Drivers of expansion and biodiversity impacts of the Pied Crow on Angulate Tortoise populations in the Western Cape

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Declaration

I know the meaning of plagiarism and declare that all of the work in the dissertation, save for that which is properly acknowledged, is my own. This dissertation has been submitted to the Turnitin module (or equivalent similarity and originality checking software) and I confirm that my supervisor has seen my report and any concerns revealed by such have been resolved with my supervisor.

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Abstract

Global biodiversity loss continues, with no foreseeable end. Efforts to limit biodiversity loss include a focus on controlling populations of alien invasive species, yet the impacts of native species increasing their ranges remain poorly explored. These native invaders can increase rapidly, with impacts comparable to those of alien invasive species. In South Africa, the Pied Crow (*Corvus albus*) represents a well-known example of a native invader, with population increases observed across much of the country. These increases have been particularly acute in largely treeless areas of the west where the development of dense linear infrastructure, such as powerlines, telephone poles, and even windpumps have provided novel nesting sites. These increases have brought Pied Crows into contact with many species that were not previously exposed to large numbers of this generalist predator. Despite growing concern about their potential ecological impacts, particularly on tortoises, empirical evidence remains limited.

This thesis examines recent Pied Crow population trends over the past 15 years and investigates the potential impacts of their expansion along linear infrastructure on a native tortoise species. I address several questions relating to drivers of Pied Crow population increases, their use of powerline infrastructure as nesting sites, and how this enables them to invade relatively undisturbed, historically treeless Fynbos and Karoo habitats.

First, using data from the Second Southern African Bird Atlas Project (SABAP2), I quantified Pied Crow population change across South Africa between 2008 and 2023 and identified three potential environmental drivers (minimum temperature, annual rainfall, and degree of human modification) associated with these trends. Reporting probabilities increased nationally by approximately 45% across the period, with large increases in the Free State (265%), Eastern Cape (81%), and Mpumalanga (74%). By biome, Albany Thicket (133%) and Grassland (89%) showed the largest increases. Increases were more pronounced in unprotected than protected areas, suggesting that anthropogenic change facilitates population expansion. Temperature, precipitation, and human modification were also associated with increasing reporting probabilities, with higher increases in cooler, drier, and more modified landscapes.

Second, I explored the impacts of Pied Crow expansion following powerline development at a wind farm, on Angulate Tortoises (*Chersina angulata*). I assessed the hypothesis that the powerline has allowed Pied Crows to nest in this area and that this has elevated crow numbers and therefore predation pressure, impacting local tortoise populations. Based on this hypothesis, I make two predictions, one temporal and one spatial. Temporally, I predict that numbers of depredated tortoises at Pied Crow nest sites along the powerline would have declined over time as tortoise numbers are being reduced by Pied Crow predation, leaving fewer to prey upon. Spatially, I predict that numbers of tortoise will be lower close to the powerline than further away from it, because predation will be greater near Pied Crow nests and be reduced further away. To test my first prediction, I used long-term data collected along the powerline over 11 years. I analysed whether the number of tortoise shells depredated and left beneath Pied Crow nests had declined over time. To test my second prediction, I explored how Pied Crow and Angulate Tortoise abundance varies with distance from the powerline, predicting that if Pied Crows are most abundant near the powerline, tortoise numbers would likely be lowest in these areas due to higher predation pressure.

I found support for my hypothesis. Depredated tortoises found beneath individual nest sites declined over time. Across all nest sites, tortoise carcass abundance decreased by approximately 31% each year. In addition, Pied Crow abundance was greatest near the powerline, decreasing 26% per km, moving away from infrastructure. The spatial tortoise response was non-linear, with abundance rising sharply beyond 4 km from the powerline, indicating increased predation pressure near infrastructure.

Together, these results suggest that climate and infrastructure development have contributed to Pied Crow expansion in South Africa, and that powerlines create elevated predation risk for native fauna, such as tortoises. This thesis represents the first evidence of Pied Crows impacting a native tortoise species in South Africa. This finding is particularly important given that South Africa is a global hotspot for chelonian biodiversity and supports some of the most threatened tortoise species in the world. Importantly, this evidence supports the justification for management intervention, such as nest and old linear infrastructure removal, where impacts on vulnerable native tortoise species are suspected.

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Chapter 1: General Introduction

1.1 Biodiversity loss and biological invasions

Biodiversity, defined as the variety of all living species on the planet, supports ecosystem functioning and processes (Hooper et al., 2005; Gamfeldt et al., 2008), and is therefore essential for supporting human well-being. The Convention on Biological Diversity (Article 2) describes biological diversity or biodiversity as "the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species, and of ecosystems (Díaz and Malhi, 2022)". This definition encompasses more than 9 million species that co-exist with human beings and form the foundation of the various organismal, genetic, and ecological diversity found on Earth (Cardinale et al., 2012). The proper functioning of Earth's various ecosystems relies heavily on the co-existence and interactions between these species (Sala et al., 2000; Thébault and Loreau, 2005). However, global biodiversity is declining at an unprecedented rate (Cardinale et al., 2012). Human-induced extinctions, resulting from both direct and indirect activity have accelerated to rates comparable to the previous five mass extinctions (Ceballos et al., 2015), with thousands of species vulnerable or threatened (Cox et al., 2022). Human activities have accelerated the loss of various taxonomic lineages and contributed to ecosystem collapse through climate change and landscape transformation (Clavel et al., 2011). This loss disrupts fundamental ecological processes like carbon storage, nutrient cycling, and pollination, potentially leading to further biodiversity decline and ecosystem collapse (Hooper et al., 2012).

Invasive species are recognised as primary drivers of biodiversity loss and species extinctions (Doherty et al., 2016; Dueñas et al., 2021; Díaz and Malhi, 2022). Traditionally, invasive species refer to non-native species that have established themselves, through either unintentional or deliberate human activities, with detrimental consequences for local ecosystems and economies (Carey et al., 2012). Invasive species negatively impact agriculture, socio-economic systems, ecosystem services, and human well-being (Dueñas et al., 2021; Shivambu et al., 2020). However, native species can also become "invasive", when they experience marked increases or range expansions due to indirect human drivers such as habitat modification and climate change (Nackley et al., 2017). These are referred to as "native invaders" (Carey et al., 2012).

1.2 Native invasions

Human activities are largely responsible for turning native species into “invaders” within their natural habitats (Nackley et al., 2017). Climate change, urbanisation, and fire suppression heighten reproduction and survivorship in certain species (Carey et al., 2012), causing population expansions (Goodrich and Buskirk, 1995; Valéry et al., 2008). Land-use changes may lead to more severe impacts by invasive native species on local animal and plant communities, owing to increased predation and competition (Didham et al., 2007). These invaders can outcompete resident communities by exploiting niches created by human activity, or by filling vacancies left by declining species (Carey et al., 2012). Such invasions threaten native biodiversity, as even slight abundance shifts can trigger cascading effects (Valéry et al., 2009). For example, removing top predators in the eastern United States caused an overabundance of White-tailed Deer (*Odocoileus virginianus*), altering forest plant species composition due to excessive browsing (Horsley et al., 2003). Ultimately, anthropogenic activity provides expansion opportunities for generalist native species, often to the detriment of others.

Birds are often native invaders, likely due to their intelligence, opportunism, and mobility. Although most birds have declined with anthropogenic change, some have exploited urban habitats (Blair, 2004; Cristaldi et al., 2017; Winarni et al., 2022). In the Sierra Nevada, brood parasitic cowbirds (*Molothrus* spp.) have expanded their range with negative impacts on the host species (Rothstein and Robinson, 1994). Similarly, in Australia, land-use changes and climate shifts have considerably favoured the Noisy Miner (*Manorina melanocephala*), leading to changes in bird species composition through interspecific competition (Bennett et al., 2015). Range expansion in the Barred Owl (*Strix varia*) provides another example, as this species has shown evidence of displacing the threatened Spotted Owl (*Strix occidentalis*) through competition for territory and prey (Gutiérrez et al., 2007). In some cases, active lethal management of these native invaders has already been conducted (Diller et al., 2016) and has proven to be effective in increasing the reproductive productivity of different species. However, the implementation of such management actions to control species populations are difficult due to societal, cultural, and legal resistance (Coates et al., 2020).

1.3 Population expansion by corvids

Several species within the Corvidae family, a group of common birds (23 genera, 129 species) have undergone significant range, and abundance shifts worldwide over the past 50 years (Marzluff et al., 2001; Marzluff and Angell, 2005). For example, corvid populations have expanded to become pests across North America (Coates et al., 2020; Harju et al., 2021; Smith et al., 2022), Europe (Vuorisalo, 2003), Australia (Everding and Jones, 2006), Africa (El-Bahrawy et al., 2007; Cunningham et al., 2015; Wilson et al., 2015), and the United Kingdom (Amar et al., 2010). Expansion is most pronounced in urban environments (Marzluff et al., 2001), likely due to the availability of nesting sites, enhanced food predictability, and reduced predators (Marzluff and Neatherlin, 2006).

Corvid expansion into previously marginal rural areas has been facilitated by livestock farming, which provides food resources, and reduced persecution (Amar & Redpath, 2002; Amar et al., 2010; Jokimäki, 2022). This global increase in range and abundance has often been associated with negative impacts, particularly the predation of endangered species (Madden et al., 2015; Holcomb et al., 2021; Moldowan, 2023). For example, two *Corvus* species, Common Ravens (*Corvus corax*) and House Crows (*Corvus splendens*), are considered to be highly problematic (Adelino et al., 2017). In North America, Common Raven populations have increased dramatically, with consequences for the Greater and Gunnison Sage-grouse (Coates et al., 2020; Dinkins et al., 2021), and the endangered Mojave Desert Tortoise (*Gopherus agassizii*) (Berry et al., 2020). While House Crows have not been considered a native invader, they have established breeding populations outside of their traditional ranges (Adelino et al., 2017) with ecological (Ryall, 1992) and economic consequences (Kamel, 2014). Given their generalist diet and high intelligence, corvids exemplify population abundance and range expansion in avifauna.

1.4 Invasive potential of *Corvus albus*

Pied Crows (*Corvus albus* Müller, 1776) have increased markedly across South Africa in recent decades (Cunningham et al., 2015). This expansion has been associated with human population growth, rising temperatures, changing precipitation, higher densities of electrical infrastructure, increased access to human waste, roads, and urbanisation (Cunningham et al., 2015; Dean and Milton, 2009; Joseph et al., 2017). In the Karoo and Fynbos shrubland biomes

of southwestern Africa, Pied Crow reporting rates suggest increased population abundance (Cunningham et al., 2015). This is particularly notable near areas with dense powerline infrastructure, suggesting their use of these structures for nesting sites (Cunningham et al., 2015).

South Africa's rising demand for electricity is driving large-scale expansion of the transmission grid (Akinbami et al., 2021). In their Transmission Development Plan for 2025-2034, the country's power utility, Eskom (2024) outlined plans for approximately 14,494 km of new powerlines to accommodate both renewable and non-renewable energy development, particularly in the Northern Cape and Limpopo provinces. This represents a ca. 44% increase to the national transmission network of 33,067 km (Eskom, 2024). Because Pied Crows benefit from the availability of nest sites provided by powerlines and pylons (Cunningham et al., 2015; Underhill, 2025), this infrastructure expansion may facilitate further population increases.

Pied Crows are widely regarded as a 'problem species' due to their mobbing, harassing, and competing with raptors for nesting sites (Cunningham et al., 2015). Tortoise predation has been widely reported across the Northern and Western Cape provinces, involving several species of conservation concern (Fincham and Lambrechts, 2014; Loehr, 2017; Durà i Franch, 2017). Pied Crows have been identified as nest predators of Kittlitz's Plover (*Charadrius pecuriaru*s) and the near threatened Chestnut-banded Plover *(Charadrius pallidus)* (Troscianko et al., 2016; Ferguson et al., 2021). Furthermore, there have been disturbing reports of Pied Crows feeding on and plucking out the eyes of new-born lambs (Jenkins and van Zyl, 2020). Consequently, expanding crow populations threaten biodiversity and agricultural productivity.

1.4.1 Human perception of *Corvus albus*

Decision-making in conservation is strongly influenced by human perception and opinion, with the media playing a major role in shaping how species are viewed and understood (Ostrovski et al., 2021). For the vast majority, the media acts as their main source of information on nature, impacting their perception of global environmental issues and species (Ostrovski et al., 2021). In movies and TV shows, crows are generally portrayed as harbingers of death, a source of bad luck, and bad omens, evoking negative feelings in most people (Król

and Hernik, 2020). These biases can have negative consequences for wildlife management, especially when there is no direct evidence of biodiversity impacts.

In a recent study, Ballejo et al. (2020) found that perceptions of the harm caused by birds were not supported by field observations of livestock predation. The study also highlighted that many farmers believed lethal control was the best solution to human-wildlife conflict. Premature decisions based solely on perception can therefore lead to unjustified actions against wildlife (Morales-Reyes et al., 2018).

Perceptions of Pied Crows vary across South Africa (Adelola, 2024), which may influence conservation efforts. Negative views of Pied Crows, especially considering their growing abundance, may lead to an overreaction by various stakeholders, including farmers, conservationists, and the general public. Understanding whether this species is indeed increasing in abundance and range, and the effects of this increase on native fauna, is key to developing conservation strategies that do not indiscriminately harm species based on public perceptions.

1.4.2 *Corvus albus* as a model species for native invasion

I investigated the driving factors behind changes in Pied Crow population abundance across South Africa. Pied Crows are widespread throughout sub-Saharan Africa, with their range extending to the southernmost point of Africa. This species is notably absent from central Kalahari and eastern Namibia (Chittenden et al., 2016). They occur across a wide range of habitats, including open savanna woodland, shrublands, farmlands, and urban areas, often associating with human settlements (Chittenden et al., 2016).

Pied Crows are monogamous, with males and females pairing for life (Chittenden et al., 2016). Their nests are built high up in trees, on electrical pylons, or windmills (Chittenden et al., 2016). A clutch of 4-5 bluish eggs with heavy speckling are laid during the breeding period from July to January (Chittenden et al., 2016). Fledglings are reared by both parents (Chittenden et al., 2016). Currently, Pied Crows are categorised as ‘Least Concern’ on the IUCN Red List (BirdLife International, 2024).

