THE EFFECT OF PIOSPHERES ON THE ECOLOGY OF INSECTIVOROUS BIRDS AND THEIR ARTHROPOD PREY

By

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PREFACE

The experimental work described in this thesis was performed on the two properties owned by Simon White in the Eastern Cape Province of South Africa. The data for the study was collected from April 2021 to October 2022.

The study was conducted under the supervision of Professor Ben Smit of Rhodes University.

These studies present original work by the author, and these have not been submitted in any other form for any other degree or diploma to any other University. Where use has been made of work of others it is duly acknowledged in the text.

All procedures related to the use of animals in these studies were approved by the Rhodes University Animal Research Ethics Committee, RU-AREC (clearance certificate 2021-4859-5909).

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ABSTRACT

Desertification is the degradation of arid ecosystems that result in the loss of biodiversity. Piospheres are areas of local degradation around a central point due to overgrazing and increased herbivore presence. There is a paucity of information regarding the effect of localised degradation on arthropods and insectivorous birds. Both of these organisms play crucial roles in ecosystem functioning and stability and can be used as models to study ecosystem functioning.

I investigated the effect of piospheres on arthropods and birds in the Eastern Cape province of South Africa. I found that the abundance and diversity of arthropods were significantly reduced inside the piospheres due to the lack of vegetation. Termites were a group specifically negatively impacted by piospheres, with a significant reduction in their presence inside the piosphere. The family composition of arthropods also changed inside and outside the piospheres, with Caelifera, Diptera and Formicidae being the most dominant groups. The diversity of birds was also significantly reduced due to the degradation inside the piospheres. Looking at insectivorous birds, I found that the reduction in both vegetation and arthropod prey availability resulted in non-random avoidance of piospheres. This shows that piospheres negatively impact both arthropods and birds. The results from my study are supported by other literature studying the effects of habitat degradation associated with desertification. Due to the similarities of degradation between piospheres and desertification I make the argument that piospheres can be studied as localised models of desertification.

The decrease in vegetation and arthropod abundance and diversity was found to further impact the feeding success of insectivorous birds. Using piospheres as a model for desertification, I found that the foraging effort of birds is significantly reduced within a degraded area due to the lack of vegetation providing safety to arthropod prey species. In addition to this, the foraging efficiency of insectivorous birds is significantly reduced inside the piospheres due to the decreased arthropod abundance and diversity. This shows that inside the piospheres birds spend less time searching for insects and have fewer successful feeds. This has implications for desertification of arid environments where birds face hyperthermia.

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CHAPTER 1:
INTRODUCTION

The loss of biodiversity and abundance of organisms has been noted and studied worldwide as the environment faces habitat loss and degradation, a changing climate, and anthropogenic disturbances (Cardinale *et al.* 2012; Allen *et al.* 2015; van Dover *et al.* 2017; Scheele *et al.* 2019). Anthropogenic disturbance is a broad term for the human population's multiple adverse effects on the environment (Forbes *et al.* 2002; Goodale *et al.* 2015; Ribeiro *et al.* 2015; Nabe-Nielsen *et al.* 2018). These adverse effects include deforestation; habitat fragmentation; urbanisation; agricultural land-use intensification; and overgrazing (Goodale *et al.* 2015; Ribeiro *et al.* 2015; Martínez-Ramos *et al.* 2016; Matuoka *et al.* 2020). Disturbances to the habitat often result in systematic loss of vegetation and primary productivity in an environment (Goodale *et al.* 2015; Ribeiro *et al.* 2015; Thom & Seidl 2015; Nabe-Nielsen *et al.* 2018; Mirzabaev *et al*. 2019; Huang *et al*. 2020). The combination of climate change and habitat degradation poses significant threats to the world's biodiversity, habitat stability and ecosystem functionality (Mantyka-Pringle *et al.* 2015; Ribeiro *et al.* 2015; Matuoka *et al.* 2020; Raven & Wagner 2021). An example of the extent to which habitat degradation can affect biodiversity can be seen in insect populations in Western and Northern Europe that face severe declines (Biesmeijer *et al.* 2006; Hallman *et al* 2017; Habel *et al.* 2019; Raven & Wagner 2020). van Strien *et al.* (2019) found that the species-specific estimates of relative population sizes of butterflies declined by 84% from 1890–2017 in the Netherlands due to habitat degradation associated with land use changes.

Arid ecosystems and drylands are also threatened by climate change and habitat degradation. Dryland ecosystems refer to ecosystems with a ratio of potential evaporation to precipitation below 0.65, according to the Aridity Index (Safriel & Adeel 2005; Maestre *et al.* 2017; Greve *et al.* 2019). Due to the low levels of precipitation, these ecosystems are especially prone to the effects of degradation and climate change (Reynolds *et al.* 2007; Bestelmeyer *et al.* 2015). Dryland and arid ecosystems are estimated to cover 40% of the global land area across the African continent, western North America, Australia, the Middle East and Central Asia (Tang *et al.* 2016; Mirzabaev *et al.* 2019; Huang *et al.* 2020). These areas also face degradation, with the term desertification being defined as the degradation of dryland ecosystems due to multiple factors, including climate change, agricultural land-use intensification and overgrazing (Glantz & Orlovsky 1983; Hoffman & Cowling 1990; Archer

& Tadross 2009; Mirzabaev *et al.* 2019; Huang *et al*. 2020). The degradation of these arid landscapes, as with other ecosystems, also results in biodiversity loss (Mirzabaev *et al*. 2019).

Desertification and biodiversity loss

Vegetation is often affected when an arid ecosystem faces desertification. Although this term is often associated with an area transitioning into a desert landscape, this is not the case. Instead, the landscape's dominant vegetation type and community can shift or change, and specific species found in the area may no longer occur there due to a change in water availability and soil nutrients (Sheffer & Carpenter 2003; von Wehrden *et al*. 2012; Zhao *et al.* 2013; Estringana *et al.* 2014; Bestelmeyer *et al.* 2015). An example of vegetation changes can be seen in grasslands affected by desertification (von Wehrden *et al*. 2012; Zhang *et al.* 2018; Jiang *et al.* 2019). It has been found that grasslands most commonly shift to sparsely vegetated lands due to a lack of precipitation, or to shrub and woodlands with less herbaceous vegetation due to a decrease in fire (Seabloom *et al.* 2003; D'Odorico *et al.* 2013; Bestelmeyer *et al.* 2013; Zhang *et al.* 2018).

Vegetation structure and composition in ecosystems are also likely to change when faced with overgrazing and trampling due to an area's high concentration of livestock (Glantz & Orlovsky 1983; Archer & Tadross 2009; D'Odorico *et al.* 2013; Huang *et al.* 2020). Overgrazing is one of the leading factors contributing to desertification in rangeland areas often resulting in livestocks' hooves cutting through plant roots, a shift in common plants, and the overconsumption of plants resulting in their inability to reproduce (Li *et al.* 2000; Ibáñez *et al.* 2007; Archer & Tadross 2009; Geist 2017; Huang *et al.* 2020). An example of how desertification affects vegetation can be seen in south-western Algeria where vegetation species richness decreased from 234 species in 1978 to 95 species in 2011 (Mirzabaev *et al.* 2019).

The changes seen in vegetation due to desertification also have further impacts on the environment. Changing vegetation type is likely to alter the soil that vegetation grows in, both due to increased soil erosion and altered soil properties (D'Odorico *et al.* 2013; Bestelmeyer *et al.* 2013; Tang *et al.* 2018). Vegetation cover is seen as the main factor that controls erosion as infiltration and runoff are affected by the vegetation in the area (Zachar 2011; Haregeweyn 2013; Zhao *et al.* 2013; Estringana *et al.* 2014). Erosion also negatively affects vegetation as it is known to deplete soil resources and decrease the quality of water due to the increased turbidity and particle-born pollutants, creating a challenging environment for vegetation to grow (Chomitz & Kumari 1998; Labrière *et al.* 2015; Abd El-Salam & Elhakem 2016).

Desertification has also been recorded to affect the physical properties of soil, with fine soil particles being found to decrease in degraded areas while sand content of soils increased, decreasing the likelihood of potential land productivity (Zhao *et al.* 2009; Sousa *et al.* 2012; Tang *et al.* 2016; Tang *et al.* 2018; An *et al.* 2019). Chemically, soil is also known to change when faced with degradation, and it was found that desertification negatively affects both carbon and nitrogen fixation which has a negative effect on the structure and functioning of an ecosystem (An *et al.* 2019). In addition, desertification has been found to decrease soil nutrients while increasing soil salinity, and interfering with the ecosystem's carbon, nitrogen and phosphorus nutrient cycling systems (Khanamani *et al.* 2017; Qiu *et al.* 2018; An *et al.* 2019). These changes in the soil further affect the microorganisms and the vegetation that relies on the soil, with the impact on vegetation growth and stability further affecting herbivorous organisms (Bestelmeyer *et al.* 2013; Khanamani *et al*. 2017; Qiu *et al*. 2018; An *et al.* 2019; Haj-Amor *et al.* 2022).

A combination of vegetation and soil degradation, and the reduction in water availability due to desertification is also likely to affect all fauna. Mammals and birds that implement evaporative cooling techniques when experiencing high ambient temperatures are likely to be affected by these affects as they implement behaviours that rely on drinking water and sufficient food sources for evaporative cooling techniques (Hetem *et al.* 2016; Albright *et al.* 2017; Schooley *et al.* 2018; Mirzabaev *et al*. 2019). The lack of natural vegetation also threatens an organism's ability to use microclimates to thermoregulate and the stability of their food sources in the ecosystem (Albright *et al.* 2017; Chillo *et al.* 2018).

Piospheres

Desertification is a degraded effect across arid ecosystem landscapes; however, it is not only at this scale that degradation affects these ecosystems. The artificial implementation of surface water available to organisms in these arid ecosystems also results in smaller-scale effects of degradation (Barker & Lange 1969; Fatchen & Lange 1979; McNaughton *et al.* 1988; Wilson 2010; Landman *et al.* 2012). The interactions of vegetation, water sources and herbivores have been intensely studied since the 1950s as the area around a water source is often degraded due to the increased presence of large herbivores that rely on the water source that result in the surrounding vegetation being disturbing (van der Schijff 1957; Barker & Lange 1969; Lange 1969; Rogers & Lange 1971). This area of degradation around a central source has been found to be comprised of concentric patterns of degradation where the highest level of degradation can be found closest to the central source, while less severe degradation of the environment is found moving outwards (Lange 1969; Fatchen & Lange 1979; Derry 2004; Shahriary *et al.* 2021). This localised pattern of degradation was termed a piosphere in 1969 (Lange 1969) and are formed due to the heavy grazing of vegetation in and around the area surrounding the central source, combined with a trampling effect caused by the hooves of large herbivores (Lange 1969; Fatchen & Lange 1979; Derry 2004; Shahriary *et al.* 2021). Since the term piosphere was coined, these landscape features have since been studied to assess the effect on vegetation, soil properties, herbivorous species, and to a lesser extent some bird communities, small mammals and arthropods (Landman *et al.* 2012; Egeru *et al.* 2015; Muvengwi *et al.* 2018; Perkins 2018; Fulton 2020; Shahriary *et al.* 2021).

The effect of piospheres on vegetation and soil properties has been studied in depth as the effect of piospheres is exacerbated depending on the vegetation and soil type (Thrash 1998; Mphinyane 2002; Barboni *et al*. 2007; Melak *et al*. 2019). It has been suggested that the herbaceous vegetation closer to the water source experiences higher levels of trampling and grazing, resulting in the area closer to the water source being dominated by annual plants instead of perennial grasses (Thrash 1998; Mphinyane 2002; Melak *et al.* 2019). Although differences were found between the annual grass and perennial grass composition in the Kalahari and Gamka Karoo, piospheres result in an overall reduction in biomass as well as the structural complexity of the vegetation (Thrash 1998; Lechmere – Oertel *et al.* 2005; Perkins 2018: Schmidt *et al.* 2019; Saayman *et al.* 2022). Woody vegetation is also affected by piospheres as the density, diversity and composition of woody vegetation was impacted by a higher presence of elephants in closer proximity to watering sources (Mphinyane 2002; Wilson 2010). In addition to this, the structural complexity of woody vegetation was also impacted as a reduction in basal area and canopy volume was seen closer to the watering holes (Mphinyane 2002; Wilson 2010).

Piospheres also affect soil properties, as was found in Canada where cattle drastically increased the ammonia (NH_3) and nitrous oxide (N_2O) in the soil, above expected levels, within a piosphere (Sheppard & Bittman 2011). In addition to this, it was also found that significantly higher levels of nitrogen and organic carbon were found in soil samples closer to the watering source, perhaps due to high levels of defecation and urination from the density of herbivores

(Stumpp *et al.* 2005; Smet & Ward 2006; Shahriary *et al.* 2012; Egeru *et al.* 2015; Jawuoro *et al*. 2017). The high density of herbivores around a central source also result in soil being compacted which affects the ability of growth of vegetation and prevents the percolation of water into the soil (Smet & Ward 2006; Shahriary *et al.* 2012; Arnhold *et al.* 2015; Egeru *et al.* 2015; Jawuoro *et al*. 2017). The exposure of the soil to erosion due to overgrazing inside a piosphere also affects the composition of the soil resulting in a much higher sand content, which significantly lowers silt and clay levels (Pei *et al.* 2008; Mohammad 2009; Jawuoro *et al*. 2017). This, with the high compaction of soil closer to the watering hole also results in reduced infiltration, which combined with the high density of herbivores further results in significantly higher pH levels of soils due to the lower surface leaching ability (Beukes & Ellis 2003; Smet & Ward 2006; Egeru *et al.* 2015; Jawuoro *et al*. 2017). These effects on soil further affect the vegetation communities that can grow in an area, as was seen in Botswana where high cattle density was associated with encroaching thorny, woody plant species, especially in the nitrogen-rich soils created by the cattle in the piospheres (Moleele & Parkins 1998; Perkins 2018). The thorny plant species were encouraged to grow in the nitrogen-rich soils, both around natural water sources available to the cattle and artificial watering points (Moleele & Parkins 1998). All these factors result in a degraded environment that is difficult for vegetation growth and creates inhospitable environments for the organisms that reside in the soil of these areas.

The effect that piospheres have on vegetation and soil properties further affects other organisms that reside in the habitat. It has been found that bird species richness and abundance decrease closer to the central point of piospheres in South American forests and the drylands of Australia and South Africa (James *et al.* 1999; Hudson & Bouwman 2007; Macchi & Grau 2012; Fulton 2020). In Australia it was found that areas of degradation resulted in a displacement of ground-dwelling birds, range changes in different species, and a change in predation rates due to the clustering of prey species at watering holes (James *et al*. 1999; Fulton 2020). Birds are generally classified according to their food sources, with insectivorous birds receiving most of their water requirements for metabolic processes from the insects (and other small arthropods) they consume (Epaphras *et al.* 2008; Macchi & Grau 2012: Smit *et al.* 2019; Czenze *et al.* 2020). In contrast, granivorous birds are more likely to rely on drinking from surface water for their metabolic requirements (Smit *et al.* 2019; Czenze *et al.* 2020). However, the presence of water holes is likely to affect both feeding guilds' food sources, as less vegetation and damaged soils are likely to lower the number of available seeds, and arthropods are also likely to decrease in abundance due to the degradation of the habitat (Macchi & Grau 2012; Fulton 2020; Fallah *et al*. 2017; Chillo *et al.* 2018; Muvengwi *et al*. 2018).

Arthropods have been found to be negatively impacted by piospheres in South America, Australia and Southern Africa (Hoffman 2008; Chillo *et al.* 2018; Muvengwi *et al.* 2018). Studying piospheres in South America, Chillo *et al.* (2018) found that most invertebrate species populations had a decreasing trend in areas that experienced continuous grazing. In Australia, a greater species richness of insects was found further away from heavily degraded areas (Hoffman 2008). While in southern Africa macro-invertebrates and termites were negatively affected by utilisation gradients associated with piospheres (Muvengwi *et al.* 2018). More research into understanding the effects of piospheres on arthropods, birds and their interspecies relationships is needed as there is still a paucity of information.

It has been suggested that continuous grazing has a negative effect on all biodiversity, including small mammals (Moleele & Parkins 1998; Chillo *et al*. 2015; Laverty & Berger 2021). Due to bush encroachment, many small animals in Southern Africa are not able to use areas as their habitat and biotic environment is being changed, which alters the microhabitats they, and their food sources require (Moleele & Parkins 1998). However, the change in vegetation composition due to increased grazing by large indigenous herbivores around a water source in southern Africa has been found to affect some bat species, increasing their activity levels and species richness around watering holes (Taylor *et al.* 2020; Laverty & Berger 2021). These changes in the landscape have also been noticed in South America, where a marked gradient of decreasing biodiversity can be seen along the piosphere during both wet and dry seasons, especially with small mammals such as rodents (Chillo *et al*. 2015). Owing to so many types of organisms being negatively affected by piospheres, it is clear that these landscape features have a negative impact on biodiversity in a similar way that desertification affects an ecosystem.

