0.72	0.30	0.48	0.36	0.40	0.29	
Feb	0.61	0.31	0.73	0.35	0.55	0.49	
Mar	0.71	0.38	0.74	0.49	0.62	0.56	
Jun			0.80		0.81	0.92	
Jul	0.78	0.88	0.91	0.99	0.89	0.96	
Aug	0.72	0.75	0.88	0.82	0.88	0.92	
Sept	0.89	0.72	0.98	0.45	0.99	1.00	
Oct	0.81	0.47	0.58	0.41	0.57		
Nov	0.95	0.85	0.36	0.72	0.41	0.34	
Dec				0.37		0.61	
Month	**AH**	**BH**	**SB**	**MB**	**LB**	**WB**	**SW**
Jan			0.01	0.03			
Feb	0.15	0.16	0.09	0.09	0.03		0.28
Mar	0.15	0.29		0.06	0.06		0.26
Jun						0.81	
Jul	0.49	0.73	0.36			1.00	0.97
Aug	0.57	0.47	0.11	0.04	0.21	0.95	0.81
Sept	0.59	0.67	0.07	0.12	0.17	1.00	0.74
Oct	0.31	0.52	0.10	0.07	0.06		0.60
Nov	0.42	0.69	0.17	0.12	0.07	0.49	0.89
Dec						0.62	

Table A3.3: Daytime buffering capacity (B_1) of all microhabitats in the mountain habitat

Month	GCE	GCW	SHBE	SHBW	SHCE	SHCW	TRBE
Jan	0.76	0.41	0.76	0.47	0.53	0.91	
Feb	1.00	0.55	1.00	0.45	0.46	0.81	
Mar	0.56	0.50	0.53	0.40	0.42	0.86	
Jun							
Jul							0.68
Aug	0.70	0.92		0.58		0.88	0.73
Sept	0.89	1.00	0.63	0.83		0.94	0.82
Oct	0.94	0.81	0.53	0.73		0.94	0.54
Nov	0.85	0.81	0.59	0.81		0.95	0.57
Dec		0.84		0.71		0.90	
Month	**RCSE**	**RCSW**	**RCME**	**RCMW**	**RCLE**	**RCLW**	
Jan	0.65	0.50	0.74	0.42	0.55	0.22	
Feb	0.95	0.43	1.00	0.46	1.05	0.32	
Mar	0.45	0.41	0.48	0.34	0.43	0.24	
Jun							
Jul	0.05		0.38		0.16		
Aug	0.26	0.43	0.64	0.53	0.33	0.38	
Sept	0.45	0.60	0.74	0.74	0.57	0.54	
Oct	0.35	0.44	0.57	0.62	0.46	0.29	
Nov	0.35	0.57	0.47	0.75	0.54	0.56	
Dec		0.45		0.65		0.35	

Table A3.4a: Nighttime buffering capacity (B_1) of vegetation microhabitats in the dune habitat

Month	GCW	GCE	SHBW	SHBE	SHCW	SHCE
Jan	0.72	0.87	0.81	0.72	1.00	1.00
Feb	1.00	0.80	0.67	0.66	0.87	0.91
Mar	0.83	0.95	0.73	0.78	0.96	0.99
Jun	1.00		0.78		0.91	
Jul	1.00		0.76		0.95	
Aug	0.98	0.86	0.72	0.78	0.95	0.98
Sept		0.86	0.79	0.78	0.96	0.99
Oct	0.99	0.97	0.76	0.92	0.99	0.98
Nov	0.95	0.90	0.80	0.81	1.00	1.00
Dec		0.94		0.78		0.98
Month	**TRBW**	**TRBE**	**TRMW**	**TRME**	**TRCW**	**TRCE**
Jan	0.99	0.99	0.96	0.99	0.94	0.98
Feb	0.48	0.48	0.87	0.93	0.77	0.86
Mar	1.00	1.00	0.93	1.00	0.88	1.00
Jun	0.97		0.94		0.91	
Jul	0.90		0.96		0.95	
Aug	0.90	0.88	1.00	0.98	0.97	0.97
Sept	0.99	0.93		0.97	0.96	0.98
Oct	1.00	0.98		1.00	0.99	1.00
Nov	1.00	0.97		1.00	1.00	1.00
Dec		0.97		1.00		1.00