The growing abundance of Pied Crows across South Africa has led to both positive and negative opinions amongst the public (Adelola, 2024), particularly regarding their perceived impacts on livestock and biodiversity. They are therefore a socially relevant focal species for

understanding human-wildlife interactions. Their wide distribution, ability to survive across a range of habitats, and association with human-modified landscapes highlight why Pied Crows are an ideal model for investigating the drivers of population expansion and the implications for biodiversity conservation in South Africa and beyond.

1.5 Aim

I aim to assess population trends of Pied Crows from 2008–2023 across South Africa, while exploring the anthropogenic and climatic factors that may have been driving these changes. Additionally, I aim to answer several key questions regarding the impacts on tortoise populations associated with increasing Pied Crow abundance because of expanding powerline infrastructure. In doing so, I aim to provide insights into not only the biodiversity impacts of Pied Crows, but also the broader impacts associated with increasing densities of powerline infrastructure across the country.

1.6 Thesis structure

My thesis has two data chapters addressing the status of Pied Crows as native invaders, and a final discussion chapter. Chapters are written using collective pronouns to facilitate future publication as co-authored papers, although I can confirm that this is all my own work. Chapters 2 and 3 are written as stand-alone manuscripts to facilitate future publication, therefore there may be overlap in information presented in the chapters. For example, both data chapters contain ecological information on corvids and *Corvus albus.* This thesis is structured as follows:

Chapter 2 analyses the current spatial distribution and recent trends in Pied Crow reporting probabilities in South Africa from 2008 to 2023, by comparing crow populations and their trends in protected versus unprotected areas, provinces, and biomes. I explore drivers by relating these changes to climate (temperature [°C], precipitation [mm]) and human development.

Chapter 3 investigates how increasing Pied Crow numbers, because of expanding powerline infrastructure, affects tortoise abundance using a powerline established in 2015 as a pseudo-experimental treatment. I analyse long-term data (2015 to 2025) on evidence of tortoise predation beneath Pied Crow nesting sites to assess whether, and to what extent, Pied Crow

populations may be impacting Angulate Tortoise populations near the powerline. I then compare Pied Crow and Angulate Tortoise abundance at varying distances away from the powerline, predicting that Pied Crow numbers will be highest near the powerline, and that Angulate Tortoises will be lower in these same areas due to increased predation. I then analyse tortoise size in relation to distance from the powerline, predicting that smaller individuals will be more abundant at greater distances where Pied Crow predation pressure is lower. Lastly, I compare the size class frequency of live and dead tortoises recorded, predicting that the current tortoise population is skewed towards larger, older individuals with declining juvenile numbers, suggesting a lack of recruitment. This approach provides a case study for understanding ecological consequences of increasing densities of linear infrastructure on native wildlife.

Chapter 4 synthesises the thesis and recommends considerations for future research.

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Chapter 2: Drivers of Recent Pied Crow Population Changes in South Africa

2.1 Abstract

Globally, bird species are undergoing rapid shifts in distribution and abundance, driven largely by climate change, land-use modification, and habitat degradation. Understanding the drivers of change typically focuses on declining or invasive species, with the expansion of common native species often overlooked. The Pied Crow (*Corvus albus*) is a common species occupying much of South Africa and is an example of a native invader. The species showed large population increases between the 1980s and 2010s, which were associated with climate change and the expansion of powerlines providing nesting and perching structures in previously treeless landscapes. With Pied Crows suspected to negatively impact biodiversity and agriculture, there is a need for consistent long-term monitoring of this native, but invasive species. Here, we examine recent (i.e., 2008–2023) population changes, using data from the Second Southern African Bird Atlas Project (SABAP2), to identify spatial patterns of change and underlying drivers over the last one and a half decades. We found a proportional increase of ca. 45% in Pied Crow reporting probabilities across South Africa over this recent 15-year period, with large increases in the Free State (265%), Eastern Cape (81%), and Mpumalanga (74%) provinces. Similarly, by biome, the largest increases were observed in the Albany Thicket (133%) and Grassland (89%). Notably, increases were more pronounced in unprotected than protected areas, suggesting this pattern may be related to anthropogenic change. Additional factors correlating with population increases were temperature, precipitation, and human modification, with greater increases in drier, cooler, and more modified pentads. Variable importance metrics (McFadden's R^2) identified minimum temperature as the most influential driver, followed by anthropogenic modification, and then rainfall. These findings suggest that both climatic factors (global scale) and human-induced landscape modification (local and regional scale) have driven Pied Crow population change in recent years.

2.2 Introduction

Monitoring biodiversity is essential to conservation, as it helps track changes in species' populations and environmental shifts, providing the information necessary to guide conservation policy and management (Schmeller et al., 2012; Lindenmayer et al., 2012). Yet, developing large-scale monitoring programmes that can track biodiversity trends across many taxa remains challenging, because long term data are needed (Proença et al., 2017). Large-scale bird monitoring programmes are therefore particularly valuable, because birds are considered useful indicators of biodiversity (Schmeller et al., 2012). These programmes not only help identify species at risk but can also document species increases at both regional and global scales (Bart, 2005).

Most large-scale monitoring efforts rely on citizen science initiatives, which allow data collection at much broader spatial and temporal scales than professional field surveys (Dickinson et al., 2010; Fraisl et al., 2022). Typically, these data are used to track trends in threatened species (Troudet et al., 2017), but monitoring population trends in widespread and common species is also important (Jones, 2011). For example, in southern Africa, one of the most important citizen science projects is the Second Southern African Bird Atlas Project (SABAP2), which collects data on bird distributions across South Africa and six neighbouring countries (Brooks et al., 2022). With the increasing availability of long-term, large-scale citizen science datasets, researchers are now better able to analyse population trends of common, wide-ranging species.

Studies exploring population expansions tend to focus on non-native, invasive species (Fennell et al., 2012). In contrast, less research has focused on range expansions of common native species (Gaston, 2011). Native invaders are species that, in response to human-driven environmental change, begin to behave like invasive species, expanding into new ranges and rapidly attaining high abundances within their native range, causing ecological or economic disruption (Carey et al., 2012; Heringer et al., 2024). These species can outcompete others (Carey et al., 2012), alter habitats, and even contribute to biodiversity loss (Nackley et al., 2017). Nevertheless, the ecological consequences of the range expansions of these so-called "native invaders" remains relatively understudied (Carey et al., 2012; Cunningham et al., 2015; Nackley et al., 2017).

Corvids represent a well-documented example of native invaders, with population increases observed worldwide. For example, over the past five decades, several native crow species have expanded across North America, Europe, Australia, and Asia (Marzluff et al., 2001; Takenaka, 2003; Harju et al., 2021; Salomon et al., 2021; Jokimäki et al., 2022). These increases are particularly prevalent in urban environments (Marzluff et al., 2001) because of the availability of nesting sites (Klausen et al., 2010), greater food availability (Kövér et al., 2019), and reduced exposure to predators (Eötvös et al., 2018). Moreover, population increases within non-urban areas have been linked to increases in livestock abundance and a relaxation in persecution (Amar and Redpath, 2002; Amar et al., 2010; Jokimäki, 2022). Global increases in corvids have often been associated with negative interactions with native fauna, including the hyperpredation of tortoises (Maldowon et al., 2023) and other endangered species, the displacement of native birds through competition for nesting sites, and reduced breeding success in some bird populations (Peery and Henry, 2010; Madden et al., 2015). For example, Common Ravens (*Corvus corax*) in the USA have been identified as predators of the endangered Mojave Desert tortoise (Berry et al., 2020). Other corvids have had similar impacts: Hooded Crows (*Corvus cornix*) are known predators of Norwegian Willow Ptarmigan eggs (Parker, 1984), American Crows (*Corvus brachyrhynchos*) are believed to be an important predator of duck eggs (Clark et al., 1995), and Steller's Jay's (*Cyanocitta stelleri*) have been identified as nest predators of Marbled Murrelets (Gabriel and Golightly, 2014). The high intelligence and sociality among corvid species allow for the efficient transmission of information, new modes of foraging, and changes in foraging behaviour (Moldowan, 2023). These factors allow corvids to take advantage of increasing urbanisation and human populations. One species that exemplifies this trend is the Pied Crow (*Corvus albus*), a generalist and opportunistic species widespread across sub-Saharan Africa (Hockey et al., 2005).

Pied Crows have shown a remarkable increase in abundance across South Africa and continue to spread into areas where they were historically scarce (Cunningham et al., 2015). Increases in Pied Crow abundance in southern Africa has been linked to various anthropogenic factors. Growing human populations create favourable conditions for this species, particularly through the expansion of infrastructure and settlements (Joseph et al., 2017). Climatic factors, such as rising temperatures and increasing precipitation, have also been associated

with increases, perhaps by altering habitat suitability or food availability (Cunningham et al., 2015). Higher densities of electrical infrastructure appear to provide perching and nesting sites (Dean and Milton, 2009; Fincham and Lambrechts, 2014; Joseph et al., 2017, Chapter 3), and increasing habitat availability, especially in the Karoo and Fynbos biomes of South Africa, where natural nest sites were historically limited due to a lack of trees (Cunningham et al., 2015). Access to anthropogenic food sources, such as human waste, is another potential driver (Igwebuike and Eze, 2010), alongside growing road infrastructure, which offers viewing perches and more foraging opportunities in the form of roadkill (Dean and Milton, 2009; Fincham and Lambrechts, 2014; Joseph et al., 2017; Adelola, 2024).

Pied Crows are often labelled a 'problem species' due to behaviours such as mobbing and harassing raptors, competing with them for nesting sites (Cunningham et al., 2015) and occasionally predating on their nests (Johnson and Murn, 2019). In addition, Pied Crows are emerging as a threat to various tortoise populations (Durà i Franch, 2017; Loehr, 2017; Moldowan, 2023, Chapter 3), as evidenced by the numerous tortoise shells found beneath some crow nesting sites (Fincham and Lambrechts, 2014; Durà i Franch, 2017; Henry, 2020, Chapter 3). Because of this, the rise in Pied Crow numbers has caused concern among conservationists (BirdLife South Africa, 2012; Adelola, 2024). In areas where livestock farming is common, Pied Crows are often blamed for lamb losses, and their growing presence around infrastructure and open farmland has made them more visible and more frequently perceived as a negative influence (Rowley 1969; de Greef, 2015; Joseph et al., 2017; Jenkins and van Zyl, 2020). This perception has fuelled growing concern in farming communities, where the species is seen as both an ecological threat and an economic problem (McGeoch and Latombe, 2016). As a result, there has been a rise in calls to control their numbers, and in some cases, landowners have resorted to poisoning or culling (Adelola, 2024).

In response to growing concerns about rising Pied Crow numbers and their potential ecological consequences, Cunningham et al. (2015) carried out the first analysis of population changes across South Africa using SABAP1 and SABAP2 data. Their analysis looked at long term population changes between two surveys separated by nearly two decades, SABAP1 (1987–1991) and SABAP2 (2008–2012), and provided a broad overview of population change up until 2012. Given ongoing changes in Pied Crow populations, especially with the expansion of powerlines to meet energy demands across South Africa and support the country's

transition to renewable energy (Eskom, 2024), an updated assessment of population trends is needed.

This study aimed to assess the current spatial distribution and recent trends in the abundance of Pied Crows and determine potential drivers of this change. Understanding these patterns is critical for conservation and management efforts, given that native invaders like Pied Crows may continue to expand their ranges and interact with native biodiversity. We use SABAP2 data from 2008 to 2023, to model spatial and temporal trends in Pied Crow occurrence among provinces, biomes, and between protected and unprotected areas. We also explore whether these changes are associated with various environmental factors, including anthropogenic development and climate over the last 15 years.

2.3 Methods

2.3.1 SABAP2 and extraction of Pied Crow data

We used data on Pied Crow occurrence from the Southern African Bird Atlas Project 2 (SABAP2: https://sabap2.birdmap.africa/). SABAP2 is a continuation of the original SABAP1 (1987–1992), which used quarter-degree grid cells (27 × 27 km) to record bird sightings (Brooks et al., 2023). SABAP2 (2007–present) introduced finer-scale spatial resolution using 5 × 5-minute grid cells called pentads (9 x 9 km), allowing more refined, year-to-year tracking of species (Brooks et al., 2022). Volunteers submit checklist cards for each pentad, recording all the species sighted (Brooks et al., 2022). Bird species lists, submitted by citizen scientists, include a minimum of 2 hours of birding and a maximum of 5 days in a "full protocol" format. Lists that do not meet these criteria are listed as "ad hoc". In this study, we only used full protocol checklists, because this ensures that survey effort is fairly standardised. Since 2014, these lists have primarily been submitted to the SABAP2 database (hosted at the University of Cape Town) using the mobile application, 'BirdLasser' (Lee and Nel, 2020, Brooks et al., 2022).

The development of BirdLasser provided a more user-friendly interface for atlassing. Its release led to an increase in checklist submissions (Lee and Nel, 2020) but may have introduced a bias that must be considered when analysing trends using reporting rates (Lee and Nel, 2020). Changes in reporting rates, which are the proportion of checklist cards for a pentad that record a species, have traditionally been used to analyse trends in the abundance

of a species between the two SABAP periods (Cunningham et al., 2015; Amar and Cloete, 2017; Lee and Nel, 2020). For this study, however, we use only SABAP2 data to analyse trends in the probability of reporting of Pied Crows during the study period, which is an alternative approach for analysing SABAP data (Lee and Nel, 2020).

We extracted Pied Crow presence-absence data from SABAP2 covering the full years of 2008–2023, as the SABAP project started mid-year 2007 (Shaw et al., 2024). To ensure adequate survey effort within a pentad across the study period, only pentads with at least 10 checklists were used, with a minimum of three visits in each half of the period, 2008–2015 and 2016–2023, similar to Shaw et al. (2024). Pentads were further filtered to include only those with at least two records of Pied Crows across the 15-year period, confirming species presence. Because the Pied Crow is a large and conspicuous bird that is not easily confused with any other species (Cunningham et al. 2015), we assumed that there were no false positives and that the species was always correctly identified.