Piospheres as models for desertification

Piospheres and desertification show similar effects of degradation on arid landscapes. Both have adverse effects on vegetation, with some areas facing regime and population shifts in the vegetation community (Moleele & Parkins 1998; Perkins 2008; von Wehrden *et al*. 2012; Zhang *et al.* 2018; Jiang *et al.* 2019). Overgrazing of vegetation by herbivores and the loss of vegetation also play essential roles in how vegetation and soil are affected in both piospheres and areas that face desertification (Smet & Ward 2006; Shahriary *et al.* 2012; Bestelmeyer *et al*. 2013; Egeru *et al.* 2015; Jawuoro *et al*. 2017; Khanamani *et al*. 2017; Qiu *et al*. 2018; An *et al*. 2019; Haj-Amor *et al*. 2022). Although more research needs to be conducted, it is clear that birds and arthropods face similar effects of loss of diversity and abundance in both areas of degradation (Macchi & Grau 2012; Hetem *et al.* 2016; Chillo *et al.* 2018; Muvengwi *et al.* 2018; Mirzabaev *et al*. 2019; Fulton 2020). Overall, desertification and piospheres have many overlapping features that show how the degradation of an arid landscape affects the ecosystem and ecosystem functioning.

The overlaps and similarities between desertification and piospheres support the idea that piospheres can act as models to study the effect of desertification at a more in-depth level (Okayasu *et al.* 2010; D'Odorico *et al*. 2013; Shahriarya *et al.* 2021). Piospheres affect a much smaller area compared to desertification allowing for in-depth studies on the effect on the environment and ecosystem functioning at a localised level which can be applied to areas facing desertification (D'Odorico *et al*. 2013; Shahriarya *et al.* 2021). Using piospheres as a model for desertification allows for both a degraded and natural area of the same ecosystem to be studied allowing for the true extent of degradation effects to be evaluated. This will allow further information on how species are affected by desertification and provide more answers as to how the degradation of arid habitats results in species loss, loss of biodiversity, and reduced ecosystem functioning.

Insectivorous birds as model species

The use of model organisms to gain an understanding of how a system and other species may also be affected is a common practice when studying environmental effects (Brown 1997; Parikh *et al.* 1997; Newman *et al*. 2007; Gregory & van Strien 2010; Parikh *et al*. 2020). In this thesis birds and arthropods are used as model taxa. Insects have a history of being used as indicators of ecosystem functioning. In South Africa, the South African Scoring System Rapid Bioassessment Method for Rivers (SASS) has been developed to assess the biota of river systems to determine the condition of the environment (Dickens & Graham 2002; Molozzi *et al.* 2012; Parikh *et al*. 2020). Terrestrial fruit-feeding insects in Northern Africa have been found to be sensitive to disturbances and were able to help evaluate various conservation strategies and their ecological impact on the area (Bouyer *et al*. 2007). Avian species can also be used as indicators for ecosystem health and sustainability (Gregory & van Strien 2010; Smits

& Fernie 2013; Fraixedas *et al*. 2020). Birds and arthropods are widely distributed and are diverse groups of organisms sensitive to environmental changes (Gregory & van Strien 2010). They are both groups of organisms that often occur in high numbers, and count data on bird species is realistic and not taxing or expensive to collect, they can be observed over a short period of time, and this allows them to be recognised as a good bioindicator group to study and work with across different biomes and environments (Newman *et al*. 2007; Gregory & van Strien 2010; Smits & Fernie 2013). Additionally, both birds and insects are expected to be highly impacted by habitat loss, increased ambient temperatures due to climate change, and reduction in water availability, making them essential organisms to understand how they are affected by desertification (du Plessis 2012; Boggs 2016; McKechnie *et al.* 2016; Pureswaran *et al.* 2018). Although birds that consume arthropods are classified as insectivorous birds, this term does include other types of arthropods and annelids and is not restricted to insects alone. Because of this, this study is not restricted to only insect groups and other arthropods are also studied.

In this thesis, insectivorous birds are studied as model species to assess how desertification affects the abundance and diversity of organisms within an ecosystem and their interspecies relationships. Furthermore, insectivorous birds feeding behaviours are used to understand how desertification affects food webs within an environment. Both the foraging effort and efficiency of insectivorous bird species is examined. Foraging effort is described as the proportion of an observational focal that a bird spent actively foraging (du Plessis *et al.* 2012). This differs from foraging efficiency which is the estimated biomass intake rate per unit foraging time, measured in grams per minute (Ridley & Raihani 2007; du Plessis *et al.* 2012). This will provide more information to enhance predictions and models created to determine the effect of desertification and climate change on organisms in arid ecosystems.

Thesis structure

This dissertation is structured in a manuscript style as two stand-alone chapters based on empirical data and a general introduction and conclusion. This inevitably results in some overlap of the introductory information.

Chapter One provides information on the effects of desertification and piospheres, and how these two classifications of degradation have many overlapping similarities as different landscape scales. An argument is made showing why these similarities and scale differences allow piospheres to be studied as models for desertification.

In Chapter Two, I investigate the effects of desertification on vegetation density, and arthropod and bird diversity and abundance in the Albany Thicket of the Eastern Cape using piospheres as a model for desertification. I hypothesise that significantly lower diversity and abundance of both avian and arthropods species will be found inside the piosphere.

In Chapter Three, I investigate how desertification affects the foraging effort and efficiency of insectivorous bird species in the Albany Thicket of the Eastern Cape using piospheres as a model for desertification. I hypothesise that the foraging effort of insectivorous bird species will be higher inside the piosphere in areas of degradation, and the foraging efficiency of insectivorous bird species will be higher outside of the piosphere due to a higher insect abundance and diversity.

Chapter Four provides general conclusions and suggestions for future research.

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CHAPTER 2:

THE EFFECT OF PIOSPHERES ON THE ABUNDANCE AND DIVERSITY OF BIRDS AND ARTHROPODS

Abstract

Desertification of arid ecosystems results in a reduction in biological productivity and biodiversity. Piospheres are localised areas of desertification resulting from an increased presence of herbivores around a central source that leads to poor soil quality and a change in vegetation structure and composition. Due to the similarities between areas affected by desertification and areas affected by piospheres, I propose that piospheres can be used for studying interspecies relationships and ecosystem function that are affected by habitat degradation. Although piospheres have been studied since the early 1970s there is still a paucity of data regarding the effect they have on organisms other than plants and herbivores, and the overall effect on the environment. I studied the effect of piospheres on arthropod and birds abundance and diversity using 13 functional water trough sites across two farms located in the Eastern Cape province of South Africa. The family composition of arthropods was also studied, as were the effects on the occurrence of insectivorous bird species. I found a significant decrease inside the piosphere in both the abundance of arthropods in summer (inside = 0.33, outside = 0.50) and winter (inside = 0.22, outside = 0.29), and diversity in summer (inside = 1.93, outside = 2.35) and winter (inside = 1.55, outside = 1.86). The diversity of birds was also significantly affected by piospheres in winter with higher diversity outside the piospheres. Termitidae, Diptera, Formicidae and Myrmeleontidae were all families of arthropods significantly affected. I also found that significant differences in the family composition of arthropods changed in summer, where 44.20% of arthropods comprised of Caelifera, Diptera and Formicidae inside piospheres was reduced to only 26.91% outside of piospheres. Similar patterns were also seen in winter. The insectivorous birds were unsurprisingly affected by this change in prey abundance and diversity inside piospheres. I found that out of the 14 species studied four species were found to avoid piospheres in summer and four species in winter. From this it is clear that piospheres affect the environment beyond herbivores and vegetation, and can be used to study how specific organisms are likely to be affected by desertification. This can be utilised for studying the effect of desertification on agricultural practices, and species conservation.

Introduction

Habitat disturbance, specifically where the systematic loss of vegetation and primary production in an area occurs, reduces the diversity of faunal species and ecosystem interactions. An example of such a disturbance includes desertification, defined as the degradation of dryland or arid ecosystems that results in the reduction of biological productivity (Glantz & Orlovsky 1983; Hoffman & Cowling 1990; Archer & Tadross 2009; Mirzabaev *et al.* 2019; Huang *et al.* 2020). Desertification results in a loss of biological productivity as there is a loss of vegetation in the area affected, a decline in soil quality, and a loss of water availability in an area (Archer & Tadross 2009; Tang *et al.* 2016; Mirzabaev *et al.* 2019). There are several factors that contribute to this degradation, including anthropogenic disturbances, wind erosion and changes in climate (Glantz & Orlovsky 1983; Tang *et al.* 2016; Mirzabaev *et al.* 2019). Some of the anthropogenic disturbances found to contribute to desertification include deforestation, and a concentration of livestock in an area which results in overgrazing and trampling of vegetation (Glantz & Orlovsky 1983; Archer & Tadross 2009; Huang *et al.* 2020).

Dryland ecosystems are estimated to cover 40% of the global land area, covering areas across the African continent, western North America, Australia, the Middle East and Central Asia (Tang *et al.* 2016; Mirzabaev *et al.* 2019; Huang *et al*. 2020). The effect of desertification has been seen in many of these areas, but in Africa, the high rates of overgrazing, poor agricultural practices, firewood harvesting, and deforestation in Angola, Zimbabwe, Zambia and Mozambique have resulted in severe water and wind erosion causing large areas of desertification (Dregne 2002; Hansen *et al.* 2013; Prăvălie 2016; Mirzabaev *et al.* 2019). This has been found to have caused nutrient depletion in these areas and reduced soil fertility (Prăvălie 2016; Mirzabaev *et al*. 2019).

Desertification is not the only degradation of drylands reported. Localised degradation of dryland habitats has been found around central sources, most commonly water sources, with the level of degradation being highest at the central source with concentric rings of less severe degradation moving away from the source (van der Schijff 1957; Barker & Lange 1969; Thrash & Derry 1999). These ecological concentric patterns of degradation were termed piospheres from the Greek word "pios" – to drink, after being studied in Australia (Lange 1969). Piospheres are formed by heavy grazing in the area surrounding a water source, combined with a trampling effect caused by the tracks of herbivores (Lange 1969; Fatchen & Lange 1979;

Derry 2004). Piospheres have been studied to understand the effect water sources have on large herbivores and the vegetation they feed on, both for indigenous large herbivores and livestock farming practices (Barker & Lange 1969; Fatchen & Lange 1979; McNaughton *et al.* 1988; Wilson *et al.* 2010; Landman *et al.* 2012). Some studies have examined the effect on specific types of plant vegetation (Clegg 1999; Parker & Witkowski 1999; Chamaillé-Jammes *et al.* 2009; Wilson et al. 2010), while others examined the effect these landscape changes have on soil properties (Simanga 2013; Mogotsi *et al.* 2015; Saayman *et al.* 2021). Although piospheres have been studied since the early 1970s, there is a paucity of information regarding the effect of piospheres on ecosystems, as most studies have focused on the relationships between vegetation and herbivores.

Research thus far conducted in piospheres shows unequivocally that piospheres change both biotic organisms and the landscape, in the same way as desertification. Since both piospheres and desertification result in the degradation of arid areas, piospheres can be seen as localised areas of desertification (Okayasu *et al.* 2010; D'Odorico *et al*. 2013; Shahriarya *et al.* 2021). If an area had multiple water sources resulting in multiple piospheres across the landscape, this would result in degradation similar to large-scale desertification (Macchi & Grau 2012; Hetem *et al.* 2016; Chillo *et al.* 2018; Muvengwi *et al.* 2018; Mirzabaev *et al*. 2019; Fulton 2020). Piospheres could thus act as a landscape-level model for desertification, which offers an opportunity for an in-depth study of the effects of desertification on the ecosystem, and the organisms that reside in it.

Birds and insects are used in this study as both groups of organisms are expected to be highly impacted by climate change, and habitat change and loss (du Plessis 2012; Boggs 2016; McKechnie *et al.* 2016; Pureswaran *et al.* 2018). Additionally, these groups play essential roles in maintaining ecosystem functioning (Chagnon *et al.* 2015; Sekercioglu *et al.* 2016; Brockerhoff *et al.* 2017; Noriega *et al.* 2018). Both birds and insects are potential flagship taxa for studying environmental change as they often occur in high numbers, are diverse and are relatively easy to observe (Rosenberg *et al.*1986; Zakaria *et al.* 2005; Newman *et al*. 2007; Gregory & Strein 2010; Smits & Fernie 2013). The relationship between birds and arthropods is also essential to study as many bird species rely on arthropods as their source of food and water and studying this relationship will allow for a greater understanding of how desertification affects ecosystem function and stability (Macchi & Grau 2012: Smit *et al.* 2019; Czenze *et al.* 2020; Wilson *et al.* 2021). In addition, few in-depth studies have been conducted to determine how desertification and/or piospheres affect these organisms and the ecosystems they reside in (Fulton 2020; Fallah *et al.* 2017; Chillo *et al.* 2018; Muvengwi *et al*. 2018).

In this study, I aim to determine the effect of piospheres and desertification on arthropods and insectivorous birds, which act as models for ecosystem functioning. This was done by studying the effect of degradation on vegetation density, the abundance and diversity of arthropods and insectivorous birds, and the drivers of insectivorous birds' presence and how this differs inside and outside the area of degradation. With these data, I aim to assess changes in abundance and diversity of birds and arthropods in relation to piospheres, and then extrapolate these data to understand how desertification may affect these organisms based on the assumption that piospheres are local points of desertification. I predict that the area inside the piospheres (inside the area of degradation) will have lower vegetation density, resulting in a lower diversity and abundance of arthropods, resulting in a lower diversity and abundance of insectivorous birds when compared to areas outside the piospheres.

Materials and methods

Study Sites

Functional concrete water troughs were located across two adjacent farms 15km northwest of Grahamstown, namely Table Farm (33° 15' S, 26° 25' E; 600m) and Draai Farm (33° 14' S, 26° 25' E; 600m), Makhanda, Eastern Cape, South Africa. Lowland areas characterise this area's vegetation with an assortment of vegetation from Karoo scrubland, thornveld, and thicket clumps. These farms fall within the Albany Thicket Biome (more recently named Subtropical Thicket Biome (Mucina & Rutherford 2006)), where the climate varies seasonally between average temperatures of 25°C in summer and 15°C in winter (World Weather Online www.worldweatheronline.com). The average rainfall for this area in summer is approximately 60 mm a month while in winter it is closer to 70 mm (World Weather Online). However, rainfall in this area is unpredictable as it faces a 25% chance of not receiving 80% of its expected mean rainfall in any given year, commonly resulting in several months of drought (Aucamp & Tainton 1984; Hoare *et al.* 2006). High temperatures exceeding 40°C in summer months occur on occasion while winter months often experience temperatures below freezing leading to frost in lower lying areas (Hoare *et al.* 2006).

Thirteen water troughs across both farms were used, which were identified as the "inside piosphere" sites. An image showing these sites locations can be seen in the appendix

(Image 1.) The water troughs supplied surface water to livestock and wildlife for the duration of the study. For each water trough, there was an "outside piosphere" site situated 1km away in a direction that did not fall within another piosphere, ensuring this was not a disturbed or degraded area, and at similar altitudes. Images showing the visual differences between inside and outside piosphere sites can be found in the appendix (Image 2). I ensured that the outside site had a similar vegetation type to the respective inside site. This resulted in a total of 26 sites (13 inside-, and 13 outside piospheres). Each site was studied in both winter (June – August 2021) and summer (November 2021 – February 2022).

Vegetation density

The vegetation density was measured at each of the 26 sites in summer and winter using a point-centred quarter method (PCQ) which is a plotless method that allows one to estimate the vegetation density by creating four quadrats around the centre point (Dix 1961). The plant closest to the central point in each quadrat was identified. Then the distance between the central point and the selected plant in each quadrant was measured, and these distances were averaged across the four quadrats to represent the average distance ($\bar{x}d$) at each sample site. Once the average distance per site was calculated, the mean area (MA) was calculated as equal to the mean distance squared ($MA = \bar{x}d^2$). The vegetation density per site was then derived by calculating the inverse of MA, resulting in the vegetation density for each site both inside and outside the piospheres, for both winter and summer. In addition to this, the vegetation ground cover was also scored with '0' showing no cover, and '10' showing 100% cover. Although this was a subjective estimate, it was done by the same observer creating a consistent estimate throughout each season, allowing vegetation ground cover to be a valuable factor to include in further analyses.