Table A3.4b: Nighttime buffering capacity (B_1) of hollow, nest and burrow microhabitats in the dune habitat

Month	AHW	SWW	WBW	WBE	SBW	SBE	MBW	MBE	LBW	LBE
Jan	0.89	1.00		0.96	0.49	0.33	0.12	0.22	0.23	0.23
Feb	0.85	0.84		0.94	0.55	0.24	0.02	0.17	0.25	0.12
Mar	0.87	0.92		1.00	0.64	0.17	0.10	0.17	0.24	0.18
Jun		0.76					0.03		0.74	
Jul	0.94	0.81	1.00				0.01		0.45	
Aug	0.91	0.80	0.96	0.97		0.06		0.19	0.38	0.47
Sept		0.84		0.99	0.16	0.20	0.09	0.28	0.42	0.49
Oct	0.98	0.94			0.10	0.14	0.02	0.12	0.31	0.31
Nov	0.91	0.90		0.99	0.13	0.02	0.14	0.19	0.34	0.33
Dec				1.00		0.24		0.38		0.29

Table A3.5: Nighttime buffering capacity (B_1) of all microhabitats in the plains habitat

Month	GC	SHB	SHC	TRB	TRM	TRC	
Jan	0.95	0.84	0.80	0.85	0.70	0.36	
Feb	0.94	0.86	0.88	0.81	0.75	0.46	
Mar	1.00	0.94	0.67	0.90	0.65	0.52	
Jun			0.82		0.81	0.65	
Jul	0.88	0.98	0.78	1.00	0.78	0.65	
Aug	0.88	0.97	0.86	0.96	0.85	0.75	
Sept	0.89	0.95	0.95	0.65	0.94	0.87	
Oct	0.82	0.75	0.86	0.89	0.90		
Nov	0.98	1.00	0.96	0.92	0.93	0.87	
Dec				0.90		0.93	
Month	**AH**	**BH**	**BM**	**SB**	**LB**	**WB**	**SW**
Jan			0.21	0.56			
Feb	0.26	0.11	0.17	0.00	0.39		0.13
Mar	0.58	0.50	0.32		0.61		0.47
Jun						0.51	
Jul	0.56	0.48		0.12		0.73	0.68
Aug	0.57	0.46	0.09	0.06	0.40	0.69	0.51
Sept	0.66	0.78	0.21	0.10	0.50	0.86	0.82
Oct	0.48	0.64	0.11	0.09	0.30		0.76
Nov	0.42	0.55	0.09	0.23	0.21	0.73	0.69
Dec						0.96	

Table A3.6: Nighttime buffering capacity (B_1) of all microhabitats in the mountain habitat

Month	GCE	GCW	SHBE	SHBW	SHCE	SHCW	TRBE
Jan	1.00	0.94	0.82	0.97	1.00	1.00	
Feb	1.00	1.00	1.00	1.00	0.67	1.00	
Mar	0.97	1.00	0.80	1.00	0.53	1.00	
Jun							
Jul							0.88
Aug	0.93	1.00		1.00		1.00	1.00
Sept	0.93	1.00	1.00	0.99		1.00	0.94
Oct	0.99	1.00	1.00	1.00		1.00	1.00
Nov	0.94	1.00	0.99	1.00		1.00	0.99
Dec		1.00		1.00		0.95	
Month	**RCSE**	**RCSW**	**RCME**	**RCMW**	**RCLE**	**RCLW**	
Jan	0.75	1.00	1.00	1.00	0.89	1.00	
Feb	1.00	1.00	1.00	1.00	1.00	1.00	
Mar	0.70	1.00	0.98	1.00	0.92	1.00	
Jun							
Jul	0.13		0.51		0.36		
Aug	0.35	1.00	0.85	1.00	0.62	0.84	
Sept	0.69	0.91	0.89	0.95	0.78	0.84	
Oct	0.57	1.00	1.00	1.00	1.00	1.00	
Nov	0.60	0.84	0.90	0.95	0.86	0.82	
Dec		1.00		1.00		1.00	