2.3.2 Environmental covariates

We assigned each pentad to a province, a biome type, and protected area status, and extracted data on five environmental variables (levels of global human modification (gHM), average temperature [°C] (T_{avg}), average minimum temperature [°C] (T_{min}), average maximum temperature[°C] (T_{max}), and mean annual precipitation [mm] (P_{avg}) experienced over the 15 years of the SABAP2 survey period). Pentads were assigned to their administrative provinces using GADM data (Global Administrative Areas, 2022) shapefiles, with each pentad allocated to the province to which most of its area belonged. Biome type was assigned using the South African National Biodiversity Institute's vegetation map (Mucina and Rutherford, 2006), with each pentad classified according to the dominant vegetation type, considering ten biome categories: Fynbos, Savanna, Grassland, Indian Ocean Coastal Belt Biome, Succulent Karoo, Nama-Karoo, Albany Thicket, Forest, Desert, and Azonal Vegetation. Lastly, pentads were classified as formally protected areas if > 50% of their area was within protected zones based on the World Database of Protected Areas (Protected Planet, 2024).

Information on the five environmental variables (gHM, T_{avg}, T_{min}, T_{max}, and P_{avg}) was extracted using the Google Earth Engine R interface, '*rgee*' (Aybar et al., 2020). The '*ABDtools*' package, a companion package for the Africa Bird Data packages, '*ABAP*' and '*CWAC*' (BIRDIE

development team, 2025), was used to calculate average values across specific spatial units, allowing extraction of levels of anthropogenic modification and mean climate values for each pentad. We extracted the median value of gHM from Kennedy et al. (2019), which represents a cumulative measure of human modification of terrestrial landscapes. This index combines five major anthropogenic stressors: human settlement (population density and built-up areas), agriculture (cropland and livestock), transportation (major and minor roads, two-track roads, and railways), mining and energy production, and electrical infrastructure (powerlines and night-time lights). The gHM values were continuous, ranging from 0.0 to 1.0 and are calculated based on the proportion of a given location that is modified by human activity (Figure 2.1). T_{avg} data were obtained from the ERA5 land dataset (Muñoz Sabater, 2019), T_{min} and T_{max} data were obtained from the TerraClimate dataset (Abatzoglou et al., 2018), and P_{avg} from the Monthly Global Precipitation dataset (Huffman et al., 2023) (Figure 2.2a, b).

2.3.3 Statistical analyses

To visualise local changes in Pied Crow reporting probabilities, we first analysed temporal trends at the individual pentad level. We fitted a separate generalised linear model (GLM) for each unique pentad, with binary presence (1) or absence (0) as the response variable, and year as the dependent variable. From each of these individual models, we extracted the slope coefficient for the continuous 'year' variable. These coefficients were mapped to display the spatial distribution of increasing (positive slopes), decreasing (negative slopes), and stable trends across the SABAP2 period (2008–2023).

We fitted three sets of generalised linear mixed models (GLMM) to analyse the current spatial distribution and trends in Pied Crow abundance from full protocol SABAP2 cards. We used the binary presence or absence of Pied Crows as the response variable with each full protocol card as the sampling unit, where the probability of presence serves as a proxy for relative abundance. All models were specified with a binomial error distribution and a logit link function. To ensure consistency, all fitted models had the same basic structure. The base structure included a random intercept for pentad to account for repeated sampling of pentads across the time frame, a fixed (before/after) two level categorical 'period' effect to adjust for a possible reporting bias introduced by the BirdLasser app in 2014 (Lee and Nel, 2020), and log-transformed (+1) "hours" of survey as an offset. As a result, the model

coefficients represented change in Pied Crow reporting probability per unit survey hour. However, for simplicity, hereafter we use the straightforward term 'reporting probability'.

Before we explored changes in reporting probability over time or in relation to our co-variates, we first explored how overall reporting probabilities vary spatially across South Africa, to better understand where crow abundances are currently highest and to quantify differences between protected and non-protected areas. To do this, we subsetted the data to include only more recent atlas data from the second half of the study period (2015–2023). We then fit separate GLMMs that included only the main effect of either province, biome, or protection status (e.g. seenbin ~ biome), using the base model structure (excluding the 'period' effect as this subset is post-2014). From these models, we extracted individual estimates of occurrence probability for each category using the '*emmeans*' function of the '*emmeans*' package (Lenth et al., 2025).

Our other analyses explored Pied Crow temporal trends between 2008 and 2023. We first explored how these trends differed across spaces, including between provinces, biomes and within and outside protected areas. For this analysis, we included a two-way interaction term between the continuous year variable and each main categorical variable. This resulted in three separate models to assess trends across provinces, biomes, and protected areas:

Model 1: $presence \sim year * province$

Model 2: $presence \sim year * biome$

Model 3: $presence \sim year * protection\ status$

Individual trends of probability of occurrence for each province, biome, and protected status were further extracted using the *'emtrends'* function within the '*emmeans*' package in R (Lenth et al., 2025).

Lastly, we undertook a "full model" approach to explore whether Pied Crow trends were associated with our environmental covariates (e.g. human modification index and climate variables). We first assessed collinearity between the predictor variables prior to fitting the models (Suppl. Table S1 for full correlation matrix). No environmental variables that were correlated with one another were included in the same model. The full model analysed how changes in Pied Crow presence over time were associated gHM and average climatic conditions and included these different variables in one model. Specifically, we examined

whether trends in Pied Crow reporting probability varied across gradients of gHM, temperature metrics (T_{avg}, T_{min}, and T_{max}), and P_{avg}, by including interaction terms between "year" and each of the covariates (i.e., year × gHM, year × T_{avg}, and year × P_{avg}). To determine the most influential temperature metric (all three were correlated with each other), we first compared three alternative versions of the full model, each using a different temperature variable: T_{avg}, T_{max}, and T_{min}. Based on the Akaike's Information Criterion (AIC), the model with T_{min} provided the best fit and was therefore kept for our final analysis (i.e., year × gHM, year × T_{min}, year × P_{avg}). All continuous predictors except year were standardised (mean = 0, SD = 1). Thus, our final model explored whether Pied Crow trends differ in warmer versus cooler areas, in wetter versus drier regions, and in more human modified versus less human modified landscapes.

For models analysing Pied Crow trends across the broad spatial groups such as biomes and provinces, we used the '*glmmTMB*' package in R (Brooks et al., 2017) and did not control for spatial autocorrelation, as these groups represent geographically clustered areas. To account for spatial autocorrelation in the model analysing spatial distribution and trends inside and outside of protected areas, and the "full" model across South African pentads, we used the R package '*sdmTMB*' (Anderson et al., 2022), which accounts for spatial autocorrelation using the stochastic partial differential equation (SPDE) approach. Since coordinates need to be in a distance-based projection, the pentad grid was re-projected to the Albers Equal Area coordinate system, which is suitable for preserving area across large regions like South Africa, which spans three Universal Transverse Mercator (UTM) zones. The projection parameters were as follows: central meridian at 25°E, standard parallel 1 at 22°S, standard parallel 2 at 38°S, and a latitude of origin at 30°S. In '*sdmTMB'*, the spatial random field is modelled as a continuous Gaussian Markov random field (GMRF) and is approximated through a triangulated mesh constructed over the study extent (Lindgren et al., 2011). We generated the mesh using projected Albers Equal Area coordinates, setting the number of nodes to 500. The optimal cutoff value for the number of nodes was determined via the '*cutoff_search*' option in '*sdmTMB'* (Anderson et al., 2022). Spatial correlation on land was constrained using barrier meshes created with the '*add_barrier_mesh*' function (Anderson et al., 2022).

For the final model used to explore the influence of covariates on Pied Crow trends, we explored the relative contribution of each predictor variable using the McFadden's pseudo-

R^2 method. First, the full model was fitted in '*sdmTMB*' using all predictors and relevant interaction terms. We then fit a series of reduced models, removing one interaction term at a time, while keeping all other terms the same. For each reduced model, McFadden's pseudo-R^2 was calculated. This metric measures the loss in model fit caused by removing a specific predictor.

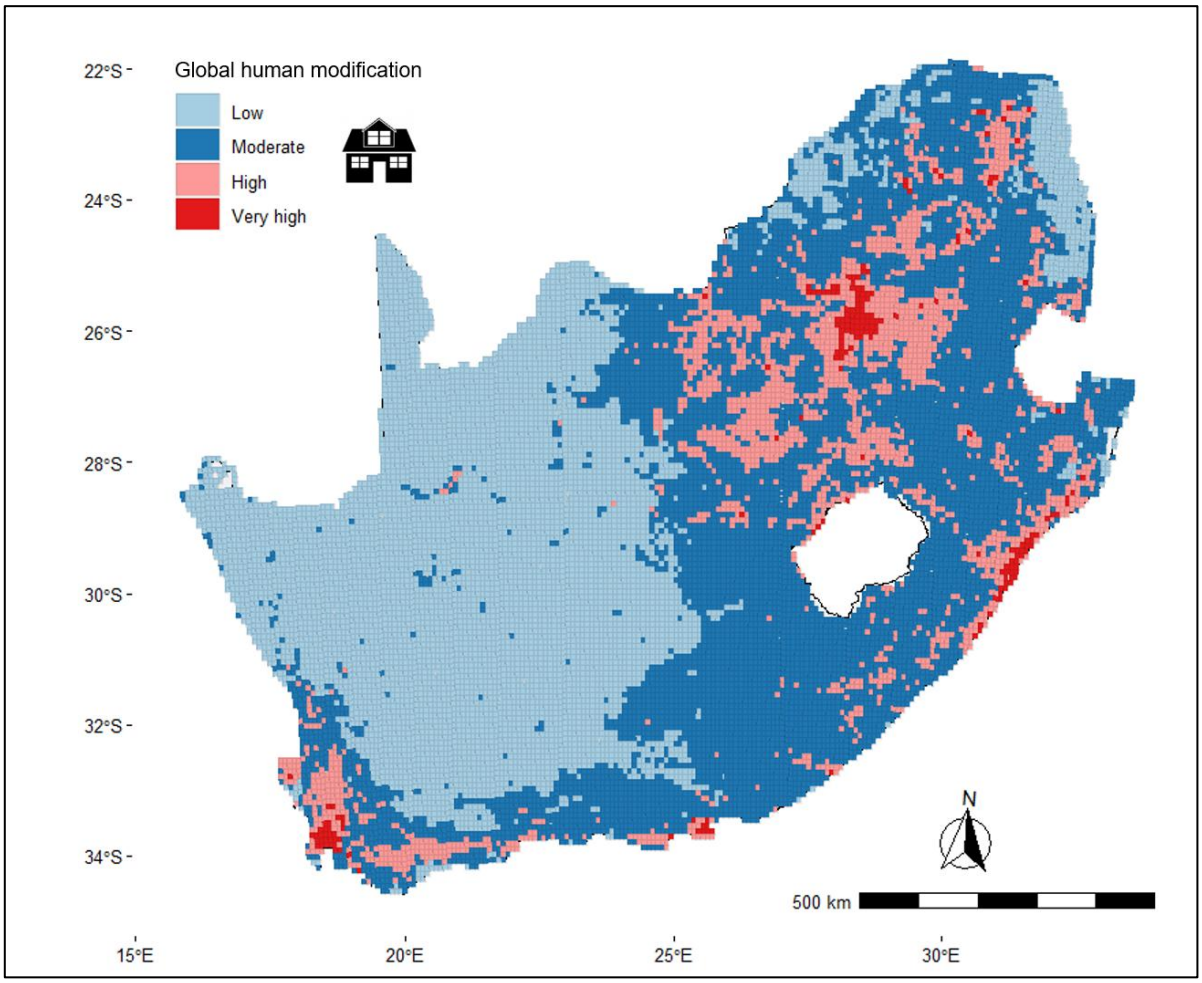

Figure 2.1. Map of South Africa displaying level of human modification (gHM) across all 9 x 9 km pentads (irrespective of whether they were used in the analysis). Each colour represents a different modification index: light blue = 0.2, dark blue = 0.5, pink = 0.7, and red = 0.9.

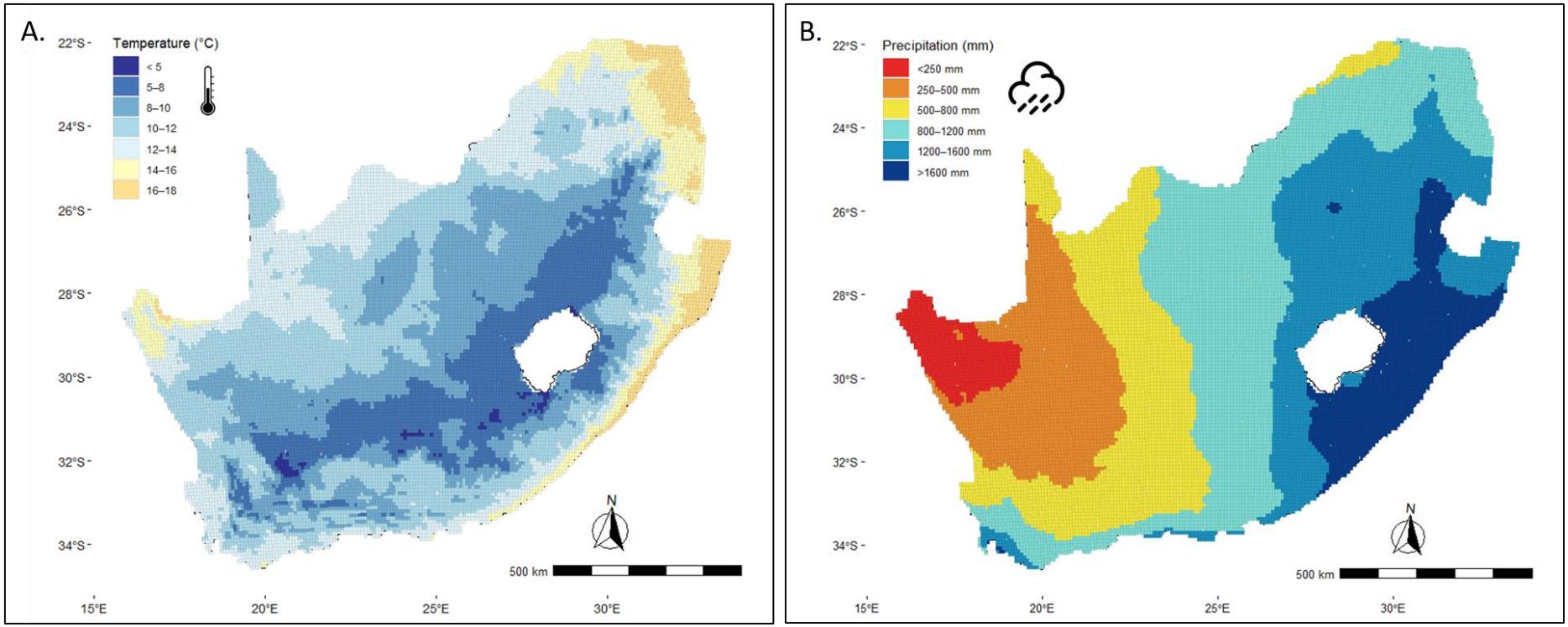

Figure 2.2. Map of South Africa displaying (a) average minimum temperature [°C] and (b) mean annual precipitation [mm] for the period 2008–2023. Temperature data were derived from the TerraClimate land dataset (Muñoz Sabater, 2019), and precipitation data from the Monthly Global Precipitation dataset (Huffman et al., 2023). All 9 x 9 km pentads are shown, irrespective of whether they were used in the analysis.