Once the vegetation density was calculated, these data were then analysed using R (R Development Core Team, 2022), where a test for normality was first run. As the data residuals of vegetation density were not normally distributed, a Kruskal-Wallis test was run to test for a significant difference in the vegetation density as a result of seasonality and the degraded habitat caused by the piospheres. A nonparametric post hoc test (Dunn's Multiple Comparison Test) was conducted to find which relationships differed significantly.

Bird abundance and diversity

Bird abundance and diversity data were collected between 08:00 am and 11.00 am to avoid hot ambient temperatures and times when birds are naturally less, or more active. At each of the 26 sites, a 12-minute bird observational focal was completed by identifying species of birds seen in the maximum radial distance of approximately 50m, counting the number of individuals present. Birds calling at the site were also identified and the number of individuals calling were estimated and added to the observations. Birds calling from an estimate of over 100m away were not included in the study. Bird abundance and diversity observations were completed for both summer and winter months to determine if there were changes in seasonal bird abundance and diversity inside and outside of piospheres. These data were then used to calculate the diversity of bird species at the site using the Shannon Diversity Index (H'), and the relative species abundance was also calculated.

For both the diversity and relative species abundance, a test for normality was conducted in R (R Development Core Team, 2022). An Analysis of variance (ANOVA) was run on the bird diversity and relative species abundance data to test for significant differences between winter and summer, and to determine if the degraded habitat found inside piospheres also had an effect. A Tukey's post hoc test was also conducted to determine where these significant differences occurred.

Arthropod abundance and diversity

Within the four quadrats used for the vegetation density analyses, a 2-minute arthropod collection was performed in each quadrat for each site, during both winter and summer. I surveyed arthropods using active searching methods such as turning over rocks, grass sweeps and net beating. Arthropods that were found were identified to suborder- or family- level. Formicidae nests and termite mounds were counted, but individual insects within these structures were not counted. The number of each suborder or family found within each quadrat was then pooled for each site. The diversity of arthropods at the site was calculated using the Shannon Diversity Index (H'), as was the relative species abundance. In addition to this, family and order composition analyses were also conducted. Arthropod diversity and abundance were collected in both winter and summer to determine if there were seasonal changes in addition to the degraded habitat around a water trough.

To test how seasonality and the degradation associated with piospheres affect the arthropod diversity and abundance, a test for normality was conducted on both data sets. An ANOVA was conducted to determine if seasonality and the habitat degradation from the piospheres significantly affected the diversity of arthropods, and a Tukey post hoc test was performed to see where significant differences were located. A Kruskal-Wallis test was performed to test for significant effects on the arthropods' relative species abundance and a Dunn's Multiple Comparison Test was conducted as a post hoc test.

In addition to this, data on the presence of termite mounds were also analysed to see if the degradation affects their abundance. These tests were performed using a Shapiro-Wilk test for normality and a Kruskal-Wallis test to determine significant differences in the data collected inside and outside the degradation area. A Dunn's Multiple Comparison Test with Bonferroni correction for p-values was then conducted as a post hoc test to determine where these significant differences occurred in the termite mound distribution.

Arthropod Family and Order composition

The number of individuals for each arthropod identification found in the four quadrats per site was pooled and the mean number of individuals per family across all 13 sites were calculated for inside and outside the piospheres for both summer and winter data. From this, the percentage of each family relative to the total percentage of families across the 13 sites for both summer and winter was calculated. A chi-squared goodness of fit test was then run to see if the family and order composition changed with the degradation of habitat found inside piospheres and how this differed from the composition of arthropod families found outside of the piospheres for both winter and summer data.

Insectivorous birds

After calculating the diversity and abundance of all birds found across the 26 sites in both summer and winter, the most commonly occurring insectivorous bird species were further analysed to determine if the difference in their presence inside and outside the piospheres was random or not. Information from these analyses shows how birds that feed on arthropods are likely to be affected by areas of degradation due to a change in their food source, as their presence will not be linked to the availability of surface water. All insectivorous bird data were transformed into presence/absence data per site, per season. Subsequently, a chi-squared goodness of fit test was run to determine if the birds' presence inside or outside of the piospheres was random or not.

If the birds' presence was not randomly related to piosphere status (inside/outside), I conducted further analyses to determine what habitat characteristics determined their presence. For these analyses I ran a generalised mixed effects model using the nlme package (Pinheiro & Bates 2000) (family binomial) on species presence/absence, against the following fixed affects: vegetation density, seasonality, arthropod diversity, piosphere status, vegetation ground cover, including "site" as a random effect. I then ran models on the six species chosen using the same fixed and random terms and computed Akaike Information Criteria (AIC) values on all models run to evaluate the influence of different factors. The AIC score was used to validate the top 2 remaining models (in some cases there are three models) against a null model testing whether a species presence inside the piospheres was independent of any of the factors tested.

Results

Vegetation density

The degradation inside the piospheres significantly affected vegetation density (Kruskal-Wallis, $\chi^2 = 18.83$, df = 3, p-value < 0.001; Fig. 1). A nonparametric post hoc test showed that during summer there was a significant decrease in vegetation density inside the piospheres compared to outside the piospheres (Dunn's Multiple Comparison Test, Z = -2.31, p-value < 0.05; Fig. 1). Similarly, a significant difference in vegetation density between winter inside and outside the piospheres was also found (Dunn's Multiple Comparison Test, Z = -3.43, p-value < 0.001; Fig. 1). This shows that the degradation within piospheres significantly impacted vegetation density in both summer and winter.

The graph depicting vegetation density for inside and outside the piospheres per season had 4 major outliers removed (3 for Winter Out; and 1 from Summer Out) as they were all over 2 standard deviation points away from the mean of their data (Fig. 1). For the data collected in summer, the mean vegetation density for inside and outside the piospheres were 0.02 plants.m^{-2} and 0.05 plants.m^{-2} respectively. In winter the mean vegetation density for inside and outside the piospheres were 0.03 plants.m^{-2} and 0.07 plants.m^{-2}, respectively. However, outside of the piospheres in both winter and summer a maximum vegetation density of 0.13 plants.m^{-2} was observed (Fig. 1).

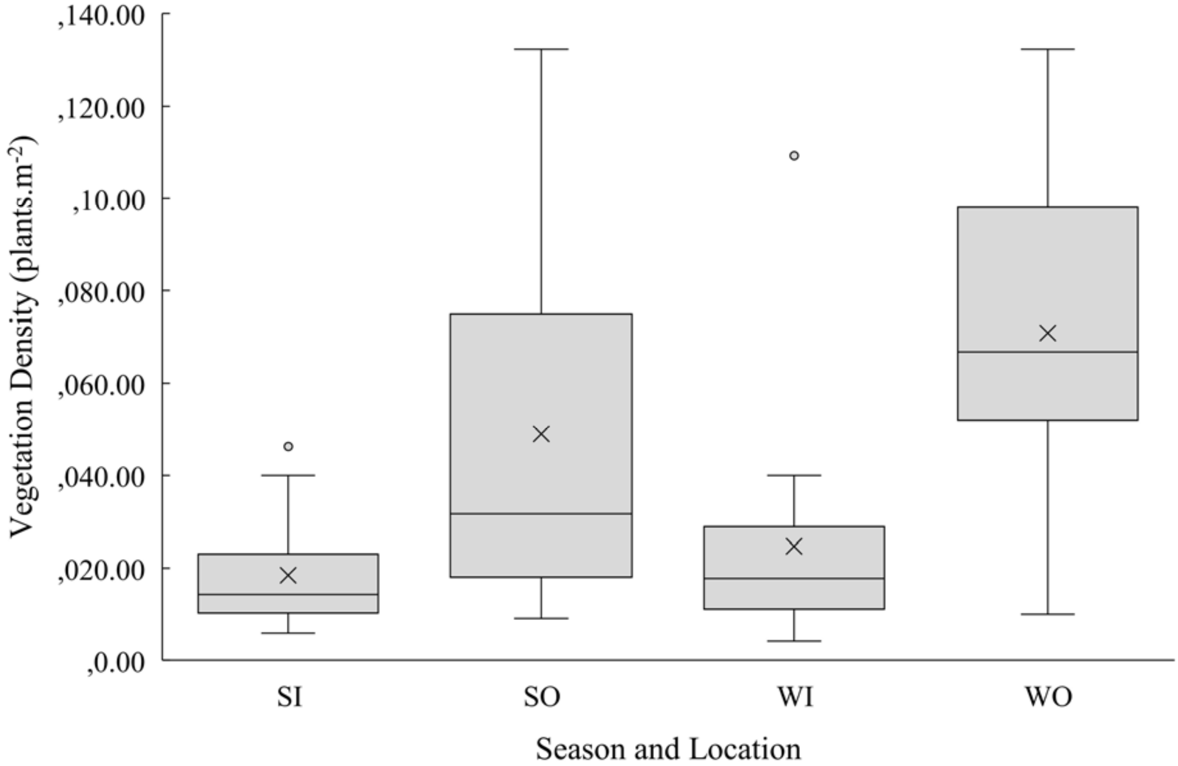

Figure 1: Vegetation density (plants.m^{-2}) as a function of seasonality and habitat degradation due to the presence of piospheres, with the season and location reading as follows: SI: Summer In, SO: Summer Out, WI: Winter In, WO: Winter Out. The box and whisker plot shows the mean (X), minimum and maximum values (seen as error bars), the first and third quartile, and the median for each data set. Outliers occurring outside of the minimum and maximum values are shown as grey circles. The Interquartile Range (IQR) can be calculated by finding the difference between quartile 1 and quartile 3.

Bird abundance and diversity

No significant difference was found in the relative abundance of birds inside or outside the piospheres across the seasons (ANOVA, df = 3, p-value = 0.32; Fig. 2). The relative species abundance of birds inside and outside piospheres during summer were only marginally different (SI = 0.15 and SO = 0.16), as were the winter values (WI = 0.17, WO = 0.19) with winter inside the piospheres IQR being slightly higher compared to winter outside the piospheres, and to the summer data.

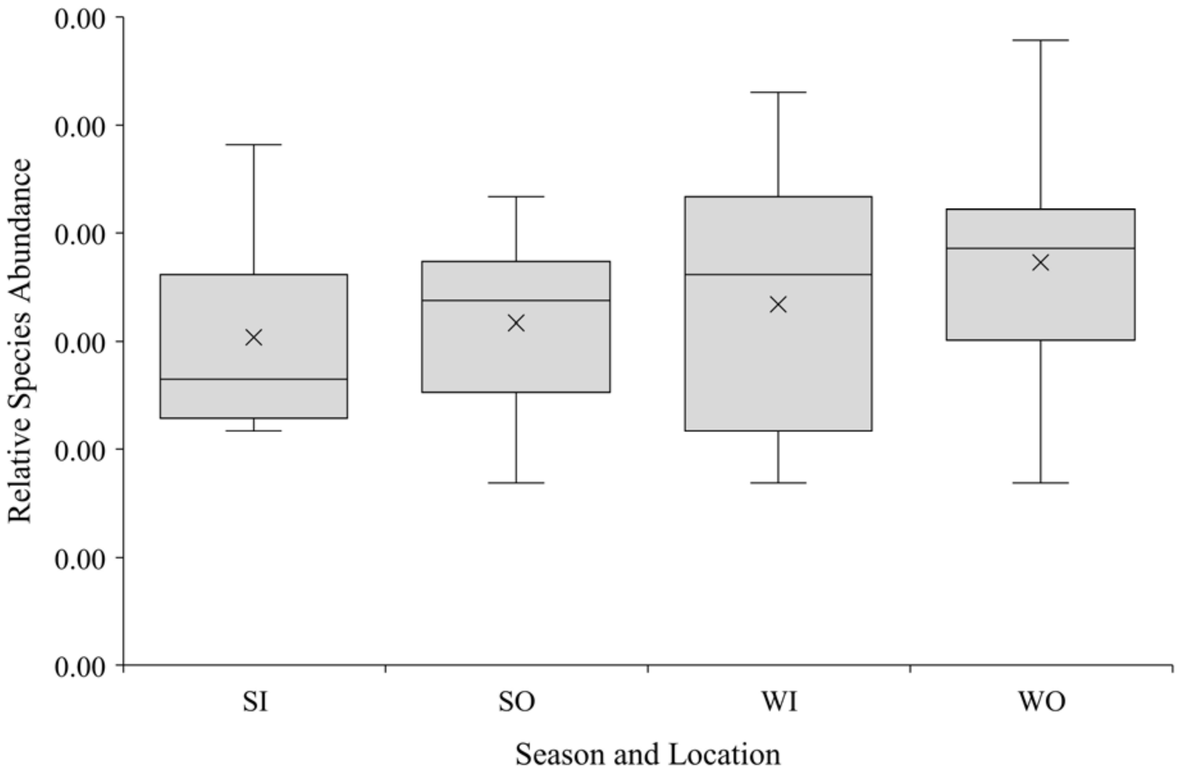

Figure 2: Relative species abundance as a function of season and habitat degradation, with the season and location reading as follows: SI: Summer In, SO: Summer Out, WI: Winter In, WO: Winter Out. The box and whisker plot shows us the mean (X), minimum and maximum values (seen as error bars), the first and third quartile, and the median for each data set. The Interquartile Range (IQR) can be calculated by finding the difference between quartile 1 and quartile 3.

The diversity of birds inside and outside the area of degradation was found to be significantly different (ANOVA, df = 3, p-value < 0.05; Fig. 3). The post hoc test showed that bird diversity was significantly greater outside compared to inside the piospheres during winter (Tukey's post hoc Test, p-value < 0.05; Fig. 3), while there was no significant difference in summer (Tukey's Post hoc Test, p-value = 0.78; Fig. 3).

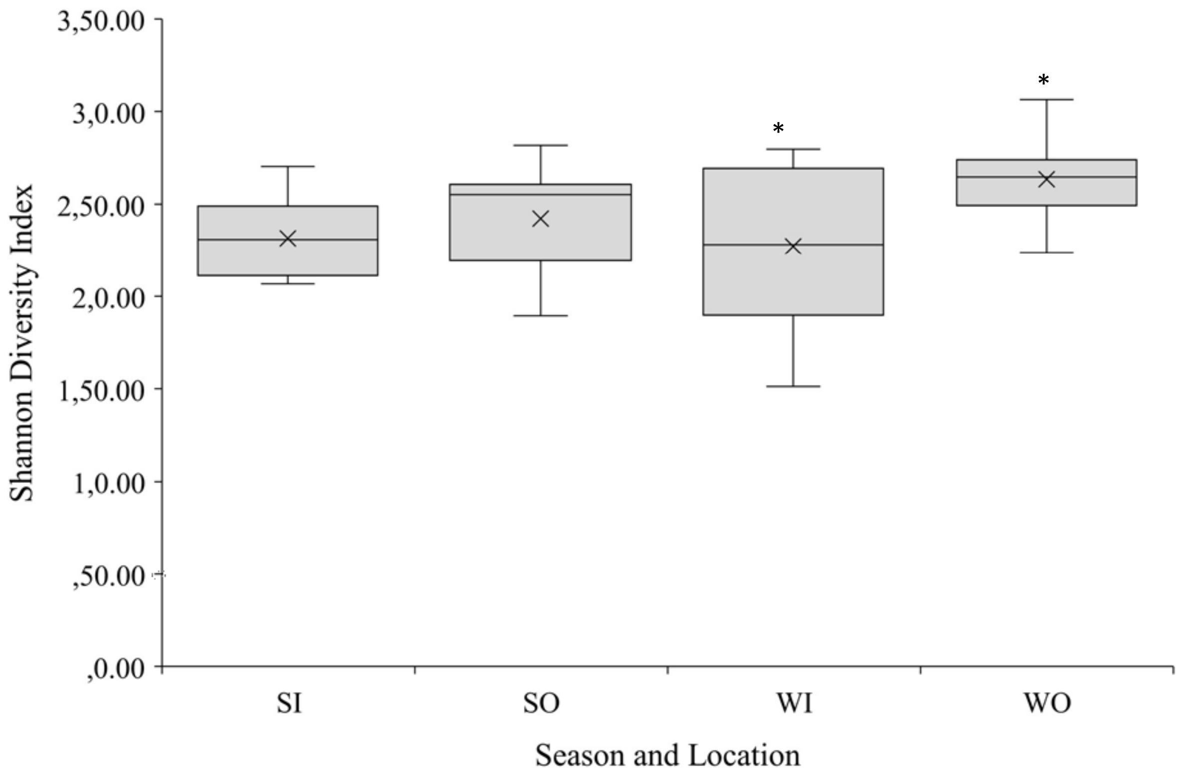

Figure 3: Shannon diversity index of bird species seen as a function of season and habitat degradation, with the season and location reading as follows: SI: Summer In, SO: Summer Out, WI: Winter In, WO: Winter Out. Asterisks are used to indicate which season and location have significant differences. The box and whisker plot shows the mean (X), minimum and maximum values (seen as error bars), the first and third quartile, and the median for each data set. The Interquartile Range (IQR) can be calculated by finding the difference between quartile 1 and quartile 3.