2.4 Results

After filtering, 2,541 pentads (15% of total pentads across South Africa) remained for analysis, covering an area of approximately 205,821 km² across South Africa (Figure 2.3; Table 2.1). Pentads included here had an average of ca. 82 cards submitted (range 10–3,154 cards). In total, 208,321 cards were used in the final analysis, which included 91,993 presences and 116,328 absences.

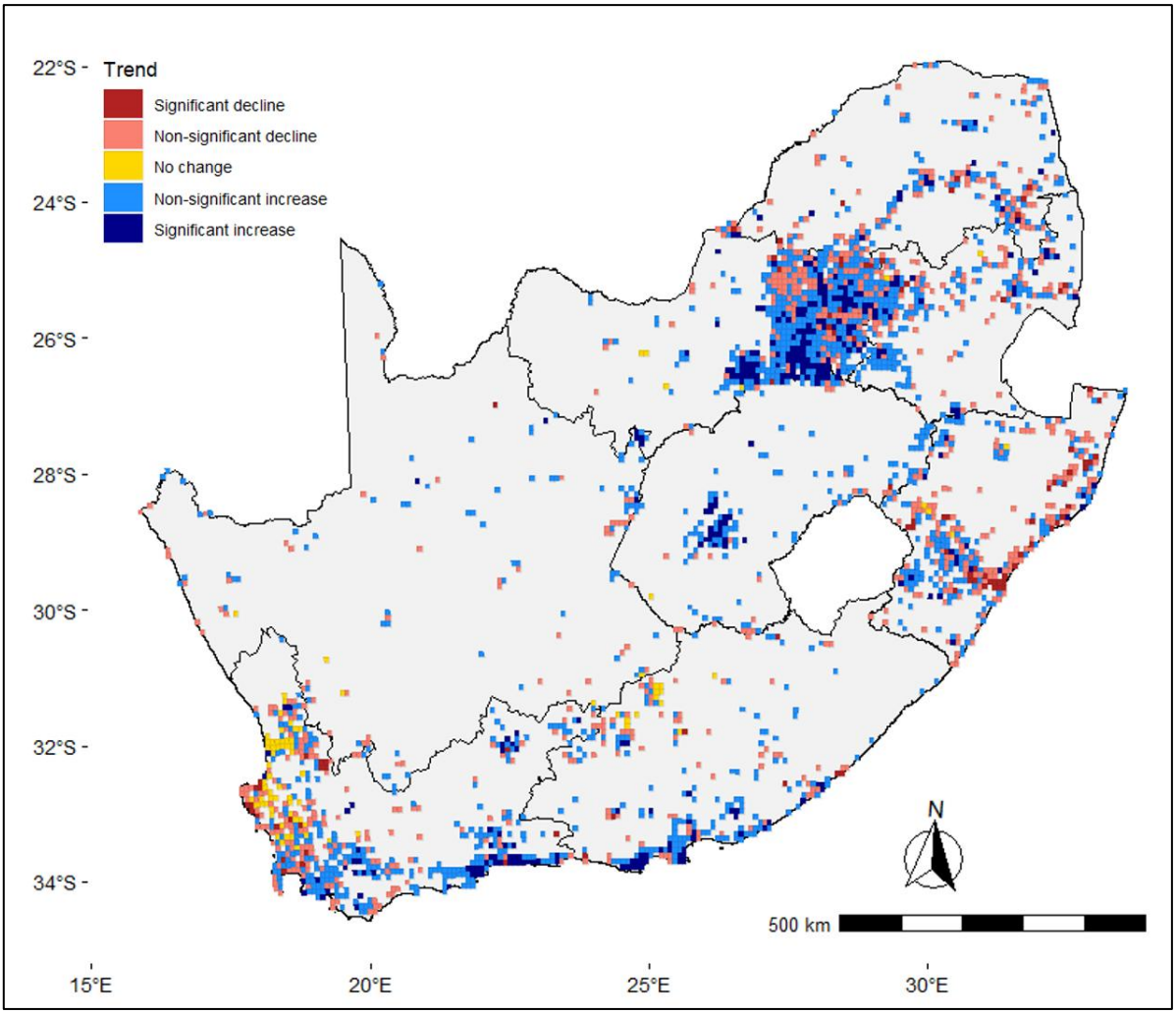

Figure 2.3. Distribution of South African pentads included in the analyses, showing changes in the probability of Pied Crow presence over the SABAP2 period (2008–2023). Generalised linear models were fitted for each pentad individually to estimate slopes. Blues indicate decreases, reds indicate increases, and yellow indicate no change.

Table 2.1. Distribution of pentads used in the analysis of Pied Crow reporting probabilities across South Africa's provinces and biomes, showing the number of pentads, total pentad area [km²], official region area [km²], and approximate percentage coverage of each province and biome. Provincial area values were sourced from provincial websites. Biome area values were calculated directly. Note: pentads are uniform grid cells that may overlap boundaries, therefore the total pentad area can slightly exceed the official provincial area, leading to coverage percentages over 100%.

Region Type	Name	Number of pentads	Total pentad area [km²]	Total region area [km²]	% Coverage
Province	Eastern Cape	260	18,721	168,966	11
	Free State	195	14,674	129,825	11
	Gauteng	239	18,385	18,178	100
	KwaZulu-Natal	364	27,269	94,361	29
	Limpopo	235	18,375	125,754	15
	Mpumalanga	228	17,586	76,495	23
	North West	296	22,794	104,882	22
	Northern Cape	147	10,935	372,889	3
	Western Cape	577	41,330	129,462	32
Biome	Albany Thicket	118	8,443	35,307	23
	Azonal Vegetation	27	1,988	26,468	8
	Desert	10	753	6,262	12
	Forest	14	1,041	4,981	21
	Fynbos	492	35,167	81,651	43
	Grassland	808	61,279	365,616	17
	Indian Ocean Coastal Belt	86	6,405	11,692	55
	Nama-Karoo	142	10,387	249,361	4
	Savanna	752	57,921	407,077	13
	Succulent Karoo	92	6,690	78,208	10

2.4.1 Temporal trends (2008–2023) in Pied Crow reporting probability across South Africa

Prior to looking at change in Pied Crow presence, we first explored varation in the current abundance of Pied Crows (using data from 2015–2023). This analysis showed significant variation in the average probability of Pied Crow reporting across South Africa's nine provinces (χ^2 = 497.37, DF = 8, p < 0.001; Suppl. Table S2). Overall reporting probabilities ranged from 0.19 - 0.70, with lowest and highest reporting probabilities found in Mpumulanga and Northern Cape, respectively (Figure 2.4a, b). Similarly, we found considerable variation in Pied Crow occurrence probabilities across South African biomes (χ^2 = 256.99, DF = 9, p < 0.001; Suppl. Table S3). Overall reporting probabilities ranged from 0.17–0.80, with lowest and highest reporting probabilities found in Forests and Succulent Karoo, respectively (Figure 2.5a, b).

Overall, the probability of Pied Crow reporting across South Africa increased over the SABAP2 survey period (p < 0.005, z = 18.1). Pied Crow presence increased proportionally by ca. 45%, or 4% per annum. Increases were concentrated within the north-eastern parts of the country, and largely urbanised areas such as Gauteng and parts of the Western Cape (Figure 2.6a, b). Declines were most prominent along the east coast of KwaZulu-Natal and in areas surrounding Gauteng (Figure 2.6a, b).

Trends in Pied Crow reporting probability differed between provinces from 2008–2023, with a significant interaction between province and year (χ^2 = 873.80, DF = 8, p < 0.001). The greatest relative change over the study period was observed in the Free State (+265%, z = 20.74, p < 0.001), followed by the Eastern Cape (+81%, z = 14.94, p < 0.001), and then Mpumalanga (+74%, z = 7.80, p < 0.001) (Figure 2.6a, b). Other provinces also showed notable increases, ranging from 67% in Gauteng (z = 18.69, p < 0.001) and 49 % in the North West (n = 296, z = 13.42, p < 0.001), to 17% in the Western Cape (z = 7.36, p < 0.001). Despite their high current reporting probability, increases in the Northern Cape (+24%, z = 4.53, p < 0.001) and the Western Cape (+17%, z = 7.36, p < 0.001) were not quite as dramatic. KwaZulu-Natal (z = -7.60, p < 0.001) was the only province to show a decline, with a 24% decrease in probability over the period. Limpopo (p = 0.07) showed no statistically significant change over the study period.

Trends in reporting probability of Pied Crow over the last 15 years differed between biomes (Figure 2.7), with a significant interaction between biome and year (χ^2 = 486.54, DF = 9, p <

0.001). The greatest increases were observed in the Albany Thicket (+133%, $z = 13.61$, $p < 0.001$), Desert (+104%, $z = 1.99$, $p < 0.001$), and Grassland biomes (+89%, $z = 21.99$, $p < 0.001$), indicating notable expansions in these regions. The Nama-Karoo (+25%, $z = 6.57$, $p < 0.001$), the Savanna (+25%, $z = 6.57$, $p < 0.001$), Fynbos (+20%, $z = 8.10$, $p < 0.001$), and Succulent Karoo (+13%, $z = 2.59$, $p = 0.01$) also displayed moderate increases, suggesting a continued spread into arid and semi-arid areas. In contrast, the Indian Ocean Coastal Belt Biome (-39%, $z = -8.29$, $p < 0.001$) was the only biome to show a decline in Pied Crow probability, while Forests ($z = -0.42$, $p = 0.64$) and Azonal Vegetation ($p = 0.08$) displayed no significant change.

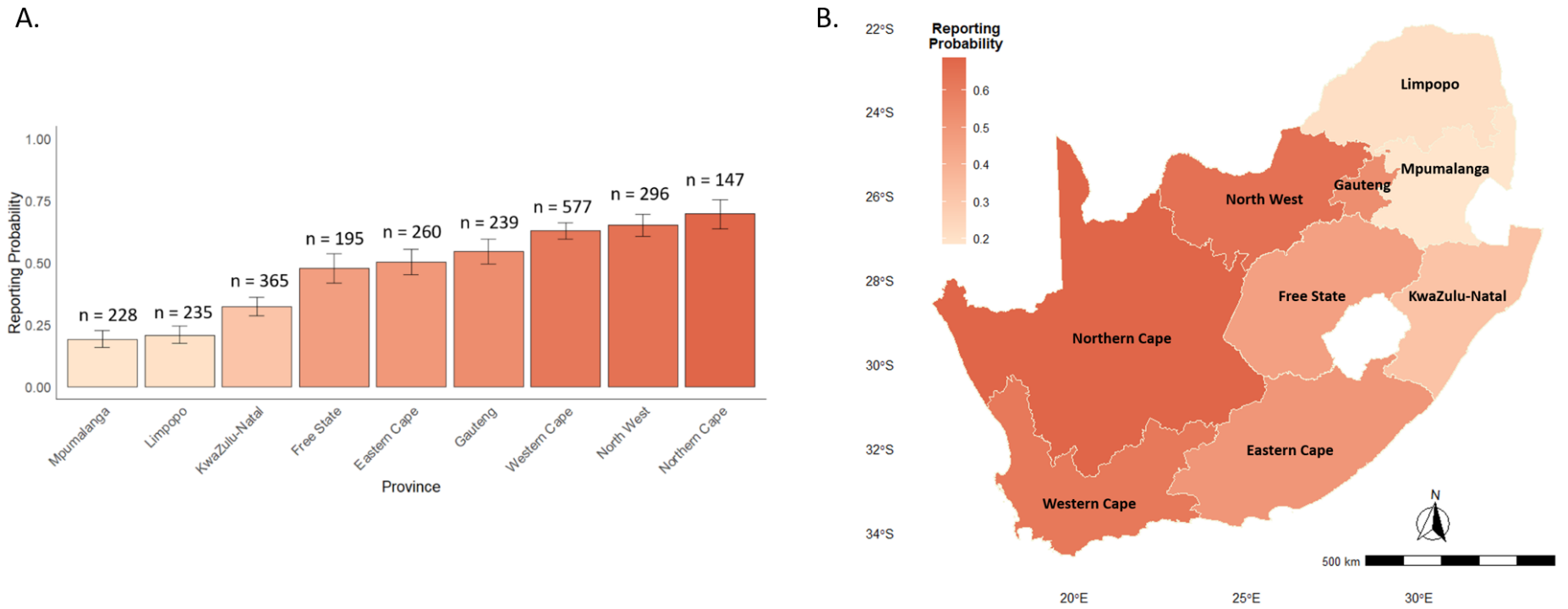

Figure 2.4. (a) Average Pied Crow reporting probabilities across South African provinces during the second half of the SABAP2 period (2015–2023), displayed as a bar chart, with error bars representing 95% confidence intervals, and numbers above bars indicating the number of pentads used for each province. (b) Map of South Africa displaying geographic distribution of average reporting probabilities of Pied Crows. In both figures, darker orange shades indicate a higher average reporting probability.

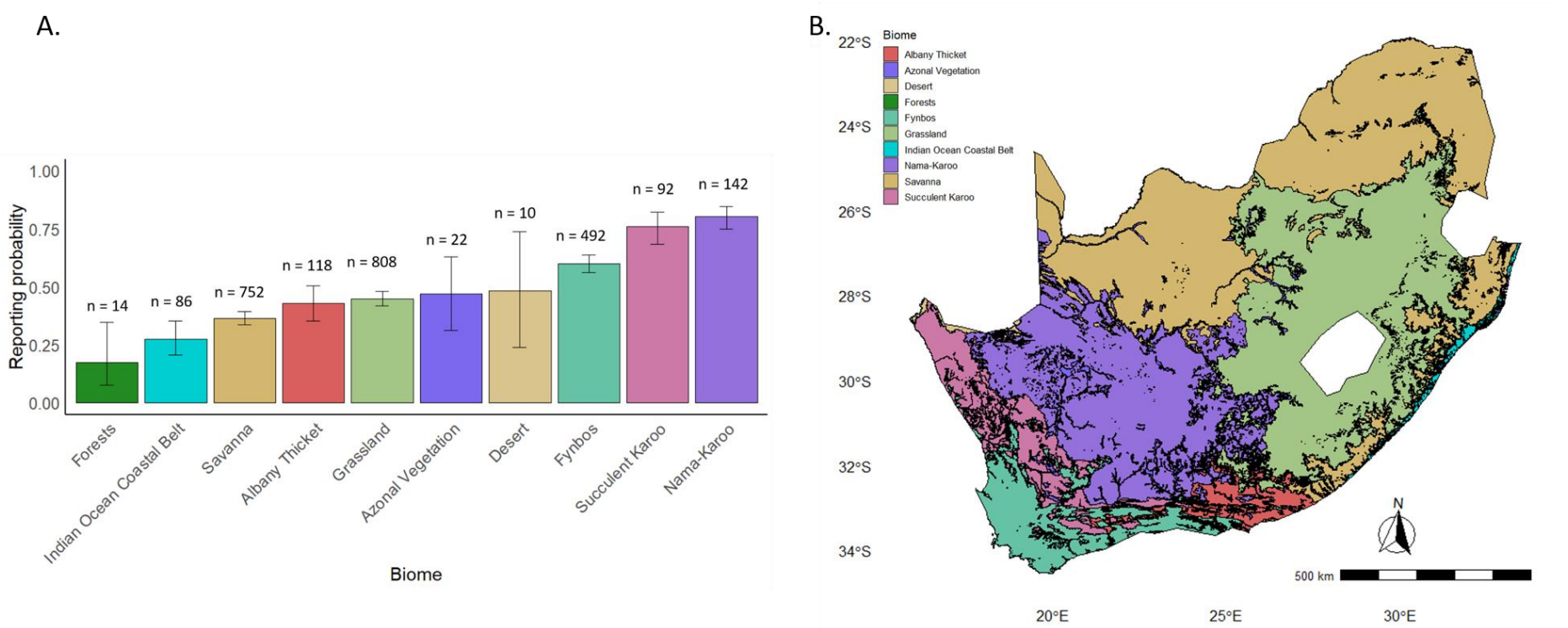

Figure 2.5. (a) Average Pied Crow reporting probabilities across South African biomes during the second half of the SABAP2 period (2015–2023), displayed as a bar chart, with error bars representing 95% confidence intervals, and numbers above bars indicating the number of pentads used for each biome. (b) Map of South Africa displaying geographic distribution of South African biomes.

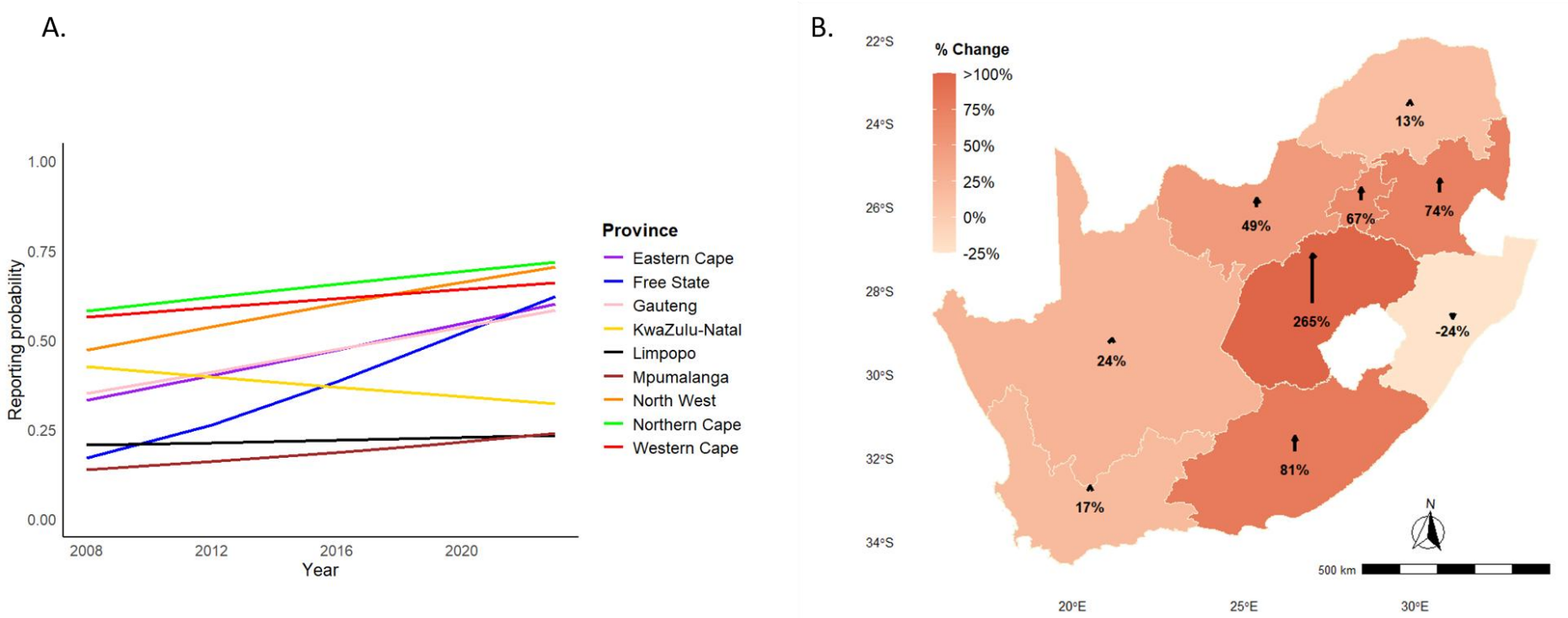

Figure 2.6. Trends in Pied Crow reporting probability across South Africa's nine provinces during the SABAP2 period (2008–2023), displayed as logistic probability curves illustrating the reporting trend for each province. (b) Map showing the overall percentage change in reporting probability. The magnitude of this change is represented by the intensity of the orange shading and the scaled length of the arrows

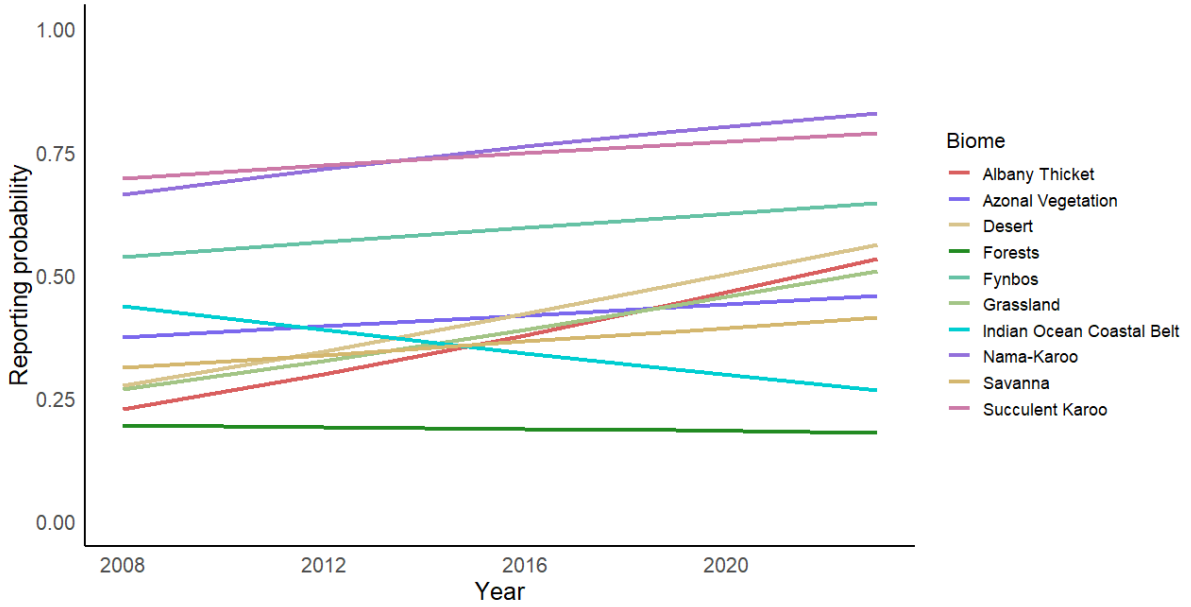

Figure 2.7. Trends in Pied Crow reporting probability across South Africa's ten biomes during the SABAP2 period (2008–2023). Lines represent logistic probability curves

2.4.2 Temporal trends (2008–2023) in Pied Crow reporting probability in relation to protected areas

Numbers of repeat visits to pentads was more intensive inside protected pentads. Pentads inside protected areas had an average of 123 cards (range 10–3,154), whereas pentads outside protected areas had an average of 76 cards submitted (range 10–2,268). As expected, given the disparity in area size of protected and unprotected areas, the number of pentads in unprotected areas (n = 2,233, area = 180,873 km²) was higher than in protected areas (n = 308, area = 24,948 km²).

We found a significant interaction between year and protection status (β = -0.042, SE = 0.004, $p < 0.001$; Suppl. Table S4), with protected areas experiencing significantly slower rates of increase in Pied Crow reporting probability. In unprotected areas, reporting probability increased by 51% ($p < 0.001$), while protected areas showed no significant trend ($p = 0.15$) (Figure 2.8).

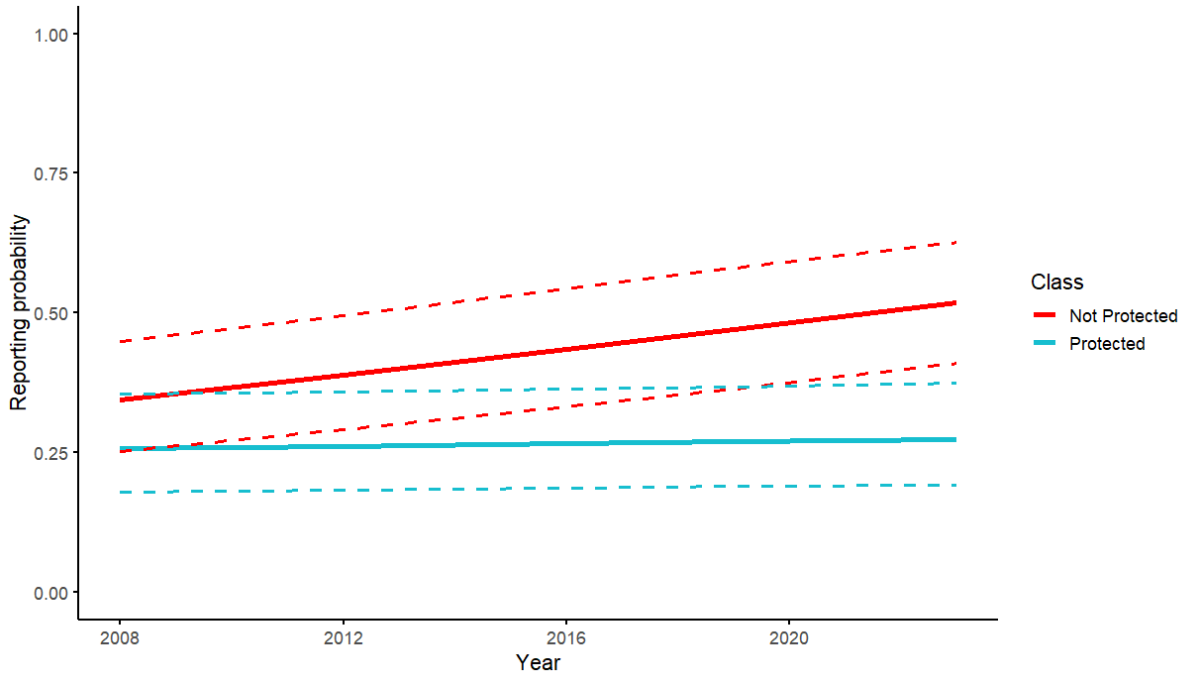

Figure 2.8. Trends in Pied Crow reporting probability across the SABAP2 period 2008–2023, in protected (red) and unprotected (blue) areas. Lines are logistic probability curves. Confidence intervals are represented by the dotted lines.

2.4.3 Associations between climate and human modification variables and trends

Trends in Pied Crow reporting probability were associated with both levels of human modification and climate conditions (Table 2.2). A significant interaction was observed between year and gHM, with Pied Crows increasing faster at greater levels of human modification (Figure 2.9). Significant negative interactions were found between year and T_{min}, and year and P_{avg}, with Pied Crows increasing faster in cooler drier areas and showing slower increases in warmer, wetter regions during the study period (Figure 2.10a, b). There was an additional negative effect associated with the introduction of BirdLasser in 2014, indicating that Pied Crow reporting probability was slightly lower post-2014, which was accounted for in all models.

Table 2.2. Results from the full model examining change in Pied Crow occurrence over time and interactions with and human modification metric (gHM), average minimum temperature [°C] (T_{min}), and average annual precipitation [mm] (P_{avg}). Continuous variables excluding year are scaled.