Arthropod abundance and diversity

The abundance of arthropods differed significantly inside and outside the piospheres (Kruskal-Wallis, $\chi2= 29.38$, df = 3, p-value < 0.001; Fig. 4). Summer arthropod data from inside and outside the piospheres were negatively significantly different, with a much higher relative species abundance occurring outside the piospheres (Dunn's Multiple Comparison Test; p-value < 0.05, Fig. 4). The winter arthropod abundance, however, was not significantly different for inside and outside the piospheres (Dunn's Multiple Comparison Test; p-value = 0.76, Fig. 4). There was no significant difference found between seasons for inside the piospheres (Dunn's Multiple Comparison Test; p-value = 0.08; Fig. 4). While the summer relative abundance outside the piospheres was positively significantly higher than winter outside the piosphere (Dunn's Multiple Comparison Test; p-value < 0.001, Fig. 4). In summer, arthropod relative abundance was greater outside the piospheres compared to inside the piospheres (SI =

0.33 and SO = 0.50; Fig. 4). The relative species abundance in winter showed a smaller difference between inside and outside the piospheres (WI = 0.22, WO = 0.29; Fig. 4).

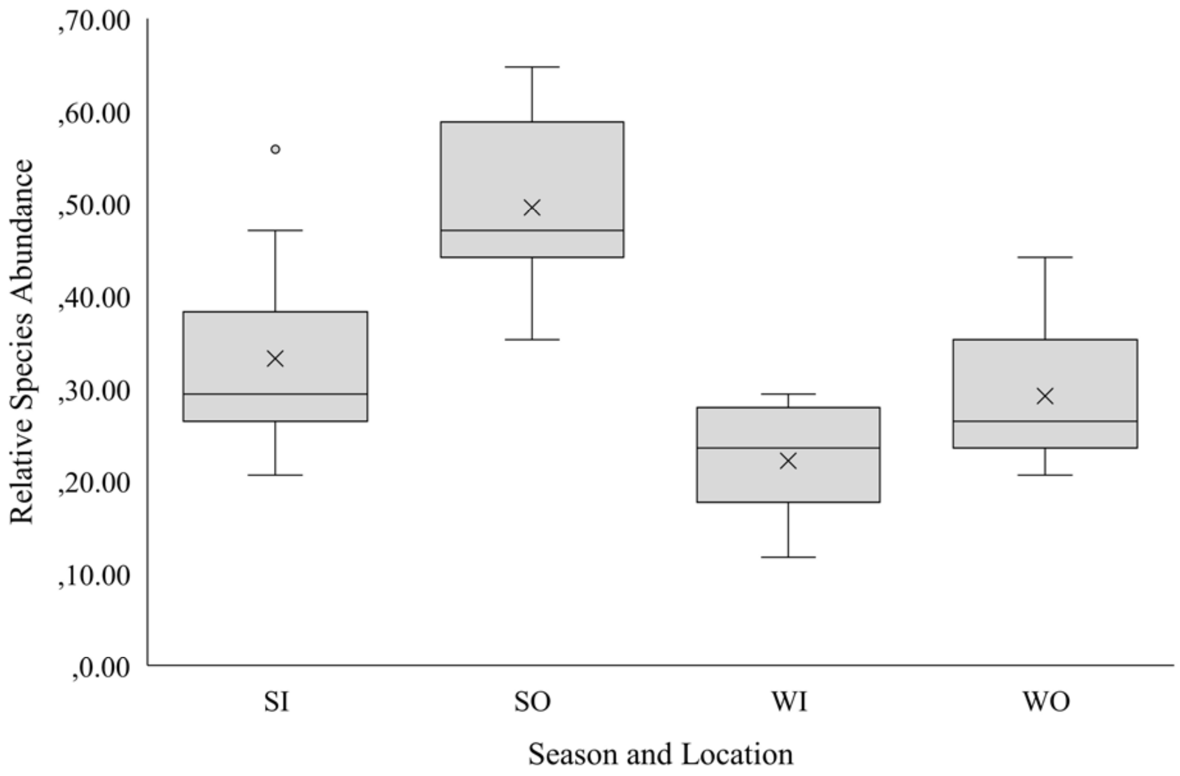

Figure 4: Seasonality and habitat degradation associated with piospheres on relative species abundance for arthropod populations found inside and outside the piospheres in summer and winter, with the season and location reading as follows: SI: Summer In, SO: Summer Out, WI: Winter In, WO: Winter Out. The box and whisker plot shows us the mean (X), minimum and maximum values (seen as error bars), the first and third quartiles, and the median for each data set. Outliers occurring outside of the minimum and maximum values are shown as grey circles. The Interquartile Range (IQR) can be calculated by finding the difference between quartile 1 and quartile 3.

Arthropod diversity varied significantly as a function of season and piosphere status (ANOVA, df = 3, p-value < 0.001; Fig. 5). Significant differences were found in arthropod diversity in winter (Tukey's Post hoc Test, p-value < 0.05; Fig. 5); and summer months (Tukey's Post hoc Test, p-value < 0.001; Fig. 5). Additionally, arthropod diversity changed significantly with seasonal change inside the piospheres from a mean diversity index value of 1.93 in summer to 1.55 in winter (Tukey's Post hoc Test, p-value < 0.05; Fig. 5). Outside the area of degradation also had significant differences in the mean arthropod diversity from 2.35 in summer to 1.86 in winter (Tukey's Post hoc Test, p-value < 0.001; Fig.5).

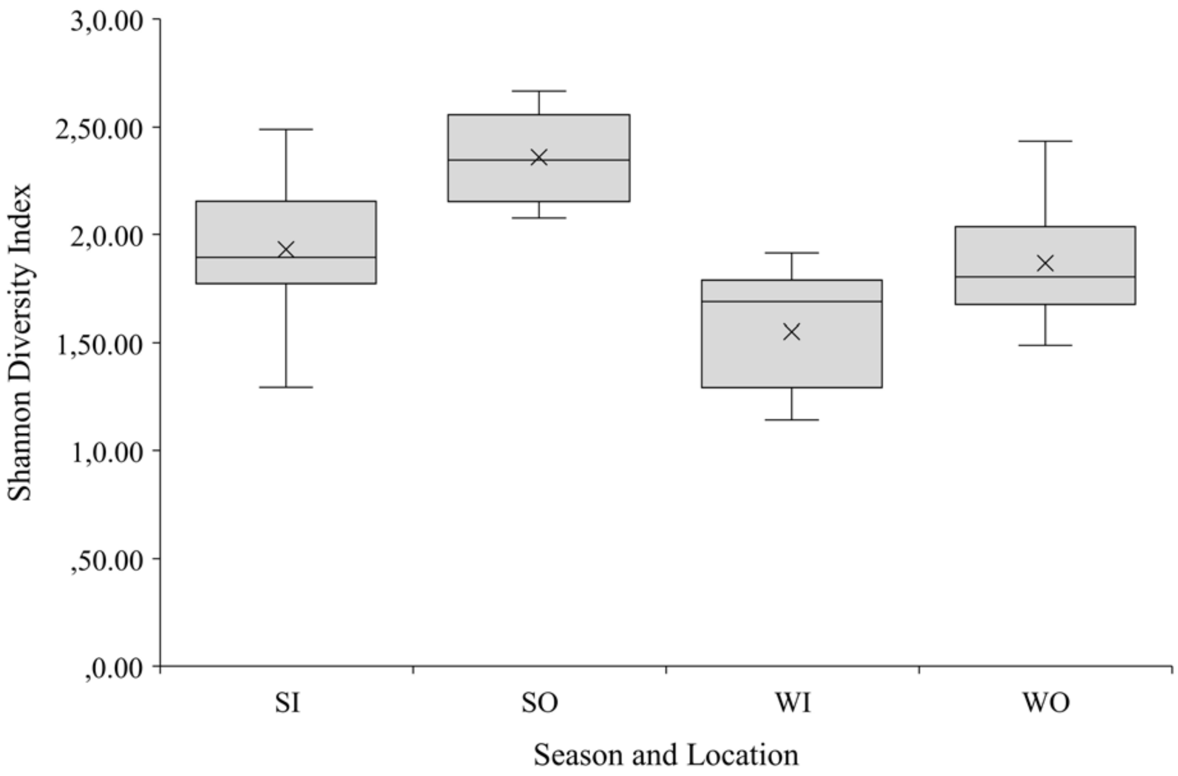

Figure 5: Shannon diversity index of arthropods seen as a function of season and habitat degradation, with the season and location reading as follows: SI: Summer In, SO: Summer Out, WI: Winter In, WO: Winter Out. The box and whisker plot shows us the mean (X), minimum and maximum values (seen as error bars), the first and third quartile, and the median for each data set. The Interquartile Range (IQR) can be calculated by finding the difference between quartile 1 and quartile 3.

During field data collection, I noticed a general lack of termite mounds inside piospheres. The distribution of termite mounds inside versus outside the piospheres was significantly different (Kruskal-Wallis, χ^2= 41.18, df = 3, p-value < 0.001; Fig. 6). From the post hoc test conducted there was no difference between seasons (inside: Dunn's Multiple Comparison Test; p-value = 1.00; outside: Dunn's Multiple Comparison Test; p-value = 1.00; Fig. 6). However, the differences between inside the piospheres and outside the piospheres for both summer and winter months were significant (summer: Dunn's Multiple Comparison Test Test; p-value < 0.001; winter: Dunn's Multiple Comparison Test; p-value < 0.001; Fig. 6).

From the 13 sites where I collected data, on average, the sites inside the piospheres for both seasons had only 0.23 ± 0.43 termite mounds, while in summer the sites outside the piospheres had 14.1 ± 3.44 on average, and winter on average had 12.3 ± 4.64 outside the piospheres (Fig. 6).

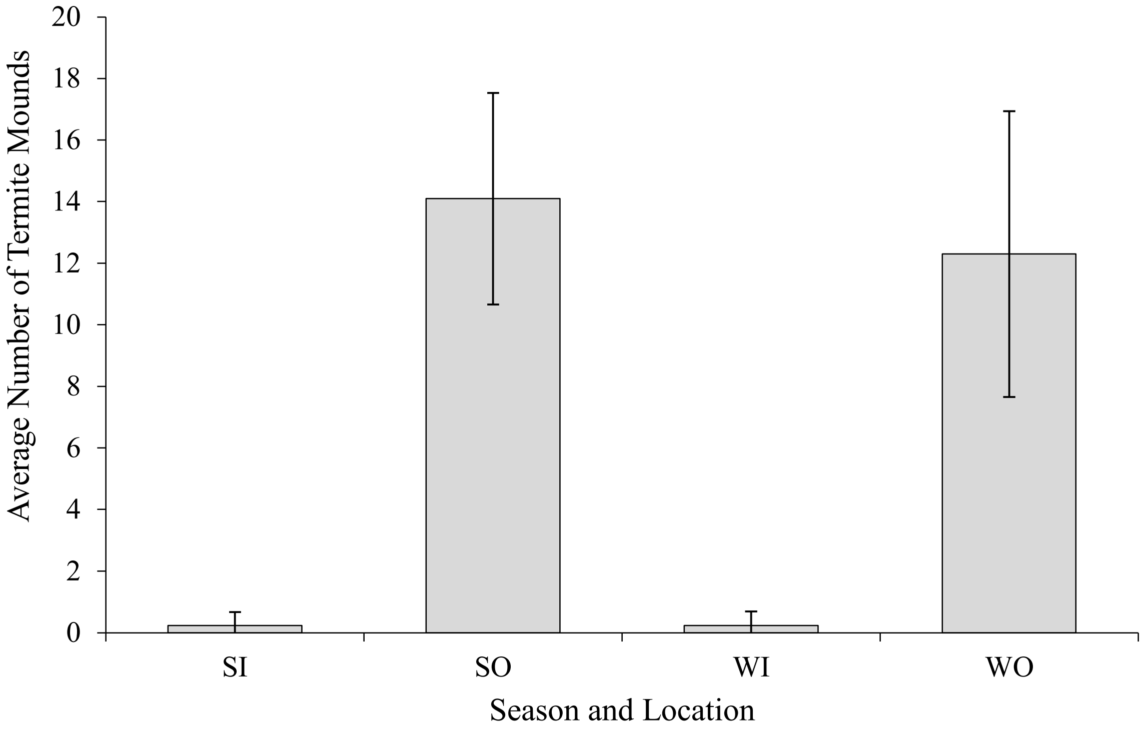

Figure 6: Effect of seasonality and habitat degradation associated with piospheres on the average number of termite mounds found inside and outside the piospheres in winter and summer, with error bars showing standard deviation (n=13). The season and location read as follows: SI: Summer In, SO: Summer Out, WI: Winter In, WO: Winter Out.

Arthropod Family and Order composition

Significant differences in the composition of the arthropods were seen inside and outside the piospheres in winter for Diptera (chi-squared goodness of fit test; $\chi^2 = 4.34$; df = 1; p-value < 0.05; Table 1), Formicidae (chi-squared goodness of fit test; $\chi^2 = 6.63$; df = 1; p-value < 0.05; Table 1), Termitidae (chi-squared goodness of fit test; $\chi^2 = 8.56$; df = 1; p-value < 0.05; Table 1) and Myrmeleontidae (chi-squared goodness of fit test; $\chi^2 = 12.83$; df = 1; p-value < 0.001; Table 1). In summer, only Termitidae showed a significant difference inside and outside the piospheres (chi-squared goodness of fit test; $\chi^2 = 15.79$; df = 1; p-value < 0.01; Table 1). For both seasons, Termitidae were found outside of the piospheres only (Fig. 6).

Table 1: Arthropod composition at family level (as percentage) found inside and outside the piospheres in both summer and winter. The chi-squared goodness of fit test values indicate significant differences within seasons for inside and outside the piospheres. Values in bold represent significant differences in family and order composition for inside and outside the piospheres.

Arthropod Identification	Summer			Winter		
	In (%) Comp.	**Out (%) Comp.**	**P -value**	**In (%) Comp.**	**Out (%) Comp.**	**P -value**
Apidae	6.17	4.89	0.7	1.59	1.71	0.95
Araneae	5.71	8.95	0.39	6.84	7.7	0.82
Armadillidiidae	3.37	1.7	0.45	0	3.14	0.07
Blattodae	2.38	1.91	0.82	1.19	2.99	0.62
Caelifera	18.66	14.97	0.52	7.46	7.84	0.92
Coleoptera	3.3	3.78	0.85	3.4	4.64	0.66
Collembola	5.47	7.41	0.59	9.16	9.07	0.98
Diptera	13.81	5.95	0.07	**18.76**	**7.98**	**0.04**
Formicidae	11.73	5.99	0.17	**21.85**	**7.82**	**0.01**
Hemiptera	4.36	6.66	0.48	2.78	3.42	0.79
Ixodida	1.49	0	0.22	2.38	0	0.12
Lepidoptera	5.3	5.23	0.98	4.97	2.9	0.46
Mantodea	0.89	2.03	0.5	1.19	1.71	0.76
Myrmeleontidae	0	0.76	0.38	**0**	**12.83**	**< 0.01**
Pentatomidae	3.86	2.25	0.51	1.78	1.71	0.97
Scorpiones	0.59	1.61	0.49	0	1.57	0.21
Termitidae	**0**	**15.79**	**< 0.01**	**0**	**8.56**	**< 0.01**
Vespidae	2.77	1.36	0.48	1.19	1.71	0.76
Other	10.15	8.76	0.74	15.46	12.69	0.6

In summer, Caelifera, Diptera and Formicidae constituted 44.20% of the species composition for inside the piospheres. This percentage was reduced to 26.91% of the species composition outside of the piospheres, with Myrmeleontidae only being found outside of the piospheres (Fig. 7). In winter, a similar pattern is observed as Caelifera, Diptera and Formicidae constituted 48.10% of the species composition inside the piospheres, while outside was reduced to 23.64% (Fig. 7). Arthropods that fall into the Myrmeleontidae classification were also only found outside the piospheres and were one of the most common families found in winter, making up 12.83% of the species composition (Fig. 7). In addition to this, in winter no Scorpiones were found inside the piospheres, but they made up nearly 2% of the species composition outside of the piospheres (Fig. 7).