Variable	Estimate (β)	SE	CI (Lower)	CI (Upper)
Year	0.04	0.00	0.04	0.05
T_{min}	0.99	0.10	0.79	1.19
P_{avg}	-0.50	0.16	-0.80	-0.19
gHM	0.30	0.05	0.20	0.40
Period (post-2014)	-0.07	0.02	-0.11	-0.02
Year × T_{min}	-0.03	0.00	-0.04	-0.023
Year × P_{avg}	-0.01	0.00	-0.01	-0.01
Year × gHM	0.01	0.00	0.00	0.01

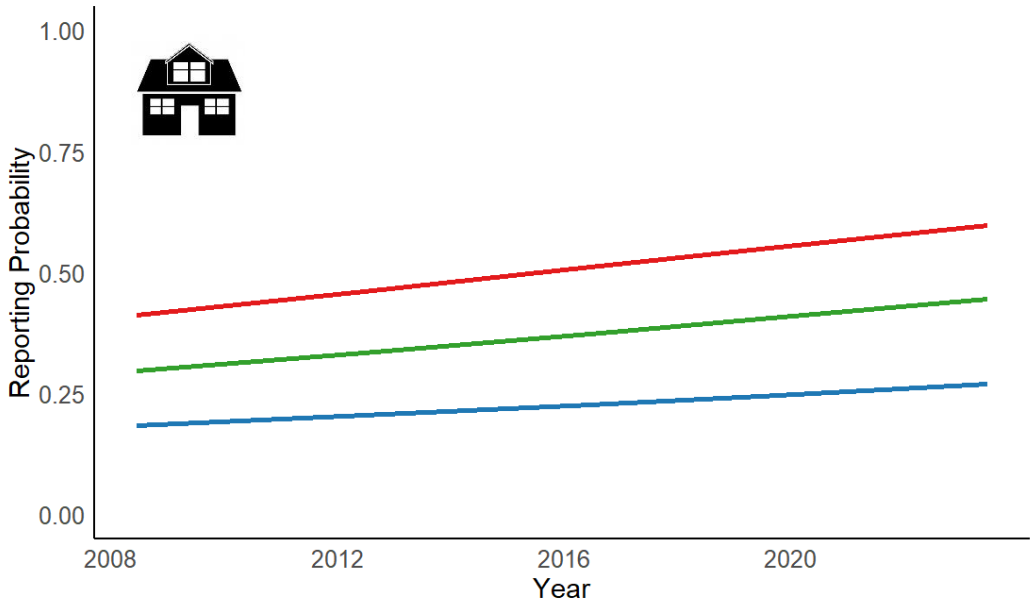

Figure 2.9. Trends in Pied Crow reporting probability across three different human modification levels, derived from model-based marginal effects using the *allEffects()* function. Each line represents a specific human modification index (gHM): blue = 0.001 (i.e., low), green = 0.5 (medium), red = 0.9 (high). Lines are logistic probability curves.

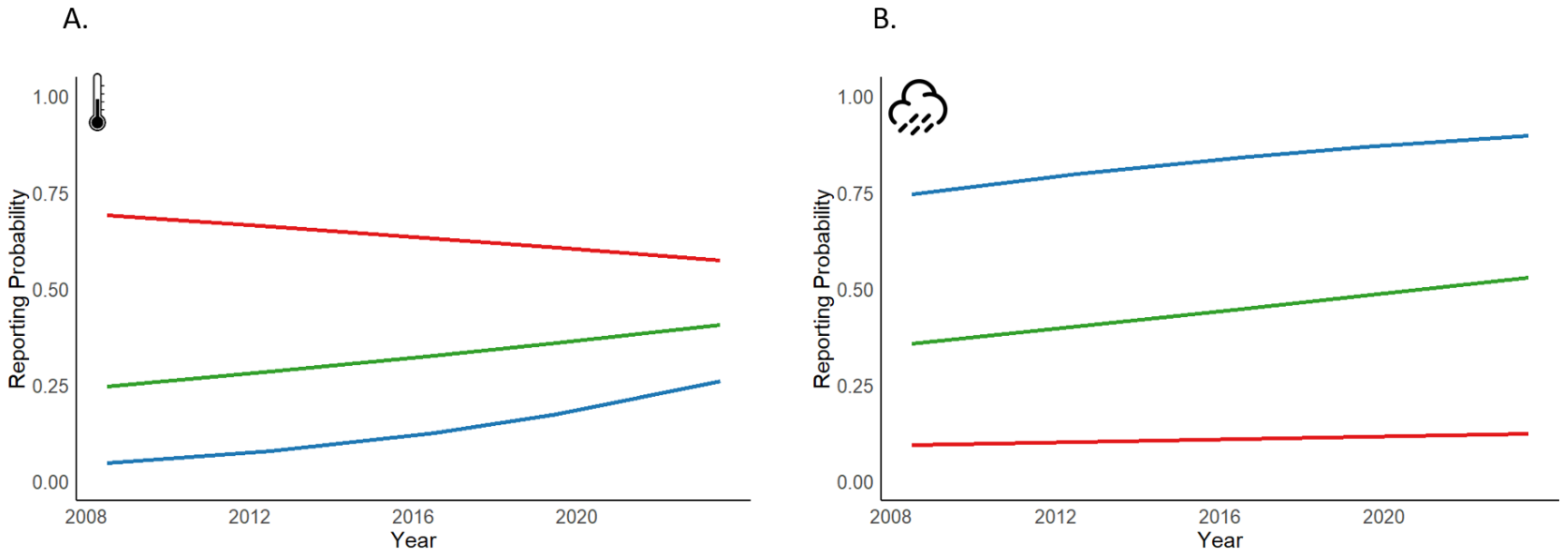

Figure 2.10. (a) Trends in Pied Crow reporting probability across three representative mean temperature levels, derived from model-based marginal effects using the *allEffects()* function. Each line represents a specific temperature [°C] (T_{min}): blue = 4.2, green = 11, and red = 18. Lines are logistic probability curves. (b) Trends in Pied Crow reporting probability across three average precipitation levels, derived from model-based marginal effects using the *allEffects()* function. Each line represents a specific mean annual precipitation measure [mm] (P_{avg}): red = 110, green = 1100, and blue = 2100. Lines are logistic probability curves.

The McFadden's pseudo-R^2 for the full model (Table 2.2) was 0.007, indicating that our fixed predictors explained only a small proportion (0.7%) of the variation in Pied Crow presence beyond the null model with random effects. Removing the interaction between T_{min} and year resulted in the largest reduction in model fit ($\Delta R^2 = 0.002$), corresponding to approximately 29% of the total explained variation by the fixed effects. This was followed by the interaction between gHM and year ($\Delta R^2 = 0.0004$; ca. 6%) and that between P_{avg} and year ($\Delta R^2 = 0.0002$; ca. 3%). Together, these interactions accounted for approximately 37% of the model's total explanatory power, with the T_{min}–year interaction contributing the largest improvement in predictive performance.

2.5 Discussion

Our study analysed more recent and fine-scale data over the past 15 years to provide an updated assessment of Pied Crow population trends. We found that Pied Crow numbers have risen markedly, showing a proportional 45% increase since 2008, a substantially faster rate than the 13% increase reported by Cunningham et al. (2015). The rate of increase varies spatially across the country, with the greatest increases occurring in the central to south-eastern regions of the country. Similar to Cunningham et al. (2015), these increases corresponded to the historically treeless biomes (e.g. Grassland), suggesting that infrastructure development in these biomes may be driving Pied Crow population increases. This is further supported by patterns observed across areas with differing levels of anthropogenic modification, where Pied Crow sightings increased faster in more human-modified landscapes.

That the geographical area representing the greatest population increase of Pied Crows in South Africa is now the central and eastern parts of the country, indicates a shift from the south-western parts, which were previously the 'centre of population growth' of the species (Cunningham et al. 2015). Despite this, Pied Crows remain most common in the Western Cape, North-West and Northern Cape provinces, as judged from their reporting probabilities of 0.63, 0.65, and 0.70, respectively. Our results suggest that rates of increase in the west have now slowed, possibly due to already high population numbers and consequently, heightened intra-specific competition (Mutshinda et al., 2023). Similar dynamics were seen in Mauritius Kestrels (*Falco punctatus*), with high densities leading to increased competition,

thereby slowing population growth through reduced breeding success (Nevoux et al., 2010). This form of density-dependent regulation limits local growth and drives expansion into sub-optimal or lower-density areas. This pattern is consistent with ecological theory predicting that population increases may slow when factors such as intraspecific competition and resource limitation intensify (Hansen et al., 1999). The eastward population expansion of Pied Crows may therefore represent a dispersal response to saturation in western areas, a process observed in other bird and mammal species undergoing range shifts (Matthysen, 2005).

Our results show that Pied Crows are expanding into regions that previously supported lower population numbers, which may have ecological and social implications. Pied Crows are known predators that can potentially alter community dynamics and threaten vulnerable species (Cunningham et al., 2015; Madden et al., 2015; Joseph et al., 2017; Loehr, 2017). In addition, as highly visible birds, they can often trigger strong emotional responses in people, which can amplify negative perceptions of their impacts (Madden et al., 2015). Indeed, their rising numbers are becoming more noticeable in local communities, with the awareness of rising populations being particularly high in the Northern Cape (Adelola, 2024), where our study shows that Pied Crow reporting probability was the highest. Interestingly, participants who were interviewed also widely agreed that Pied Crows display strong negative impacts on biodiversity within this same region (Adelola, 2024). Thus, as populations continue to increase, the geographical variation of this increase highlights both the adaptability of the species and emerging ecological and social pressures across different regions.

At the provincial scale, Pied Crow trends appear to be strongly associated with the change in patterns observed in their dominant biomes. The Free State and Eastern Cape, largely comprising the Grassland biome, showed the most rapid increases. As demonstrated by Cunningham et al. (2015), Pied Crows have increased in the shrubland biomes of South Africa, particularly in response to rising powerline densities, which provide perching and nesting sites in the absence of natural structures. We found similar trends in the historically open and treeless Grasslands, which are now highly modified, as reflected by the gHM index (Figure 2.1). The expansion of anthropogenic features has long been recognised as critical to not only Pied Crow success (Cunningham et al., 2015; Dean et al., 2018) but also various other bird species that exploit human resources (Chace and Walsh, 2006; Benmazouz et al., 2021).

Increases were more pronounced outside protected areas, while population trends within protected areas were relatively flat. This supports the hypothesis that anthropogenic development may actively facilitate Pied Crow population growth by providing reliable and consistent food sources, nesting opportunities, and reduced predation pressures. Protected areas host a large amount of biodiversity, particularly other bird species, including raptors (Santangeli and Girardello, 2021), which may prevent Pied Crow increases through competition. These findings were further validated by our other finding; that Pied Crow trends were positively associated with the human modification index. Thus, it appears that roads, powerlines, rubbish dumps, agriculture and settlements which are more abundant outside of protected areas have likely provided foraging and nesting opportunities, allowing the crow population to expand. Increasing Pied Crow reporting probability outside of defined protected areas could pose a major issue for many endangered and threatened species, especially reptiles. Because South Africa's current protected network fails to mitigate extinction risk for many of these taxa and given that they face many other threats pertaining to human infrastructure (Tolley et al., 2019; Lee et al., 2021), they may be particularly vulnerable to Pied Crow predation, which may accelerate their decline in human-modified regions. Carrying out a population viability analysis on impacted tortoise species would be a critical starting point to understanding the long-term population-level impacts of this type of predation pressure.

Pied Crows showed a faster rate of increase in cooler areas (areas with lower average minimum temperatures), likely because warmer regions, such as the Northern Cape, already had high population numbers at the start of the study period. This suggests that temperature is not a strong limiting factor for population growth. While previous studies indicated Pied Crows may prefer certain temperature ranges (Cunningham et al., 2015), our results suggest that they are now more strongly influenced by habitat availability and rainfall patterns. Temperature could therefore reflect areas where population growth is still possible, with cooler regions offering more room for expansion as warmer areas have already reached high densities. Habitat availability and rainfall patterns could therefore be direct limits on population growth.

We found that Pied Crow population increases were greatest in drier regions, while wetter regions showed slower increases. This suggests that very high annual precipitation may act as

a limiting factor on Pied Crow population growth, potentially through effects on prey availability and vegetation suitability. This finding likely explains the decline observed in the high-rainfall province of KwaZulu-Natal. Climate variability acts as a major driver of species population dynamics by influencing food availability, vegetation structure, and nesting opportunities (Salomon et al., 2021). In addition, arid and semi-arid regions are frequently associated with agriculture and farming (McNeely, 2003), which provide additional food resources and nesting opportunities to Pied Crows and many other avifauna. Similar patterns have been observed for Hooded Crows (*Corvus cornix*), who have shown population expansion into the Negev desert, highlighting adaptation to arid environments with low vegetation cover (Salomon et al., 2021). It is important to note, that the driest parts of South Africa, particularly the Northern Cape which makes up the desert and Karoo biomes, are characterised by fewer well-sampled pentads (Table 2.1), which is most likely a result of the relative inaccessibility of these areas . As a result, the pattern of stronger population increases in these drier areas may under- or over-estimate the observed trends in the most arid parts of the country.

While our main model identified statistically significant relationships between Pied Crow trends and anthropogenic and climatic predictors, the overall proportion of variation explained was relatively low and likely due to the influence of unmeasured fine-scale ecological and behavioural drivers (e.g., habitat structure and competition for local resources). In this context, broad environmental variables such as rainfall, temperature, and the gHM index likely capture some components of variation, but are insufficient to fully capture fine-scale processes affecting the observed patterns (Wiens, 1989). Consequently, model predictions at finer spatial scales should be interpreted with caution, particularly regarding the relative importance of individual predictors.

Our results show that Pied Crow populations continue to expand across South Africa, with growth strongest in the central and south-eastern regions, particularly in biomes with low vegetation and human-modified landscapes. Rising reporting probability appears to be driven by a combination of anthropogenic development in different biomes, density-dependence, and climate: Pied Crows thrive in open, human-altered areas, as long as they have access to nesting sites and abundant food, whereas high rainfall and dense vegetation seem to limit their success. These patterns extend the earlier work of Cunningham et al., (2015) by showing

not only that populations remain on the rise, but also that the geographic focus of growth has shifted. Continued monitoring will be critical to determine whether declines in wetter regions such as KwaZulu-Natal are isolated and whether expansion into central and south-eastern regions persists.

The continued population increase of Pied Crows driven by human-induced environmental change, alongside growing evidence of predatory interactions with native fauna, presents the story of just one emerging native invader. Rather than representing an isolated case, this pattern aligns with global evidence that many avian generalists are responding positively to human-altered landscapes (Clavel et al., 2011; Benmazous et al., 2021), where increased resource availability, novel nesting opportunities, and reduced ecological constraints facilitates increases in abundance and range expansion (Benmazouz et al., 2021). In addition to the more than 30 corvid species documented in urban environments (Benmazous et al., 2021), similar responses have been reported across several other avian taxa associated with anthropogenic habitats. Gulls (*Larus* spp.) exploit human-altered environments and have demonstrated population increases across many coastal cities (Belant, 1997). Even raptors, such as Black Kites (*Milvus migrans*), sometimes show higher abundances in urban areas (Rashid et al., 2025). These patterns reflect the long-term human influence on bird communities, where a subset of highly adaptable and generalist species is becoming increasingly dominant, with potentially severe implications for community composition, species interactions, and ecosystem functioning. This prompts reconsideration of the emphasis placed on biogeographic origin versus ecological impact when assessing the invasive potential of a species in different ecosystems.

2. 6 References

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Chapter 3: Powerlines facilitate predation of Angulate Tortoises by Pied Crows

3.1 Abstract

Anthropogenic infrastructure can facilitate avian species expansion by providing nest sites and perches for foraging. This can lead to negative interactions between species that have not co-existed so closely in the past. In South Africa, Pied Crow (*Corvus albus*) populations have increased, helped by structures like powerlines, telephone poles, and windpumps in treeless landscapes. As generalist predators, Pied Crow population increases pose threats to a variety of vertebrate and invertebrate species, including the region's unique tortoise fauna. This study uses the development of a powerline at a wind farm to investigate whether Pied Crow expansion along energy infrastructure may impact local Angulate Tortoise (*Chersina angulata*) abundance. We hypothesise that this newly erected powerline has allowed Pied Crows to breed and increase in population in a historically treeless area, and that this has elevated predation pressure and reduced local tortoise abundance. If this is the case, we make two predictions. We first predict that the number of tortoises at Pied Crow nest sites would decline over time (2015–2025; temporal change) as the Pied Crows should find it increasingly hard to find young tortoises. Second, we predict that Pied Crow abundance would be highest near the powerline, and that correspondingly, tortoise abundance would be lowest in these same areas (spatial variation). At an individual nest level (n=88), tortoise shells found under Pied Crow nest sites declined over time, supporting our temporal hypothesis. Similarly, when modelling the cumulative number of shells found under all potential nests over time, a decline was also apparent. Interestingly, tortoise fatalities were not evenly distributed across the study site: eight nest sites, representing only 9% of all structures, accounted for 50% of recorded tortoise deaths, potentially indicating that tortoise predation is limited to individual Pied Crow pairs rather than being a universal behaviour. Pied Crow abundance was highest near the powerline and decreased ca. 26% per kilometre with increasing distance. In contrast, tortoise abundance was highest further away from the powerline. The relationship with tortoise abundance was non-linear and suggested a sudden increase in tortoise abundance at distances beyond 4 km from the powerline. This raises the possibility that linear infrastructure such as powerlines can lead to a higher predation risk for tortoises. This has major implications for conservation, as the large-scale development of powerlines, and the persistence of obsolete infrastructure across the country may place increasing predation pressure on native tortoises. Management interventions when erecting powerlines should

consider the potential for negative impacts by Pied Crows and implement preventative measures such as the removal of nests or the dismantling of old telephone poles.

3.2 Introduction

Over the past century, human activities have altered ecosystems globally, driving the sixth mass extinction, a period of accelerated biodiversity loss (Pievani, 2013). Changes in land use, habitat fragmentation, climate change, and the spread of invasive species have all driven biodiversity decline (IPBES, 2019; Hald-Mortensen, 2023), particularly for specialist species with narrow niche requirements (Ramiadantsoa, et al., 2018; Correll et al., 2019). In contrast, some adaptable, generalist species have thrived in these changed environments (McKinney and Lockwood, 1999; Banks-Leite et al., 2014), often replacing specialist species, and potentially affecting ecosystem functioning and services (Clavel et al., 2011).

Native generalists can exploit various habitats and human-provided resources (Boarman, 2003; Gibson, 2011), often reaching high population densities, exerting negative ecological impacts, including predation on vulnerable species, competition for resources, and habitat degradation (Moore et al., 2023). Such species are described in the literature using a variety of overlapping terms, including “abundant vertebrates” (Goodrich and Buskirk, 1995), “subsidized predators” (Soulé, 1988), and “invasive species”. Indeed, much of the associated research has focused on alien invasive species (Fennell et al., 2012), with less attention given to the ecological consequences of native generalists becoming overly abundant in their indigenous habitats (Simberloff, 2011) or expanding their ranges. The impacts of these invasive or subsidised species are not confined to colonised areas (Boarman, 2003), making them challenging for conservation management. Spillover predation occurs when subsidised predators surviving on anthropogenic waste and other resources move into surrounding habitats (Boarman, 2003). Unlike non-subsidised predators, these species can fall back on anthropogenic waste in the absence of natural resources (Moldowan, 2023). This subsidy can lead to hyperpredation, where sustained predator populations exert pressure on rare native prey (Courchamp et al. 2000).

Corvids are highly mobile birds, typically occupying large home ranges and travelling considerable distances to forage (Moldowan, 2023). Their intelligence (Heinrich

and Bugnyar, 2007), coupled with strong social behaviour facilitates the rapid transmission of information and the spread of new foraging strategies (Moldowan, 2023). Corvid species are thus able to benefit from human-modified landscapes (Benmazouz et al., 2021). They exploit anthropogenic food and water sources and use buildings, power-poles, and other structures for perching, nesting, and roosting (Marzluff, 2001; Davis et al., 2018; Benmazouz et al., 2021).

Corvids are widespread, with several species having shown rapid population growth within and outside of their native ranges (Amar et al., 2010, Cunningham et al., 2015; Coates et al., 2020; Harju et al., 2021; Moldowan, 2023). For example, American Crows (*Corvus brachyrhynchos*) have expanded and reached high densities in the urban areas of North America (Marzluff et al., 2001), the exotic House Crow (*Corvus splendens*) has become one of the dominant species in some cities across South Africa (Nxele and Shivambu, 2018) and Kenya (Ryall, 2010), Common Ravens (*Corvus corax*) have shown population increases across North America since the mid-20th century (Coates et al., 2020), and Australian Ravens (*Corvus coronoides*) have shown increasing populations across their native range (Burbridge and Kuchling, 2004). These increases are accompanied by various ecological impacts such as hyperpredation on vulnerable and largely sedentary species like tortoises (El-Bahrawy et al., 2007; Berry et al., 2020; Moldowan, 2023), nest predation and competition with native fauna (Marzluff and Balda, 1992; Johnson and Murn, 2019), and reduced nest survival (Coates et al., 2020).

In South Africa, Pied Crows (*Corvus albus*) have demonstrated large-scale population expansion, which continues today (Chapter 2), and are considered native invaders (Cunningham et al., 2015). They have a generalist diet, including carcasses, reptiles, seeds, fruit, grains, and live prey, allowing them to benefit from waste at garbage sites, landfills, and roadkill (Igwebuike and Eze, 2010; Joseph et al., 2018; Adelola, 2024). In addition, increases in Pied Crow abundance are associated with the construction of powerlines in historically treeless areas, which provide nesting and perching sites (Cunningham et al., 2015; Dean et al., 2018). Consequently, their South African population increased by more than 13% between 1987 and 2012 (Cunningham et al., 2015), and recent assessments find an even greater increase, with a ca. 45% proportional increase between 2008 and 2023 (Chapter 2). Conservationists, farmers, scientists, and members of the public have therefore become

increasingly concerned about this expansion as Pied Crows can prey on endangered reptiles, raptors, and livestock (Amar and Redpath, 2002; Jenkins and van Zyl, 2020; Adelola, 2024).

Like other corvids, Pied Crows are notorious for preying on various tortoise species (El-Bahrawy et al., 2007; Loehr, 2017; Moldowan, 2023). South Africa hosts the greatest number of tortoise species globally, many of which occur in the Western Cape (Branch et al., 1995), an area that has also shown a surge in Pied Crow numbers to some of the highest levels of abundance in the country (Cunningham et al., 2015; Chapter 2). The proliferation of artificial nesting sites provided by powerlines, telephone poles, and windpumps, exacerbated by the non-removal of obsolete infrastructure, has allowed Pied Crows to colonise these areas, increasing interactions with tortoises that are vulnerable to predation (Cunningham et al., 2015; Underhill, 2025). Corvids use a range of techniques to prey on tortoises, including puncturing the inguinal pocket, extracting the entire carcass from the carapace, and dropping them from great heights (Moldowan, 2023). Despite evidence of increasing predation pressure on various tortoise species (e.g. Angulate Tortoise, *Chersina angulata;* Common Padloper, *Homopus aerolatus;* Tent Tortoise, *Psammobates tentorius*; Karoo Padloper; *Chersobius boulengeri,* and Speckled Padloper, *Homopus signatus)* across the country (Fincham and Lambrechts, 2014; Durà i Franch, 2017; Loehr, 2017; Tolley, 2019), the biodiversity impacts of Pied Crow population expansion remain poorly explored (Adelino et al., 2017). Consequently, BirdLife South Africa has highlighted the need for further investigations into the negative impacts of expanding Pied Crow populations on biodiversity, including tortoises (Jenkins and van Zyl, 2020).

In this study, we use the establishment of a powerline in 2015 at a wind farm as a pseudo-experiment to investigate the cascading impacts of Pied Crow population expansion facilitated by powerline infrastructure, on local Angulate Tortoise abundance. Using a long-term dataset (11 years; 2015 to 2025) of tortoise fatalities recorded beneath nests, we analyse temporal trends in predation, predicting that absolute numbers of kills should decrease over time as tortoises become locally depleted. We then determine how Pied Crow abundance varies with distance from the powerline, predicting that Pied Crow abundance would be greatest near the structure due to its provision of nesting and perching sites. We then assess the spatial distribution of Angulate Tortoise populations relative to the powerline, predicting that tortoise abundance should be negatively correlated with Pied Crow

abundance and therefore lowest in areas near the powerline. We then examine tortoise size in relation to distance from the powerline, predicting that smaller individuals (most vulnerable to crow predation) will be more abundant at greater distances from the powerline where Pied Crow abundance is lower. Finally, we compare the size class frequency of recorded tortoises, predicting that the current tortoise population is skewed towards larger, older individuals with declining juvenile numbers, which would suggest a lack of recruitment. By combining these spatial and temporal patterns, this study aims to address a key knowledge gap regarding the ecological consequences of native Pied Crows in anthropogenic landscapes and provide critical insights for the conservation of South Africa's endemic tortoises.

3.3 Methods

3.3.1 Study site

This study was conducted at the Sere Wind Farm (-31.50 S, 18.11 E), a commercial-scale wind energy facility on the Atlantic coast near Lutzville, South Africa (Figure 3.1). The site is owned by the state energy company Eskom covering approximately 3,600 hectares. The farm consists of 46 wind turbines and a 44 km, 132 kV powerline, with pylons spaced roughly every 360 m (approximately 105 pylons, based on satellite counts). The study area is in the Fynbos and Succulent Karoo biome. The Fynbos biome is characterised by evergreen shrubland with a minor grassy component adapted to the Mediterranean climate, while the Succulent Karoo occurs in a semi-arid climate and supports shrubland and a variety of succulent plants. The areas surrounding the wind farm are largely used for livestock farming and agriculture. The site experiences an average annual rainfall of 140 mm, with July generally being the wettest month (18 mm) and January the driest (0 mm) (https://gis.elsenburg.com/apps/cfm/). Average temperatures range from 14°C during the cooler months to 23°C in the warmer months (Western Cape Department of Agriculture, 2025), although temperatures can reach 40°C.

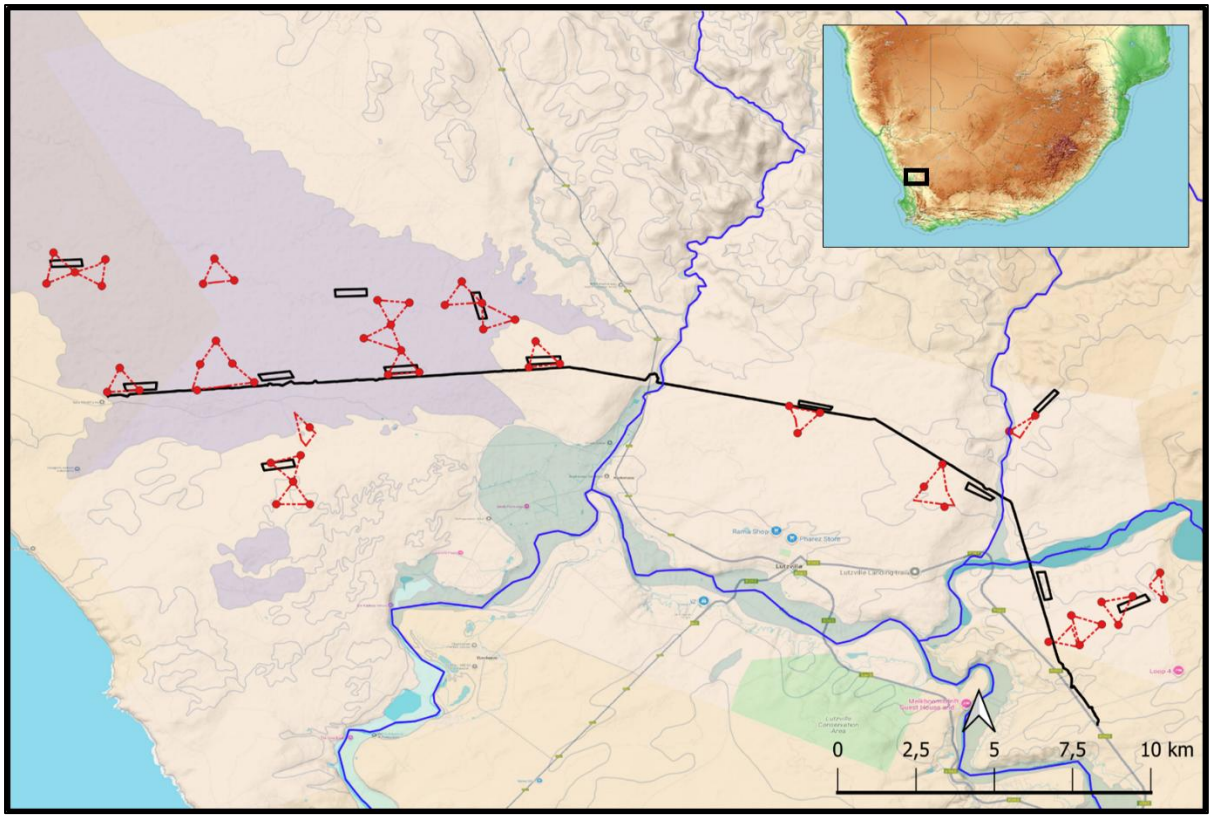

Figure 3.1. Map of study area showing location of the powerline (black line), crow point counts (red-filled circles) and tortoise transects (red dotted lines). Additional tortoise transects carried out in one month (August) are represented by black rectangles. Different base colours indicate biome type, with purple representing the Fynbos biome, green representing Azonal Vegetation, and beige representing Succulent Karoo biome. Rivers are indicated by blue lines.