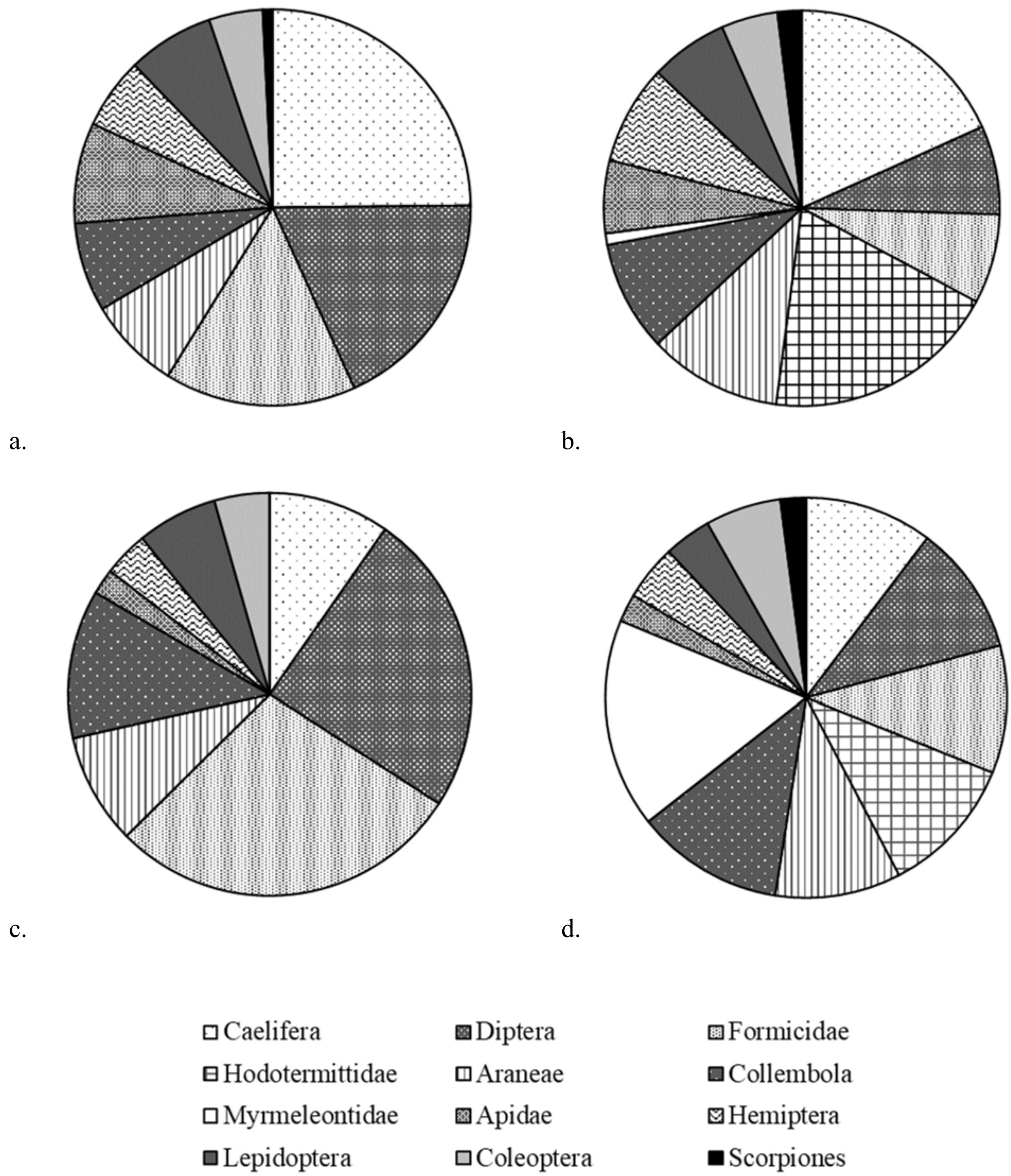

Figure 7: Composition of the 12 arthropod identifications that comprise the most commonly occurring arthropods for a. Summer Inside, b. Summer Outside, c. Winter Inside, d. Summer Outside, showing how the species that form the arthropod population changes according to the degraded habitat and season.

Insectivorous birds

It is clear that some insectivorous bird species occur inside and outside the piospheres differently, and that these occurrences are not random (Table 2). African Pipit (*Anthus* *cinnamomeus*) (chi-squared goodness of fit test, $\chi^2 = 9.46$, df = 3, p-value < 0.05) and Karoo Scrub Robin (*Cercotrichas coryphoeus*) (chi-squared goodness of fit test, $\chi^2 = 15.33$, df = 3, p-value < 0.001) occur more commonly outside of the piospheres in both summer and winter, and this distribution was not random.

In summer, both Eastern Clapper Lark (*Mirafra fasciolata*) (chi-squared goodness of fit test, $\chi^2 = 8.23$, df = 3, p-value < 0.05) and Spike-heeled Lark *(Chersomanes albofasciata)* (chi-squared goodness of fit test, $\chi^2 = 8.67$, df = 3, p-value < 0.05) were found outside the piospheres rather than inside. In winter, Familiar Chat *(Oenathe familiaris)* (chi-squared goodness of fit test, $\chi^2 = 7.71$, df = 3, p-value < 0.05) and Neddicky *(Cisticola fulvicapilla)* (chi-squared goodness of fit test, $\chi^2 = 9.30$, df = 3, p-value < 0.05) also showed non-random distribution, showing a preference for occurring outside the piospheres. Other insectivore species occurrences were considered to be random (Table 2).

Piosphere status (inside/outside) was the only factor that significantly affected the presence of *M. fasciolata*, and *O. familiaris* (Table 3). Season (summer/winter) and vegetation density significantly affected the presence of *C. coryphoeus, C. fulvicapilla*, and *C. albofasciata* (Table 3), while vegetation ground cover score only significantly affected *A. cinnamomeus* (Table 3).

Table 2: Number of presences recorded for each insectivorous species relating to season, and the results from the chi-square goodness of fit test analysing if presence for inside and outside the piospheres were random occurrences or not. Significant findings are emphasised.

Species	Summer			Winter		
	Inside	**Outside**	**P-Value**	**Inside**	**Outside**	**P-Value**
African Pipit *(Anthus cinnamomeus)*	**1**	**6**	**0.05**	**0**	**6**	**0.01**
Bar-throated Apalis *(Apalis thoracica)*	3	5	0.83	4	4	0.67
Bokamkierie *(Telophorus zeylonus)*	10	11	0.48	10	12	1
Chinspot Batis *(Batis molitor)*	4	1	0.18	3	2	0.66
Chestnut-vented Warbler *(Sylvia subcaerulea)*	2	5	0.74	6	10	0.76
Southern Fiscal *(Lanius collaris)*	4	5	0.26	5	6	0.32
Eastern Clapper Lark *(Mirafra fasciolata)*	**0**	**7**	**< 0.01**	2	4	0.41
Familiar Chat *(Oenathe familiaris)*	3	6	0.32	**0**	**6**	**0.01**
Karoo Prinia *(Prinia maculosa)*	7	5	0.56	3	4	0.71
Karoo Scrub Robin *(Cercotrichas coryphoeus)*	**1**	**7**	**0.03**	**0**	**10**	**< 0.01**
Neddicky *(Cisticola fulvicapilla)*	12	6	0.15	**1**	**8**	**0.02**
Rock Martin *(Ptyonoprogne fuligula)*	2	4	0.41	4	9	0.17
Spike-heeled Lark *(Chersomanes albofasciata)*	**0**	**5**	**0.02**	1	4	0.18
Tawny-flanked Prinia *(Prinia subflava)*	5	3	0.48	2	3	0.65

Table 3: AIC values of the top three models influencing presence inside the piospheres for common insectivore bird species. The different variables in each model are presented for each species as well as the corresponding significant values of the fixed effects.

Species	Model Number	Variables	AIC	P – value
African Pipit *(Anthus cinnamomeus)*	1	Vegetation Ground Cover Score	0.00	**0.04**
		Vegetation Density		0.14
	2	Arthropod Diversity	1.56	0.37
		Vegetation Ground Cover Score		0.14
		Vegetation Density		0.17
	3	Season	1.90	0.47
		Vegetation Ground Cover Score		**0.05**
		Vegetation Density		0.15
Eastern Clapper Lark *(Mirafra fasciolata)*	1	Piosphere Status	0.00	**< 0.01**
	2	Vegetation Ground Cover Score	0.13	0.11
		Vegetation Density		0.38
		Piosphere Status		**0.01**
	3	Vegetation Ground Cover Score	0.30	0.23
		Piosphere Status		**0.03**
	4	Vegetation Density	0.88	0.39
		Piosphere Status		**< 0.01**
Familiar Chat *(Oenathe familiaris)*	1	Piosphere Status	0.00	**< 0.01**
	2	Season	1.36	0.32
		Piosphere Status		**< 0.01**
	3	Vegetation Density	1.97	0.58
		Piosphere Status		**< 0.01**
Karoo Scrub Robin *(Cercotrichas coryphoeus)*	1	Vegetation Density	0.00	**0.03**
		Piosphere Status		**0.02**
		Season		**0.02**
Neddicky *(Cisticola fulvicapilla)*	1	Season	0.00	**0.01**
	2	Vegetation Density	1.12	0.34
		Season		**< 0.01**
Spike – heeled Lark *(Chersomanes albofasciata)*	1	Piosphere Status	0.00	**0.01**
		Vegetation Density		**0.03**
		Season		**0.01**

Discussion

My findings show a clear effect of the degradation associated with piospheres on vegetation, birds, arthropods and therefore on the ecosystem that they are found in. There was significantly lower vegetation density occurring inside the piospheres, and both bird and arthropod diversity was significantly lower inside the piospheres. Although the birds' relative species abundance was not significantly affected by the habitat degradation, arthropods occurred in significantly lower abundances inside the piospheres than outside. Piospheres specifically played a strong role in the distribution of termite mounds. Termites were present in all outside sites but were only found in 10% of all inside sites in my study. Insect composition at a family level was significantly affected by the degradation of piospheres, specifically the groups Diptera, Myrmeleontidae, Termitidae, and Formicidae. Insectivorous birds were also found to be significantly affected by piospheres as several species were absent inside the piospheres. From the models run, these absences are likely to be due to the piosphere status, vegetation and seasonality. This shows, (1) that piospheres have an apparent effect on the biodiversity and biomass that occurs within an area of degradation, (2) that piospheres allow for the study of interspecies relationships, and (3) that piospheres do exhibit similar environmental constraints as desertification.

Vegetation density

The difference in vegetation density inside and outside the piospheres was used to ensure that the areas being studied were exhibiting the characteristic traits of piospheres (Clegg 1999; Parker & Witkowski 1999; Chamaillé-Jammes *et al.* 2009; Wilson *et al.* 2021). The significant decrease in vegetation density closer to a watering hole (inside the piospheres) observed showed that piospheres were clearly established in the study area, and that these areas did face landscape level degradation due to the presence of watering holes (Thrash 1998; Mphinyane 2002; Barboni *et al*. 2007; Melak *et al*. 2019). The similarity in the vegetation density inside the piospheres for summer and winter are clear indicators of piosphere presence as it would be expected that a much higher density of vegetation would be found in summer months (Mphinyane 2002; Lechmere – Oertel *et al*. 2005; Hoare *et al.* 2006; Barboni *et al*. 2007; Melak *et al*. 2019).

The lack of vegetation associated with the inside of piospheres has many effects on the organisms that utilise vegetation cover (Hoffman 2008; Chillo *et al.* 2018; Dalerum *et al.*

2018). Arthropods are likely to be affected by the lack of cover and microsites associated with the loss of vegetation (Fallah *et al.* 2017; Chillo *et al.* 2018; Dalerum *et al.* 2018; Muvengwi *et al.* 2018). Herbivorous organisms have also been found to change their distribution due to the changing composition and lack of growth of vegetation associated with piospheres (Smit *et al.* 2007; Epaphras *et al.* 2008; Loarie *et al.* 2009).

Bird abundance and diversity

No significant differences were found looking at the abundance of birds inside and outside of the piospheres. This is not what I expected, since the lack of vegetation should result in lower abundance of birds inside the piosphere. However, it is likely that the overall abundance of birds measured was overlooking the fact that different feeding guilds of birds would be affected by piospheres differently.

Granivorous birds gain their water requirements through drinking surface water while insectivorous birds gain their water requirements through their prey (Smit & McKechnie 2015; Smit *et al.* 2019; Czenze *et al.* 2020). The granivorous birds may have been in higher abundance inside the piospheres due to their drinking needs, while other bird species were higher in abundance outside of the piospheres in the less degraded areas (Macchi & Grau 2012; Fulton 2020). This pattern was observed in Shark Bay Australia, where species such as Crested Pigeon (*Ocyphaps lophotes*) were in greater abundance near the watering hole, while Silvereyes (*Zosterops lateralis*) and Australasian Pipits (*Anthus novaeseelandiae*) decreased in abundance inside the piosphere (Fulton 2020).

The diversity of birds was found to be significantly affected in winter by the piospheres. Although I expected both seasons to be affected it is likely that only winter depicted significant results as less granivorous species would regularly require drinking water for maintaining water balance causing them to be found more commonly outside of the piospheres, increasing the diversity of birds seen (Macchi & Grau 2012; Smit & McKechnie 2015; Smit *et al.* 2019; Czenze *et al.* 2020; Fulton 2020). Similarly to my results looking at the abundance of birds inside and outside the piospheres, closer analyses to feeding guilds may yield more significant results looking at bird diversity (Macchi & Grau 2012; Fulton 2020).

Arthropod abundance and diversity

Arthropod abundance and diversity were significantly impacted by piospheres in both summer and winter. Arthropods are ectothermic and their activity and breeding levels peek in the warmer summer months accounting for the lower abundance of arthropods in winter compared to summer (Tauber & Tauber 1976; Wolda 1988; Fitzgerald *et al.* 2021). Ectotherms rely on microsites and external cover provided by vegetation to regulate their body temperatures (Wolda 1988; Gollan *et al*. 2008; Fallah *et al.* 2017; Muvengwi *et al.* 2018; Fitzgerald *et al.* 2021). Additionally, the majority of insects are herbivorous, relying on vegetation for energy and required nutrients (Holland *et al.* 2007; Orre *et al.* 2009; Raupp *et al.* 2010). With decreased vegetation cover and density, it is likely that the area inside a piospheres is unable to support high arthropod abundance due to lack of available habitat and food source.

The abundance and diversity of arthropods in summer inside the piospheres is similar to what was found outside the piospheres in winter which indicates the lack of abundance of arthropods inside the piospheres. This poses a threat to the ecosystem as arthropods play important roles within the environment (Scudder 2017; Jankielsohn 2018; Pureswaran *et al.* 2018). Arthropods have even been recorded as the biological foundation for all terrestrial ecosystems due to their roles in nutrient recycling, pollination, seed dispersal, and soil structure (Scudder 2017). Additionally, their high abundance and diversity play vital roles in providing food source to many organisms (Scudder 2017; Jankielsohn 2018; Pureswaran *et al.* 2018). The loss of these important organisms inside piospheres pose a great threat to stability of the ecosystem.

The lack of termite mounds inside the piospheres is a testament to both the stability of the environment within the piospheres and the impact that trampling from increased large herbivore presence has on the environment. It has been found that termites are particularly sensitive to physical disturbances such as trampling and overgrazing in studies in Australia (Abensperg-Traun *et al.* 1996; Holt *et al.* 1996) and north-eastern Brazil (Vasconcellos *et al.* 2010). In all three of these above-mentioned studies the abundance of termites was significantly lower in areas of higher degradation (Abensperg-Traun *et al.* 1996; Holt *et al.* 1996; Vasconcellos *et al.* 2010). As is with all the arthropods in this study, termites may also be affected by the removal of vegetation affecting microsites and the quantity and quality of feeding and nesting sites (Vasconcellos *et al.* 2010). This important group of insects play crucial roles in nutrient cycling, aeration of soils, and enriching the soil with nutrients and minerals (van Huis 2017). The loss of these insects in an area that already faces nutrient depletion and a reduction in soil fertility due to habitat degradation poses major threats to the stability of the ecosystem and future agricultural practices in the area (Prăvălie 2016; Mirzabaev *et al*. 2019).

Arthropod Family and Order composition

The Eastern Cape faced a high number of locust swarms during my summer data collection period resulting in the high number of Caelifera found both inside and outside the piospheres (Sgqolana 2022; van der Spuy 2022). In both summer and winter nearly 50% of all insects found inside the piospheres were classified as Caelifera, Diptera, and Formicidae. Diptera species are likely to constitute a higher percentage of the arthropod composition inside the piospheres due to their biological connections to livestock and herbivores (Jahnke 1976; Foil & Hogsette 1994; Stoffolano *et al.* 1995; Paliy *et al.* 2021). Some Diptera species rely on faeces as a food source required for breeding, while others rely on animal blood (Jahnke 1976; Foil & Hogsette 1994; Stoffolano *et al.* 1995; Paliy *et al.* 2021). These zoophilic Diptera are likely to be a higher percentage of arthropod composition due to the higher presence of herbivores inside the piospheres closer to the watering source (Abensperg-Traun *et al.* 1996; Macchi & Grau 2012). Formicidae species are likely to constitute a higher percentage of arthropod composition inside the piospheres in both seasons as the reduced vegetation, debris, and leaf litter has been shown to be beneficial to Formicidae feeding behaviour (Lassau & Hochuli 2004; Radnan & Eldridge 2017).

Outside of the piospheres the percentage of arthropod composition of Caelifera, Diptera, and Formicidae remained high at nearly 50%, but dropped significantly to nearly 25% in both seasons. This decrease is likely to be due to an increased presence of vegetation and lack of disturbance that allows for the support of other arthropod Families and groups. Myrmeleontidae and Scorpiones are two groups that occur in high abundance outside of the piospheres and are not found inside the piospheres. A contributing factor to this distribution of Myrmeleontidae could be due to the predatory juvenile larval form that dig pits to trap passing insects (Heinrich & Heinrich 1984). These feeding traps are likely to be too disturbed and unsuccessful inside the piosphere due to an increase in large herbivores and a lack of insect abundance (Thrash & Derry 1999). Their adult forms however, are winged and feed on nectar and pollen, showing a reliance on vegetation, further explaining their occurrences only outside of the piospheres (Stelzl & Gepp 1988). Scorpiones are also predatory arthropods and have also been recorded to be negatively impacted in disturbed habitats (Abensperg-Traun *et al.* 1996).

Insectivorous birds

In both seasons *A. cinnamomeus* and *C. coryphoeus* were found outside the piospheres not randomly, while the distribution of *M. fasciolata* and *C. albofasciata* in summer, and *O. familiaris* and *C. fulvicapilla* in winter was not random. This shows that these species were selecting to occur outside of the piospheres in these seasons. The models that investigate why these species may be following this pattern show that vegetation cover played a significant role in affecting the distribution of *A. cinnamomeus*, while the piosphere status (inside/outside) influenced the distribution of *M. fasciolata* and *O. familiaris*. A combination of season and vegetation density influenced *C. coryphoeus*, *C. fulvicapilla*, and *C. albofasciata*.

Anthus cinnamomeus is a terrestrial foraging insectivore that is known to consume insects and spiders in the short grass and shrubs it resides in, with long grass negatively affecting their feeding strategies (Peacock BirdPro). The model run highlights the importance of vegetation ground cover to the distribution of the species and shows that *A. cinnamomeus* may occur within piospheres that are less heavily degraded due to the shorter vegetation associated with intense grazing, however the reliance on arthropods as a food source may contribute to the species being found outside the piospheres (Peacock BirdPro).

Mirafra fasciolata is also a terrestrial forager but this species is known to forage at the base of vegetation structures (Ginn BirdPro). Piosphere status (inside/outside) was the main factor influencing this species occurrence outside of the piosphere, suggesting that there may be another factor linked directly to the piosphere status that was not included in the model. This may be the requirement for both arthropod prey and specific vegetation structures (Ginn BirdPro).

Oenathe familiaris is known to perch in higher vegetation and dash down to the ground to capture prey items (Dean BirdPro). Similarly to *M. fasciolata*, piosphere status (inside/outside) was the main factor contributing to the distribution of *O. familiaris*. Due to the nature of this species a combination of vegetation requirements for perching behaviour and arthropods for prey species may be an underlying factor contributing to this species selecting for outside the piospheres.

Cercotrichas coryphoeus is a species known to run between patches of vegetation where they move underneath shrubs and bushes which are used for sheltered preening behaviours (Oatley BirdPro). The data show that vegetation density, season and piosphere status (inside/outside) contribute to the non-random distribution of *C. coryphoeus* outside the piospheres, which makes sense when looking at their preening behaviour (Oatley BirdPro).

Cisticola fulvicapilla sings from open perches and relies on the undergrowth of shrubs and bushveld for foraging but can use more open spaces easily and is known to use altered habitats such as gardens and cleared bush areas (Peacock BirdPro). The models run on my *C. fulvicapilla* data showed a preference for occurring inside the piospheres in summer and outside the piospheres in winter with season being the highest contributing factor. *Cisticola fulvicapilla* breed from October to January (summer) and are often found calling from the tops of open perches; perhaps this means that the more open areas of sparsely situated vegetation associated within piospheres act as a perch for the species to attract mates and display mating behaviours from (Peacock BirdPro). In winter months they were found outside of the piospheres where they are more likely to be able to forage successfully.

Chersomanes albofasciata is commonly found in areas with open ground as the species seldom perches and are terrestrial foragers (Ginn BirdPro). *Chersomanes albofasciata* is a very territorial species often found in pairs or small groups that maintain their territories year-round, and termites are known to be one of their main food sources (Ginn BirdPro). From the models run, a combination of season and vegetation density influenced their non-random distribution outside of the piospheres. It is likely that in the sparsely vegetated habitat of the Albany Thicket the birds do not need to feed in open spaces such as piospheres, and that the main factor resulting in the species not being seen inside the piospheres in this study is due to the lack of termites inside the piospheres.

Insectivorous birds are clearly affected by piospheres beyond a reduction in food source. It is likely that desertification will also affect the temperature, vegetation structure and community more than localised piospheres do, adding more complexities to the birds' responses (du Plessis *et al*. 2012; Martin *et al.* 2015; McKechnie *et al*. 2016; Pattinson & Smit 2017). Understanding these threats at a local scale may allow for a greater understanding when faced with large-scale desertification which may allow for the conservation of species.

Piospheres have detrimental effects on vegetation density, and arthropod and bird abundance and diversity. Due to the similarities of piospheres and areas that face desertification similar patterns of loss of diversity and decrease in abundances are likely to be seen. Bush encroachment in the Chihuahuan Desert resulted in similar findings to my study, with reduced avian abundance, richness and diversity in the area (Whitford 1997). It is clear that piospheres and desertification both result in a loss of biomass and biodiversity. Because of the similarities in soil response, vegetation response, and the response of organisms I believe that one is able to study the localised effects of habitat degradation using piospheres, and individual organisms' responses to piospheres, and extrapolate these data to understand how the area may respond when faced with desertification (Hanan *et al*. 1991; Okayasu *et al*. 2010). This may be beneficial to both agricultural practices and species conservation in areas likely to be affected by desertification and climate change.

Further studies on how different habitats and species may respond to piospheres and desertification need to be conducted. Although similar patterns of diversity and abundance loss may be common across different areas faced with degradation, it cannot be assumed that all groups of organisms or all habitats will exhibit the responses shown in these data. I suggest a comparative study between two similar habitats populated with different organisms is conducted to assess how different environments are affected by piospheres and desertification. An example of this could be done comparing the drylands of the Albany Ticket and the Kalahari and how similar, and different arthropods and bird species respond to landscape level degradation.

Summary

My findings are consistent with my hypothesis and predictions that piospheres will negatively impact vegetation density, resulting in a lower diversity and abundance of arthropods, which would result in a lower diversity and abundance of insectivorous birds inside the piospheres when compared to areas outside the piospheres. I observed that piospheres show similar effects to that of desertification and that results obtained when studying localised desertification using piospheres can be extrapolated to understand the effects of desertification on a larger area. My results suggest that ecosystem functioning and the stability of food webs within piospheres is at risk due to the changing relationships between vegetation, arthropods, and bird species. On a global scale, I believe that other arid areas will show similar results, even if specific species may respond differently when studied. I suggest that studies on birds and arthropods be performed in arid landscapes where conservation practices are being implemented to understand further the effects of water provisioning, degradation, and desertification. This is likely to be beneficial to both agricultural practices and species conservation in areas likely to be affected by desertification and climate change.

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CHAPTER 3:
THE EFFECT OF PIOSPHERES ON THE FORAGING EFFORT AND EFFICIENCY OF INSECTIVOROUS BIRDS

Abstract

Habitat degradation that results in a reduction in food and water availability and vegetation cover is likely to elicit behavioural changes from the organisms that reside in the habitat. Arid areas that face desertification can be studied using piospheres as a local scale model of degradation. Degraded habitats that result in a loss of arthropod abundance and diversity threatens insectivorous birds that rely on arthropods for both their food and water requirements. In this chapter, I use piospheres to model the effects of desertification on insectivorous birds feeding behaviour to gain understanding of the effect of a degraded habitat without the need for an increase in thermoregulatory behaviour. By understanding how insectivorous birds feeding behaviour changes in a landscape with a reduced food source allows for more accurate assumptions and predictions to be made as to how they are likely to be affected by the increased temperatures associated with climate change. Both the foraging effort and efficiency of several bird species were monitored using focal observations inside and outside 13 piospheres located in the Eastern Cape province of South Africa. Using binomial generalised linear mixed effects models a significant difference in foraging effort was found across all species as it increased from 80.48 ± 6.15 % inside the piosphere to 85.18 ± 4.50 % outside the piosphere. Both *Apalis thoracica* and *Prinia maculosa* showed similar results, while *Melaniparus afer* had too small a data set for significant results. Linear mixed effects models were used to find a significant difference between the overall foraging efficiency inside the piospheres (17.80 ± 2.90 $mg.min^{-1}$) and outside the piospheres (55.20 ± 15.61 $mg.min^{-1}$). All three species also had higher foraging efficiency outside of the piospheres than inside. These data show that piospheres can be used to model the localised effects of desertification as similar data has been found in previous studies on desertification. It is important to understand how insectivorous birds are affected by a reduction in food resources for the conservation of species and the environment. This information shows that previously modelled data that shows the effects of desertification and climate change on available suitable habitat for insectivorous species needs to include information regarding food, water and shelter availability for more accurate results.

Introduction

Many of the environmental fluctuations and changes that animals experience worldwide result from climate change and the degradation of natural ecosystems. These anthropogenically driven factors threaten water and food availability, and suitable habitat for many organisms (Pattinson & Smit 2017; Conradie *et al*. 2019; Mirzabaev *et al*. 2019; Huang *et al*. 2020). In arid ecosystems, the combination of climate change and desertification results in a loss of biological productivity (Glantz & Orlovsky 1983; Hoffman *et al.* 1989; Archer & Tadross 2009; Mirzabaev *et al.* 2019; Huang *et al.* 2020). This loss of biological productivity is observed as a decline in vegetation, a decline in soil quality, and a loss of water availability in an area (Archer & Tadross 2009; Tang *et al.* 2016; Mirzabaev *et al.* 2019). One of the contributing anthropogenic disturbances is the intensive use of rangelands by livestock with larger herds than the area can support (Archer & Tadross 2009; Huang *et al.* 2020).

The degradation of arid landscapes at a local scale can be seen around central points that are over-utilised by grazing animals—often around water sources—where concentric rings of degradation are termed piospheres (van der Schijff 1957; Barker & Lange 1969; Lange 1969; Thrash & Derry 1999). Parallels between piospheres and desertification can be made as there is a systematic loss of biological productivity within an arid ecosystem, albeit at a smaller scale (Hanan *et al.* 1991; Okayasu *et al*. 2010). Both desertification and piospheres result in a reduction of available food to herbivores and the soil quality within the area, therefore, potentially changing ecosystem functioning (McNaughton *et al.* 1988; Clegg 1999; Parker & Witkowski 1999; Chamaillé-Jammes *et al*. 2009; Wilson 2010; Landman *et al.* 2012). Due to these similarities, piospheres have been used as indicators of desertification in previous studies (Glantz 1977; Dregne 1983; Pickup *et al.* 1998; Washington-Allen *et al.* 2004). It is expected that climate change will exacerbate the degradation of arid ecosystems resulting in organisms changing and adjusting their behaviours to warmer ambient temperatures, changes in vegetation structures and communities, and food and water availability (Thrash and Derry 1999; Matchett *et al.* 2009; du Plessis *et al.* 2012; Cunningham *et al.* 2013; Conradie *et al.* 2019).

In arid ecosystems where bird species are already vulnerable to hyperthermia and lethal dehydration, the additional challenges brought about by climate change, such as increasing average ambient temperatures and the degradation of the landscape resulting in a loss of vegetation and food and water availability, pose a significant threat (du Plessis *et al.* 2012;

Albright *et al.* 2017; Conradie *et al.* 2019). When faced with increased temperatures birds implement heat-dissipating behaviours that are both energetically costly to maintain, such as gular fluttering and panting, and result in water loss, such as evaporative cooling mechanisms (Calder 1974; Wolf & Walsberg 1996; du Plessis 2012; McKechnie *et al.* 2016). Because insectivorous birds require insects as a source of both energy and water, which are crucial for thermoregulation, insectivorous birds in arid ecosystems that face degradation of habitat are likely to change their feeding behaviours to meet energy and water requirements at higher temperatures (du Plessis *et al.* 2012; Cunningham *et al.* 2013; Pattinson & Smit 2017). In addition to this, the reduction in surface water availability and vegetation is likely to result in a loss of arthropod prey that insectivorous birds rely on for their food and water intake (Smit & McKechnie 2015; Fallah *et al*. 2017; Muvengwi *et al.* 2018).

The changes in prey availability and the relative costs and benefits of having to both thermoregulate and increase foraging effort due to climate change and desertification are likely to have a negative effect on insectivorous bird populations (du Plessis *et al.* 2012; Cunningham *et al.* 2013). Research on the effects of climate change on birds in arid ecosystems has greatly increased since the year 2000. Whereas some studies model the effects of increasing temperatures and access to available, suitable habitat (Rodenhouse *et al* 2008; Şekercioğlu *et al.* 2012; Albright *et al.* 2017; Conradie *et al.* 2019; Northrup *et al.* 2019) other research studies how bird behaviour is likely to change and how behaviour adaptations are likely to occur due to their changing environments (Dunn *et al.* 2010; du Plessis *et al.* 2012; Cunningham *et al.* 2013; Cunningham *et al.* 2015; Pattinson & Smit 2017). However, many of these papers are limited by the implicit assumption that water and food availability will remain the same, which is unlikely when the ecosystem faces desertification (Clegg 1999; Chamaillé-Jammes *et al.* 2009; Fallah *et al*. 2017; Muvengwi *et al.* 2018). Because of these limitations, it is important to understand how insectivorous birds feed in a degraded habitat without the additional pressure of thermoregulation at higher temperatures to assess how climate change and habitat degradation affect their feeding behaviour. By understanding how their foraging behaviour changes in a degraded landscape (where prey items and vegetation are limited), more accurate assumptions and predictions can be made as to how insectivorous species are likely to be affected by the increased temperatures associated with climate change.

In this chapter, I determined how the desertification of arid ecosystems affects the foraging behaviour of insectivorous birds using piospheres in the Eastern Cape province of South Africa as a model for desertification. I hypothesized that piospheres decrease the energy water resource landscape for insectivorous birds. I expected that birds' foraging effort would be higher inside the piosphere and degraded area due to a lack of invertebrate prey and that foraging efficiency would show a higher mass gain per minute of foraging time outside of the degraded areas.

Methods

Study Sites

This study took place across two farms in the Eastern Cape Province of South Africa, namely Table Farm (33° 15' S, 26° 25' E; 600m) and Draai Farm (33° 14' S, 26° 25' E; 600m). Thirteen functional concrete water troughs were found in lowland areas characterised by a vegetation mosaic of Karoo scrubland, thornveld, and thicket clumps. In this area of the Subtropical Thicket Biome (previously called the Albany Thicket Biome) the average rainfall in summer is approximately 60 mm a month while in winter it is closer to 70 mm (World Weather Online). However, rainfall in this area is unpredictable as it faces a 25% chance of not receiving 80% of its expected mean rainfall in any given year, commonly resulting in several months of drought (Aucamp & Tainton 1984; Hoare *et al.* 2006). High temperatures exceeding 40°C in summer months occur on occasion while winter months often experience temperatures below freezing leading to frost in low lying areas (Hoare *et al.* 2006). Due to the stark contrasts between seasonal temperatures, the data for this study were collected between August and September in 2022 on clear days with little to no cloud cover or wind. Thirteen water troughs across both farms were used, which were identified as the "inside piosphere" sites (Image 1). The water troughs supplied surface water to livestock and wildlife for the duration of the study. For each water trough, there was an "outside piosphere" site situated 1km away in a direction that did not fall within another piosphere, ensuring this was not a disturbed or degraded area. This resulted in a total of 13 inside-, and 13 outside piospheres sites. A comparison of the inside and outside sites can be seen in Image 2.

Behavioural observations

Focal observations were conducted on commonly occurring insectivorous bird species at each inside and outside piosphere sites. Once an individual bird was identified it was followed on foot from a distance of 5m to 10m. This distance ensured that the individual's behaviour was not influenced by my presence during the observation. However, I was still able to see each successful feed and estimate the size of the insect prey. The focal was conducted by continuously recording each behaviour displayed by an individual for roughly 20 minutes using a digital voice recorder (Olympus VN-540PC 4GB Digital Voice Recorder). Because continuous recording was used each activity was recorded roughly every five seconds, and the data were analysed in five-second intervals. If the individual moved outside of the focal area or was interrupted by my presence before 14 minutes of the focal was completed the observation was abandoned.

Focal observations were completed on clear sky days with little to no cloud or wind and were started at 08:00 with no focals starting after 11:00. This was done so that the influence of weather and time of day on bird behaviours were minimal to ensure that behavioural differences did not occur due to weather or time of day.

During these focal observations, the following behaviours were noted: successful feeding, handling a prey item, beak-gleaning, preening, calling, hopping, flying, pecking, active searching, and mating behaviours. The difference in the feeding and handling categories was determined if the bird was actively feeding on the prey item or if they were holding the item while moving. Mating behaviours were classified as individuals seen interacting with another individual of the same species and displaying other territorial behaviours. If a successful feeding event took place, the size of the prey item being handled was categorised according to predetermined size classes as small, medium or large. In the smaller bird species, if a peck was observed followed by beak-gleaning behaviour, it was determined to be a successful feed of a small food item. Since the same individual conducted all observations, the qualitative nature of these categories was consistent.

Several different types of insects were captured and weighed using a New Horizon Digital Food Scale (0.01g – 500g). From these measurements, the insects were classified using the same small, medium or large categories to determine an estimated average weight for each size class.

Foraging effort

Foraging effort is defined as the proportion of time an observed bird during a focal spent actively foraging. Active foraging in this case included all categories of activity except preening, mate behaviour and calling. From the data collected, a binary system was implemented that allowed for activities contributing to foraging effort equal to “1”, while activities not included in active foraging were equal to “0” for each 5s interval. The total foraging effort was summed for each focal and converted into minutes and divided by the total time of the focal, resulting in the percentage of the total time a bird spent actively foraging in an observation period.

From the 13 sites the average of each species was calculated for both inside and outside the piospheres and 95% confidence intervals were also calculated. A binomial generalised linear mixed effects model using the lme4 package (Bates *et al.* 2011) was run within the R statistical environment (R Development Core Team, 2022) for all individual focal observations to determine an overall effect of the piospheres (in/out) on foraging effort (presence/absence) of insectivorous birds, with location (inside or outside the piospheres) as a fixed effect in the model, with site and species as random effects. The same test was also completed on the data collected for each species that contained more than one focal for inside and outside the piospheres—namely the Karoo Prinia (*Prinia maculosa*), Bar-throated Apalis (*Apalis thoracica*), and Grey Tit (*Melaniparus afer*) — with site as the random effect. This was to determine if piospheres caused a difference in the foraging effort within a species.

Foraging efficiency

Foraging efficiency is defined as the biomass intake rate per unit of foraging time (Ridley & Raihani 2007; du Plessis *et al.* 2012). For foraging efficiency, the foraging effort per successful feed within a focal was calculated which was then divided by the estimated weight of the size class of the prey item.

Linear mixed effects models were run using the nlme package, with each successful feeding event for a species during the focal (Pinheiro & Bates 2000) as the dependent value, using the R statistical environment (R Development Core Team, 2022). Location (inside and outside the piospheres) was used as the fixed effect, while site and species were used as random effects in an overall model run on all the focal observations to determine the effect of piospheres on insectivorous birds foraging efficiency. For the separate models run for the *P. maculosa*, *A thoracica*, and *M. afer* to determine the effect of piospheres within a species, only site was used as a random effect.

Results

Five different species were recorded during the observations (Table 1). The Southern Fiscal (*Lanius collaris*), Fiscal Flycatcher (*Melaenornis silens*) and Fork-tailed Drongo (*Dicrurus adsimilis*) had small data sets, therefore I did not conduct "within species" analyses on their foraging effort and foraging efficiency. However, their data were used, combined with data from *P. maculosa*, *A thoracica*, and *M. afer*, to assess how overall bird foraging effort and efficiency was affected by areas of degradation.

Table 1: Number of focal observations recorded for each species, and their location (inside the piospheres, or outside the area of degradation).

Species	*Inside Piospheres*	*Outside Piospheres*
Bar-throated Apalis *(Apalis thoracica)*	2	4
Fiscal Flycatcher *(Melaenornis silens)*	1	0
Fork-tailed Drongo *(Dicrurus adsimilis)*	1	1
Grey Tit *(Melaniparus afer)*	1	4
Karoo Prinia *(Prinia maculosa)*	8	2

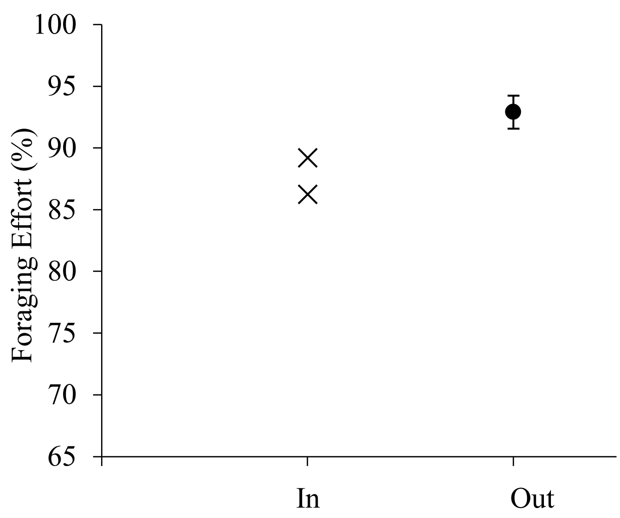
Foraging effort

Apali thoracica was only recorded at two sites inside the piospheres (one full focal each) with foraging efforts being recorded at 89.21 % and 86.24 %, respectively. Outside of the piospheres, *A. thoracica* had a mean foraging effort of 92.91 ± 1.33 % (n = 4). It was found that the piospheres had a positive significant effect on the foraging effort of *A. thoracica* (bGLMM, $\chi^2_{1,\ 1330} = 3.08$, $P < 0.05$; Fig. 1a)

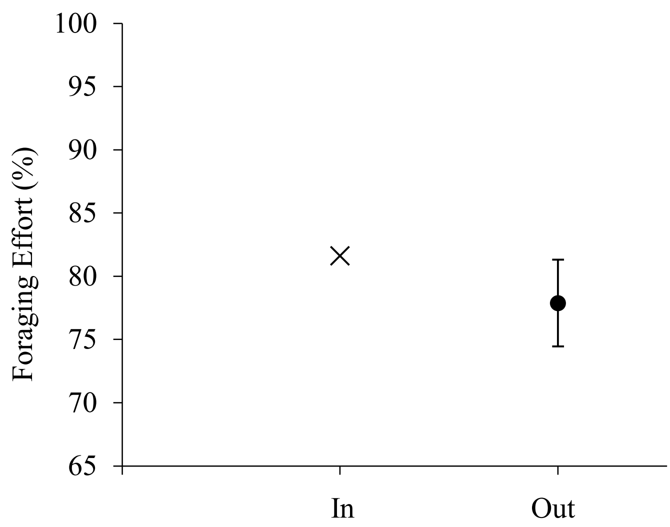
Inside the piospheres, the *M. afer* was only recorded in one full focal with a foraging effort of 81.65 %, while outside the piospheres a mean foraging effort of 77.89 ± 3.43 % was recorded (n = 4). There was no significant difference in foraging effort inside versus outside piospheres (bGLMM, $\chi^2_{1,1016} = 1.56$, $P = 0.21$; Fig. 1b).

Prinia maculosa was recorded during two full focals outside of piospheres with foraging effort percentages of 85.63 % and 74.89 %, respectively. Inside piospheres, the mean foraging effort for *P. maculosa* was lower at 69.03 ± 7.10 % (n = 9). This species' foraging effort was significantly lower inside the piospheres than outside of the piospheres (bGLMM, $\chi^2_{1,2040} = 9.72$, $P < 0.001$; Fig. 1c).

a)



b)



c)

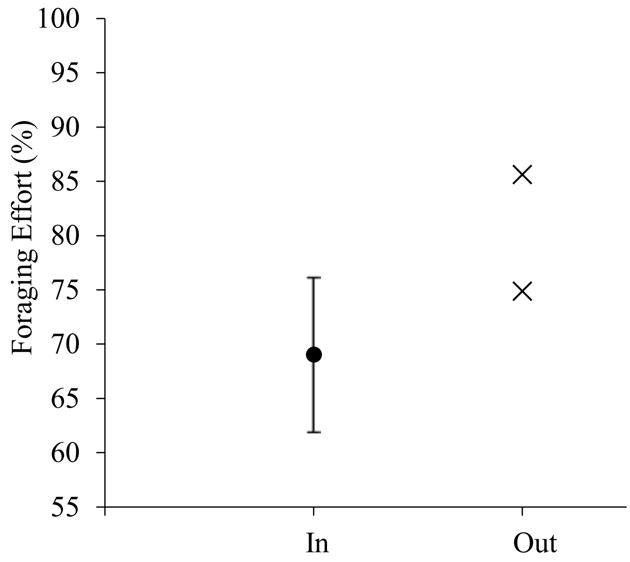


Figure 1: Percentage foraging effort for inside and outside the piospheres for a) Bar-throated Apalis (*Apalis thoracica*); b) Grey Tit (*Melaniparus afer*); and c) Karoo Prinia (*Prinia maculosa*) collected between August and September in 2022. Data presented in black circles represent foraging effort pooled across focals ± 95% CI, while data presented by crosses represent foraging effort from individual focal observations for the species.

The mean foraging effort across all species inside the piospheres (80.48 ± 6.15 %) was lower than that recorded outside the piospheres (85.18 ± 4.50 %), and this was a significant difference (bGLMM, $\chi^2_{1,\,5375} = 12.55$, $P < 0.001$; Fig. 2).

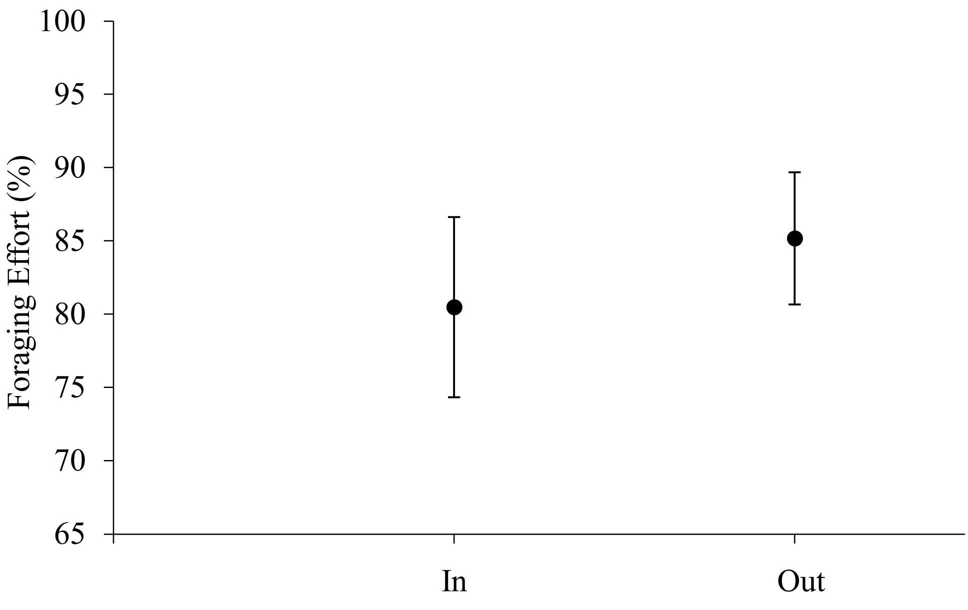


Figure 2: Percentage foraging effort for inside and outside the piospheres for all focal observations conducted (n=13). Data presented are means ± 95% confidence intervals.

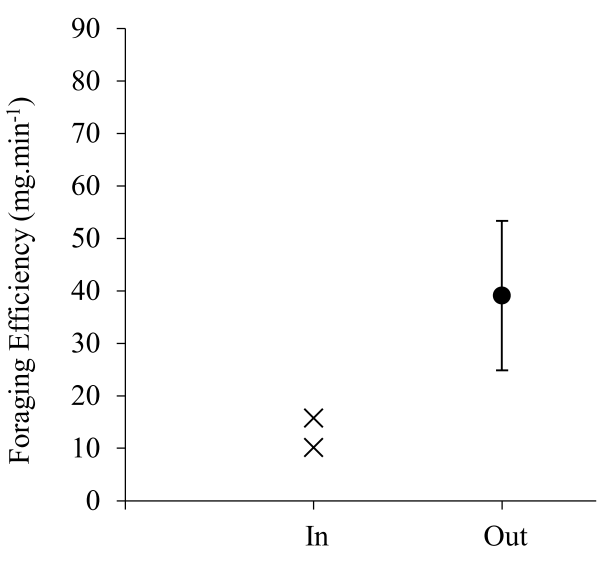
Foraging efficiency

For *A. thoracica*, two focal observations were conducted within piospheres where the mean foraging efficiency per focal was 15.70 $mg.min^{-1}$ and 10.13 $mg.min^{-1}$, respectively. Foraging efficiency of *A. thoracica* inside the piospheres was significantly lower compared to outside of the degraded area in this species (39.12 ± 14.25 $mg.min^{-1}$, n = 4) (LME, $\chi^2_{1,114} = 6.12$, $P < 0.05$, Fig. 3a).

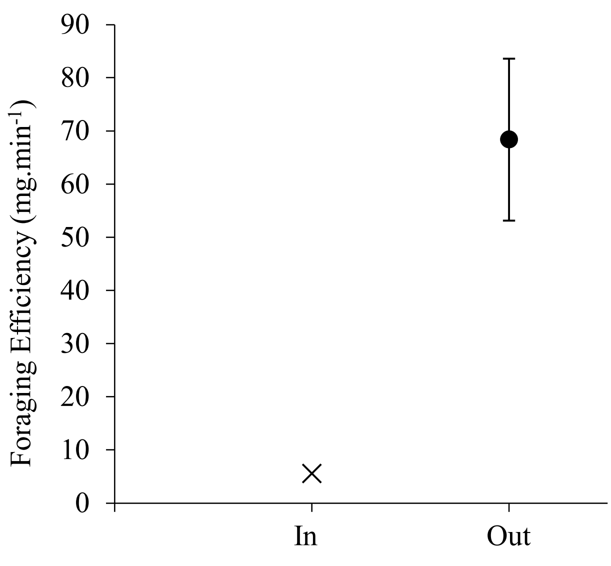
Prinia maculosa had a mean foraging efficiency inside the piospheres of 21.40 ± 2.90 $mg.min^{-1}$ (n = 8) while the foraging efficiency over two focals outside the piospheres was significantly higher at 84.02 $mg.min^{-1}$ and 40.75 $mg.min^{-1}$ (LME, $\chi^2_{1,85} = 5.58$, $P < 0.05$, Fig. 3c).

Inside the piospheres, foraging efficiency for *M. afer* during one focal was 5.55 $mg.min^{-1}$, whereas the average foraging efficiency was 68.38 ± 15.21 $mg.min^{-1}$ (n = 4) outside of the piospheres. However, foraging efficiency of *M. afer* inside compared to outside of the piospheres, was not statistically significant (LME, $\chi^2_{1,45} = 1.83$, $P = 0.18$, Fig. 3b).

a)



b)



c)

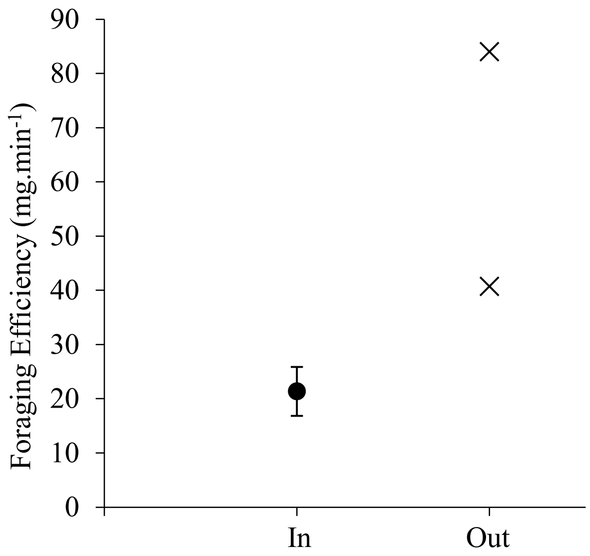


Figure 3: Foraging efficiency (mg.min^{-1}) for inside and outside the piospheres for a) Bar-throated Apalis (*Apalis thoracica*); b) Grey Tit (*Melaniparus afer*); and c) Karoo Prinia (*Prinia maculosa*) collected between August and September 2022. Data presented in black circles represent the foraging effort ± 95% CI, while data presented by crosses represent the foraging effort recorded from individual focal observations for the species.

The mean foraging efficiency across all focal observations, for species pooled (Table 1), recorded inside the piospheres was 17.80 ± 2.90 mg.min^{-1}, while the mean foraging efficiency outside the piospheres was 55.20 ± 15.61 mg.min^{-1}. There was a significant difference in foraging efficiency between inside and outside piospheres when the data for all species were pooled (LME, $\chi^2_{1,278} = 16.05$, $P < 0.001$, Fig. 4).

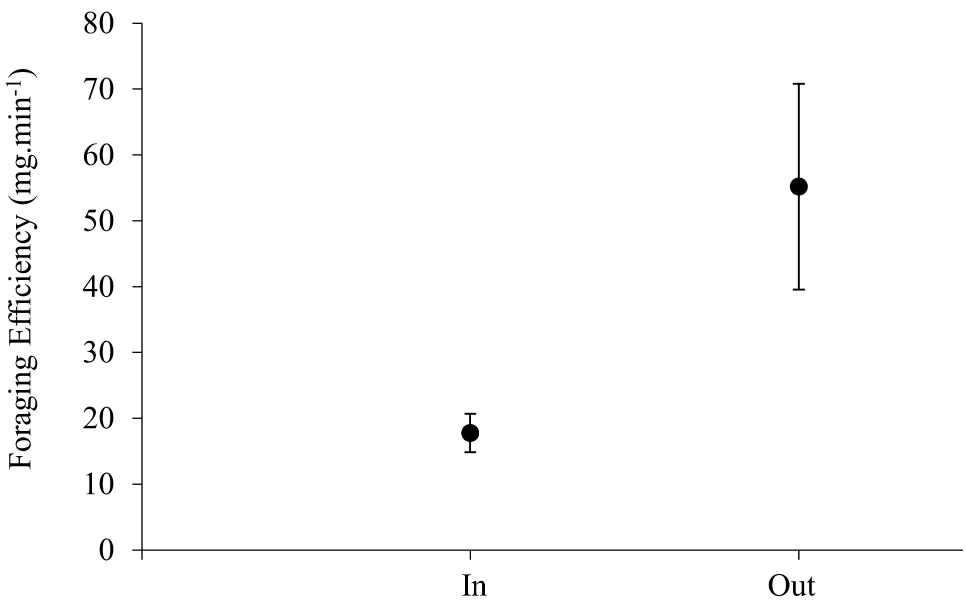


Figure 4: Foraging efficiency (mg.min^{-1}) for inside and outside the piospheres for all focal observations conducted (n=13). Data presented are means ± 95% confidence intervals.

Discussion

My data reveal that foraging effort inside a degraded area is generally significantly lower than outside a degraded area. A significantly lower foraging effort was found outside the piospheres for *P. maculosa*. Importantly, my research showed that foraging efficiency was significantly lower—specifically for *A. thoracica* and *P. maculosa*—inside piospheres than outside piospheres. These findings support my hypothesis that desertification can negatively impact the energy water resource landscape for insectivorous birds in arid environments.

Foraging effort

The foraging effort inside the piospheres was significantly lower than outside the piospheres and this differs from what I expected. I expected that the decrease in arthropod prey and vegetation associated with the degradation of the environment would have resulted in insectivorous birds having to forage more to find food (Hoffman 2008; Chillo *et al.* 2018; Muvengwi *et al*. 2018). The foraging effort patterns for *P. maculosa* were, however, consistent with my predictions. The data collected in this study did not cover enough information to assess why the foraging effort was not increased with less prey available to the birds.

Several reasons may contribute to these findings. Firstly, the decrease in vegetation associated with piospheres and arid system degradation may provide less cover for insects to conceal themselves from potential predators. Having less vegetation may make foraging for birds easier because outside the piospheres birds have to search for prey in vegetation that provides insects with cover and refuge making it more challenging to capture prey (Crowder & Cooper 1982; Savino & Stein 1982; Babbit & Tanner 1997). A study on Bluegill Sunfish (*Lepomis macrochirus*) showed that dense structure in an environment inhibits predation of smaller organisms while sparse vegetation and structure in an environment allows predator species efficient foraging even if the area is inhabited by fewer, smaller prey organisms (Crowder & Cooper 1982). Although this was an aquatic study, I believe similar principles may apply to terrestrial systems. In addition, the reduction in vegetation cover and refuge for insectivorous birds inside piospheres increases their own risk of predation while foraging.

Many animals use vigilant behaviour as a predator avoidance strategy while others use this behaviour for conspecifics (Tätte *et al.* 2002; Beauchamp 2009; Beauchamp 2010). Although vigilant behaviour was not specifically recorded in this study, behaviours such as calling and conspecific behaviour were recorded. I found that calling across all species occurred 3% more on average in focal observations conducted inside piospheres. Calling plays an important role in predator avoidance in many different organisms as well as birds (Leavesley & Magrath 2005; Hollén & Radford 2009; Gill & Bierema 2016). It is not known if this behaviour provides selfish or altruistic benefits of survival (Hollén & Radford 2009), but it is clear it plays an important role in how individuals interact with one another, intra- and interspecifically. (Leavesley & Magrath 2005; Gill & Bierema 2016).

Calling plays different roles in different bird species (Marler 1957; MacArthur 1964; Marler 2006). In *M. afer* and *A. thoracica* calling serves to remain in contact with mates while foraging which was observed to be done in pairs (Krebs 1971; van Dijk *et al.* 2015; Lee *et al.* 2018). This is suspected to differ from *P. maculosa* which were found calling from the tops of trees and bushes for territorial behaviour displays and pair bonding (Rowan & Bruekhusen 1962).

Another factor that may have caused a difference in foraging effort inside the piosphere could be related to the reduction in shaded microsites, and thus differences in thermoregulatory demand. Although no thermoregulatory behaviour was observed, perhaps because observations were conducted during the morning and not during the heat of the day, a reduction in vegetation cover that would provide cooler microsites to birds in shaded environments is significantly reduced inside the area of degradation (Martin *et al.* 2015; Perkins 2018; Melak *et al.* 2019; van de Ven *et al.* 2019; Saaymen *et al.* 2021). An increase in thermoregulatory behaviour results in reduced foraging in bird species found in arid ecosystems due to thermal constraints (Wolf & Walsberg 1996; Wolf 2000; Williams 2001; Martin *et al.* 2015). For example, Rufous-eared Warbler (*Malcorus pectoralis*) experienced a 56% decrease in foraging effort on hot days and an increase in the time spent exhibiting thermoregulating behaviours in the southern Karoo of South Africa in a similar, albeit drier landscape to my study sites (Pattinson & Smit 2017). Similar results were also seen when studying the effect of temperature on the Western Australian Magpie (*Cracticus tibicen dorsalis*) (Edwards *et al.* 2015). In this study, I expected to see more thermoregulatory behaviours and less foraging behaviours where shaded microsite availability was reduced.

Foraging efficiency

The significantly lower foraging efficiency inside the piospheres was expected due to the lack of vegetation cover that provides a food source for insects (Hoffman 2008; Chillo *et al.* 2018).

Studying the changes in vegetation due to utilisation gradients in South America, Chillo *et al.* (2018) found that most invertebrate species had a decreasing trend in areas that experienced continuous grazing. Initially, I predicted that the foraging efficiency would be higher outside the piosphere as insectivorous birds would exhibit higher foraging effort with unsuccessful feeds inside the piosphere. However, this higher foraging effort inside the piosphere was proven not to be the case. This highlights that even though the foraging effort was higher outside the piosphere, the food rewards (mg) per minute of searching were significantly higher than inside. This shows just how stark the contrasts are between the degraded environment inside compared to outside a piosphere.

Although there were limited data collected on the different species occurring inside the piospheres due to the difficulty in finding species that are commonly found both inside and outside the piospheres, my findings show a clear trend across all focal observations. I believe that the *M. afer* foraging efficiency data was not significantly different inside and outside the degraded area due to the paucity of data for inside the piospheres, and that if more focals could be conducted, a significant result would be seen.

My findings convincingly showed that a degraded landscape results in a significant reduction in foraging efficiency for insectivorous birds. My data were collected when birds experienced cooler temperatures than they would during summer months, and hotter parts of the day. This significant result shows that degradation alone is likely to affect insectivorous birds in the long term as they will struggle to forage successfully, likely leading to poor body condition and issues with maintaining metabolic requirements (du Plessis *et al.* 2012; Cunningham *et al.* 2013; Pattinson & Smit 2017; Conradie *et al.* 2019). Additionally, my results can explain the patterns of habitat use I observed in Chapter 2, with many species showing the avoidance of piospheres. Therefore, these results provide evidence that the patterns of spatial use are likely to be strongly related to foraging ecology, and energy and water balance requirements. It is expected that habitat degradation combined with the increased temperatures associated with climate change will further decrease the foraging efficiency found inside the piosphere (du Plessis *et al*. 2012; Cunningham *et al*. 2013; Martin *et al.* 2015; Pattinson & Smit 2017). This poses major threats to insectivorous birds' ability to breed, provide parental care to offspring, and ability to manage metabolic requirements that are crucial for thermoregulation which will be of huge importance in their survival (du Plessis *et al*. 2012; Martin *et al.* 2015; McKechnie *et al*. 2016; Pattinson & Smit 2017).

The broader scale implications of these results show how habitat degradation and desertification threaten arthropod and avian species at a greater level than previously understood. My study was conducted in an area that exhibited a patchy habitat where there are areas of less degraded habitat that insectivorous birds are able to forage in. This allows insectivorous birds to avoid areas where energy and water intake will be too low. However, if the degradation becomes larger scale and the entire landscape becomes degraded, I predict further reductions in avian energy and water intake to take place. Examples of this include increased intra- and interspecific competition and over-exploitation of food resources in the area. If degradation of the landscape occurs, it seems reasonable to predict that the effects of reduced foraging efficiency and/or avoidance of the habitat will become widespread.

More research needs to be conducted on more species of insectivorous birds and cover different feeding guilds. I also believe that similar studies need to be conducted in other habitats as different ecosystems may have different ecological drivers and responses to disturbance. For example, if this study were to be repeated in the Kalahari, I would expect lower foraging effort in degraded areas due to the birds' need to thermoregulate more in the hotter environment. My thesis focused on arthropods and insectivorous birds and how they are affected by piospheres and desertification. It is also important to understand how granivorous birds would respond to degraded habitats as their reliance on surface water for thermoregulation would change the outcome of the results.

Summary

My findings are consistent with my hypothesis and predictions that desertification and habitat degradation result in a loss of biodiversity and biomass, and that the degradation of arid landscapes will affect the insectivorous birds' ability to forage successfully (Pattinson & Smit 2017; Conradie *et al*. 2019; Mirzabaev *et al*. 2019; Huang *et al*. 2020). I observed that piospheres can be used to model landscape-level degradation and that these results can be extrapolated to understand the effects of desertification. I also showed that desertification and degradation have a significant impact on foraging effort and efficiency of two study species, as well as insectivorous birds in the Albany Thicket overall. My results suggest that previous studies where food and water sources were implicitly assumed to be stable when modelling the effects of climate change on insectivorous birds depict a best-case scenario. On a global scale, I believe that arid areas will show similar results when studied and suggest that similar studies be performed in arid landscapes where conservation practices are being implemented to understand further the effects of water provisioning, degradation and desertification. More investigations studying the effects on granivorous birds, the same species of insectivorous birds in different habitats, and different species in different ecosystems also need to be explored.

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CHAPTER 4
CONCLUSIONS AND SUGGESTIONS FOR FUTURE RESEARCH

Effect of piospheres on arthropods and birds

The localised degradation associated with piospheres significantly impacts vegetation density, with much lower vegetation density occurring inside the piospheres (Thrash 1998; Lechmere – Oertel *et al.* 2005; Perkins 2018: Schmidt *et al.* 2019; Saayman *et al.* 2022). My study shows that this reduction in vegetation inside the piospheres significantly impacts the arthropod abundance and diversity. It is suggested that because piospheres are associated with this decrease in vegetation due to intense grazing, trampling and changes to soil structure and soil composition, this significant reduction in arthropod abundance and diversity will be observed across all habitats where piospheres occur (Abensperg-Traun *et al.* 1996; Holt *et al.* 1996; Thrash & Derry 1999).

Termites were a group notably affected by piospheres in this study as they were found occurring outside of the piospheres in high numbers but in only 10% of inside piosphere sites (Fig. 6). The composition of arthropod families was also affected by the degradation associated with piospheres. This reduction in arthropod abundance and diversity, and shift in family composition poses major threats to the ecosystem functioning and environmental stability as insects are a food source to many organisms and play crucial roles in the ecosystem (Jankielsohn 2018; Pureswaran *et al.* 2018). Bird abundance and diversity were also affected by the piospheres, specifically insectivorous birds which were the focus of this study. This is unsurprising due to the changes seen in the arthropods that occur within piospheres.

The insectivorous birds were observed to avoid piospheres due to both the change in vegetation and the observed arthropod changes related to the degradation inside a piosphere (Whitford 1997, Fulton 2020). From my study it is clear that the main reason why the insectivorous birds studied occurred outside the piosphere relates to the changes in vegetation and the reduction in arthropod abundance and diversity.

I suggest that more species are studied in this regard to gain further understanding of the response of arthropods and their insectivorous predators to piospheres, and localised degradation. I also suggest that similar studies are conducted in other habitats and environments and that it is not assumed that all environments and species will respond in similar ways. However, it is expected that similar patterns will emerge.

Insectivorous birds feeding behaviour

The changes in vegetation and arthropod abundance and diversity observed due to the piospheres did significantly affect the feeding behaviour of insectivorous birds. My study shows that foraging effort of insectivorous birds in the Albany Thicket is significantly decreased inside the piospheres. It is suggested that this is due to a lack of vegetation available to arthropod prey as cover, meaning that insects that do occur inside the piospheres face a much higher predation risk (Crowder & Cooper 1982). The foraging efficiency recorded in my study also shows a reduction occurring inside the piospheres. This is most likely a result of low abundance of arthropods due to the degradation of the habitat (Abensperg-Traun *et al.* 1996; Holt *et al.* 1996; Thrash & Derry 1999). These data provide more insight into the patterns of avoidance of insectivorous birds seen in Chapter 2 of this thesis.

This has many implications for the survival of insectivorous species in arid environments. All insectivorous birds are threatened by this reduction in foraging efficiency in a degraded habitat as all metabolic requirements to thermoregulate are usually met by the consumption of arthropod prey (Smit *et al.* 2019; Czenze *et al.* 2020). This knowledge of feeding behavioural changes needs to be considered when modelling the effects of desertification and climate change on insectivorous birds as it is likely to affect the outcomes of shifting suitable habitat predictions such as the study conducted on Southern Pied Babblers (*Turdoides bicolor*), Southern Yellow-billed Hornbills (*Tockus leucomelas*) and Southern Fiscals (*Lanius collaris*) (Conradie *et al*. 2019).

I suggested that more research on more species of insectivorous birds needs to be conducted and that research also needs to cover different feeding guilds, such as granivores. Additionally, I believe that similar studies need to be repeated in different habitats and ecosystems as different ecological drivers may alter responses to disturbance. An example given includes conducting research in the Kalahari, as I would expect a lower foraging effort in this habitat in degraded areas due the hotter environment. My thesis focused on arthropods and insectivorous birds and how they are affected by piospheres and desertification. It is also important to understand how granivorous birds would respond to degraded habitats as their reliance on surface water for thermoregulation would likely change the outcome of the results.

Using piospheres as models for desertification

The effects seen on vegetation, arthropods, birds, and insectivorous birds shows the great threat to the environment associated with piospheres. It is clear that desertification is likely to result in similar effects to what was seen in this thesis, and that piospheres can be used to model how species and local ecosystems are likely to respond to desertification (Hanan *et al*. 1991; Okayasu *et al*. 2010). From the data presented here degradation of the landscape in the area of Albany Thicket may well lead to a loss of arthropod abundance and diversity, and this will likely result in affecting the feeding success and effort of insectivorous birds in the area, negatively impacting the ecosystem functioning and stability. The use of piospheres as models for desertification allows for further in-depth studies of the effects of habitat degradation that can allow for a greater knowledge on how habitats and ecosystems may be affected (Hanan *et al*. 1991; Okayasu *et al*. 2010). I believe that studying piospheres is an appropriate way to understand how desertification may affect an environment. This has further implications for possible preventative measures that can be determined and implemented in an attempt for species conservation and land preservation.

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Appendix

Image 1: Image depicting the 13 inside piosphere sites across both farms in the Eastern Cape, South Africa. Map Data @ 2023 AfriGIS (Pty) Ltd.

(a)

(b)

Image 2: Image depicting the degraded landscape seen inside the piospheres (a) in comparison to outside the piosphere (b) where natural vegetation is found (Balmer, NL).