3.3.2 Data collection

Tortoise predation at Pied Crow nesting sites

Staff from The Endangered Wildlife Trust (EWT) collected depredated tortoise shells under Pied Crow nests to assess tortoise predation as part of the Environmental Management Programme for the Sere Wind Farm. In the first two years (2015–2016), surveys were conducted monthly, and from 2017 to the present, these surveys were only conducted every four months. During sampling, a team of four observers drove along the powerline access road, stopping at every pylon that contained a bird nest (active or inactive). Each pylon was assigned an identification code, which is typically linked to the Pied Crow nest located on that pylon. Some pylons had more than one nest. For some counts of depredated tortoises under nest sites at pylons, only a grid reference was given, rather than attributing these data to a

pylon identification number. In these cases, we used the grid reference to allocate these observations to the closest known pylon.

At each nest and during each sampling event, a GPS coordinate was recorded, and a 20 m radius was systematically searched around the nest for evidence of tortoise predation. All visible tortoise carapaces were counted and collected. Data collection was typically completed for the entire length of the powerline within a single day.

Although most nests belonged to Pied Crows, they could also include nests used by other species e.g., Greater Kestrel (*Falco rupicoloides*). When a species was seen at the nest, it was assumed to be the "owner" and the nest was assigned to that species. However, because Pied Crows were the species of interest during surveys, and occupied most nests, any nests without species ID were assumed to belong to Pied Crows. Only years in which pylons were classified as having Pied Crow nests were retained, resulting in 88 probable nest sites used in the analysis.

Pied Crow and Tortoise surveys

Angulate Tortoise surveys were conducted monthly over six months between August 2024 and February 2025, with Pied Crows surveyed between September 2024 and February 2025, to investigate how proximity to the powerline influences species abundance (Table 3.1). Pied Crow sampling was carried out using point counts, and tortoise sampling was conducted on triangular or rectangular transects (Figure 3.1). For both species, sampling locations were established at different distances from the main 44 km powerline, measured using the ruler function in Google Earth Pro. To account for other structures, proximity to the nearest infrastructure feature (road, turbine, or farmhouse) was also calculated. Although accessibility influenced the placement of transects and point counts, which potentially introduced a minor spatial bias towards more accessible areas, the sites were intentionally selected to span a range of distances and habitats to reduce this bias.

Pied Crows were sampled using point counts located at the corners of triangular transects used for tortoise surveys, with points spaced at least 1 km apart to ensure independence. At each point, a 10-minute count within a 1 km radius was conducted, but Pied Crows observed outside of an 800 m radius were removed to ensure counts better reflected distances from the powerline. Most points were surveyed at least three times during the study period. At the

start of each point count, environmental variables including temperature [°C], wind speed [km/h], and cloud cover [%] were recorded. We also calculated time since sunrise for each observation using the package '*suntools*' (Bivand and Luque, 2024), in R (R Core Team, 2022). These were conducted over six months, between September 2024 and February 2025. We completed 179 point counts, situated between 0.003 km–5.5 km (median = 1.56 km) from the powerline. Surveys were typically carried out between 06:00 and 16:00, depending on the time of sunrise, under temperatures ranging from 12.6–39.9°C (mean = 26 °C).

Angulate Tortoises were sampled using walked transects. Surveys for tortoises were refined following the initial sampling period. In August 2024, surveys were carried out along 2.5 km long rectangular transects. From September 2024 onwards, triangular transects were used to allow more efficient spatial coverage. Each side of the triangle represented a ca. 1km transect, though occasionally shortened where fences or roads obstructed the route. Each triangle 'transect set' typically equated to ca. 3 km of total sampling effort. Each side of the triangle was analysed independently as a transect unit. Lengths of these transects therefore ranged between 115 m to 2,500 m (median = 1000 m). GPS devices were used to measure distances. Transects were walked slowly (ca. 2 km/h) by one person (Y.S.) scanning on both sides of the transect to maximise detections. For each tortoise detected, GPS coordinates, sex, and straight carapace length (SCL, measured along the plastron, mm) were recorded. Sex was determined by examining the plastron and gular, with males having a concave plastron and a lengthened gular, and females having a flat plastron.

At the start of each transect, and every 250 m thereafter, vegetation cover was estimated using a rapid 5 × 5 m grid survey, with cover visually estimated in 5% increments. The height of the tallest vegetation within each grid was also recorded. In addition, for each survey conducted along a triangular transect, environmental variables including temperature [°C], wind speed [km/h], and cloud cover [%] were recorded. We also calculated time since sunrise for each observation using the package '*suntools*' (Bivand and Luque, 2024). These transects were conducted over seven months between August 2024 and February 2025.

A total of 17 triangular sampling transect clusters were established along the powerline (Figure 3.1). Across all survey's triangles and rectangles, we completed 283 transects, covering ca. 257 km, equivalent to ca. 128 hours of active searching. Transects were situated between 0.38 km and 5.1 km from the powerline (median = 1.47 km), capturing areas near to and far

from the powerline. Surveys were typically carried out between 06:00 and 16:00, depending on the time of sunrise, under temperatures ranging from 10.8–39.3°C (mean = 26.8 °C).

Due to anemometer battery failure on 30 October 2024, missing temperature data for eight transects and six point counts were derived from the ERA5-Land dataset (Muñoz et al., 2019) using Google Earth Engine (Gorelick et al., 2017). For this we determined correlations among climate variables obtained from ERA5-Land temperatures and our field measurements using linear regression. We then used these correlations to generate predicted temperature values for these eight transects and six point counts with missing field measurements (Suppl. Table S5).

Table 3.1. Number of surveys carried out at each distance category from the powerline. Values indicate the total number of replicated surveys completed at each point count location. In total, 53 point-count locations were surveyed, each with the number of replicates below.

	Distance from powerline (km)	**Number of unique point counts/transects**	**Total number of surveys**
Pied Crow point counts	0–1	17	68
	1.1–2	12	45
	2.1–3	9	33
	3.1–4	6	15
	> 4	9	18
Tortoise transects	0–1	33	111
	1.1–2	16	60
	2.1–3	19	64
	3.1–4	13	25
	> 4	14	23

3.3.3 Statistical analyses

All statistical analyses were conducted in R (R Core Team, 2022). Model selection for all analyses was performed using the '*dredge*' function from the '*MuMIn'* package (Bartoń, 2025) with the best-fitting model selected based on the lowest Akaike's Information Criterion (AIC), with the best models considered to be those within ΔAIC of 2.

Tortoise predation beneath Pied Crow nesting sites

Temporal trends in tortoise fatalities were analysed using generalised linear mixed models (GLMMs) with a negative binomial distribution and a log-link function. Pylon identity was included as a random term to account for repeated observations at the same nest sites. Year and season were included as fixed effects, with seasons defined by month: spring (September–November), summer (December–February), autumn (March–May), and winter (June–August). The statistical significance of the seasonal effect was assessed using a Likelihood Ratio Test. To account for unequal number of days elapsed between surveys in the first two years (surveys done monthly) compared to those in the following years (typically every three months), the log-transformed (+1) number of days since the previous survey was included as an offset, i.e. more tortoises may be found beneath each nest site due to longer time periods between surveys. Consequently, the first survey at each nest site was removed before modelling, as no 'time since previous survey' could be calculated for those first observations.

To account for potential spatial autocorrelation in the number of tortoise shells found under nests, we used the R package '*sdmTMB*' (Anderson et al., 2022), which accounts for spatial autocorrelation using the stochastic partial differential equation (SPDE) approach. Since coordinates need to be in a distance-based projection, coordinates were re-projected to the Albers 25E coordinate system. In '*sdmTMB'*, the spatial random field is modelled as a continuous Gaussian Markov random field and is approximated through a triangulated mesh constructed over the study extent (Lindgren et al., 2011). We generated the mesh using projected Albers Equal Area coordinates, setting the number of nodes to 420. More nodes equate to a finer mesh. Although finer meshes generally produce a more accurate SPDE approximation, they also increase computation time and can lead to overfitting (Anderson, et al. 2022). Setting the number of nodes to 420 produced the best balance between model stability and computational efficiency. The optimal cutoff value for the number of nodes was determined using the '*cutoff_search*' option in '*sdmTMB*' (Anderson et al., 2022). Spatial correlation was constrained using barrier meshes created with the '*add_barrier_mesh*' function (Anderson et al., 2022).

Because Pied Crow pairs may have multiple nest sites, which may increase over time since the powerline has been erected, a decline in tortoise carapaces beneath a specific nest could

reflect abandonment of older nest sites rather than a decline in predation. To address this, an additional cumulative analysis was performed to determine changes in the number of tortoise carapaces across the entire powerline over time. However, this analysis assumes that Pied Crow abundance remained fairly constant over time, or at least that their abundance does not decline. Tortoise fatalities were first aggregated by year, and a separate negative binomial model was fitted, with Year included as a fixed effect. The first (2015) and the final (2025) years were excluded due to incomplete sampling. To account for changes in survey effort, as the first two years were sampled monthly, 2017 was sampled only thrice, and subsequent years were sampled quarterly, we fitted an additional model to a subset of the data excluding the first three years. This model was fitted using '*glmmTMB*' (Brooks et al., 2017).

Exploring Pied Crow abundance in relation to powerline distance

We first tested for collinearity among predictor variables (distance to powerline, distance to other infrastructure, temperature, time since sunrise). All pairwise correlations were < 0.50, indicating acceptable collinearity levels (Suppl. Table S6).

We used GLMMs to determine Pied Crow abundance at varying distances from the main powerline (Table 2.1). Counts were analysed using negative binomial distribution with a log-link function which best fitted the distribution of the data. Point Count ID was included as a random term to account for repeated measures at the same location across the four months. Environmental variables including distance to other infrastructure [km], temperature [°C], wind speed [km/h], time since sunrise [h], and month were included as fixed effects to control for their potential influence on crow counts. Two models were fitted: the first assumed a linear effect of distance, and the second included a 2nd-degree polynomial term for distance to allow for non-linear relationships. We tested the final model for residual spatial autocorrelation (Moran's I) using the '*DHARMa*' package (Hartig, 2025), which was not detected and thus we did not control for spatial autocorrelation. The model was fitted using '*glmmTMB*' (Brooks et al., 2017).

Exploring Tortoise abundance in relation to powerline distance

We first tested for collinearity among predictor variables (distance to powerline, distance to other infrastructure, temperature, average vegetation cover, and time since sunrise). All

pairwise correlations were < 0.50, indicating acceptable collinearity levels (Suppl. Table S7 for full correlation matrix).

Similarly, we used GLMMs to investigate tortoise abundance at distances from the main powerline and other infrastructure, specifying a negative binomial distribution with a log-link function. Transect ID was included as a random term for repeated measures. We also ran a model with Triangle ID as an additional random term. However, since the random effect for triangle ID explained no variance (random-effect variance = 0), it was removed from the final model. The best global model (ΔAIC = 3.1) included a 2nd-degree polynomial for distance to powerline to test for non-linear relationships, along with distance to other infrastructure [km], temperature [°C], time since sunrise [h], month, average maximum height [cm], and average vegetation cover [%] as fixed effects. The log-transformed transect length (+1) was included as an offset to standardise between surveys of different lengths. We then once again tested the final model for residual spatial autocorrelation (Moran's I) using the '*DHARMa*' package (Hartig, 2025), which was not detected and thus we did not control for spatial autocorrelation. The x and y coordinates were specified as the midpoints for each transect. The model was fit using '*glmmTMB*' (Brooks et al., 2017).

To investigate whether tortoise size varied in relation to distance to the powerline, an additional Linear Mixed Model (LMM) was carried out using SCL [cm] as the response variable and distance to the powerline as the fixed effect. Transect ID was included as a random effect to account for repeated counts from the same transect. The model was fitted using a Gaussian distribution with an identity link function.

3.4 Results

3.4.1 Tortoise shells beneath Pied Crow nests

A total of 3,182 tortoise fatalities were recorded across 88 monitored pylons with nests from mid-2015 to mid-2025. Fatalities were not uniformly distributed: eight pylons (ca. 9% of nest sites) accounted for 50% of all fatalities. Over the entire 10-year period, we recorded a mean of 36.1 ± 70.3 fatalities under nests (range = 0–450).

At an individual nest site level, there was a significant decline in tortoise fatalities with year (β = -0.25, z = -6.20, p < 0.005), indicating the number of tortoise shells beneath pylons

decreased over time (Figure 3.2). For each year, tortoise fatalities decreased by approximately 22%.

There were significant differences in the tortoise fatality counts between seasons ($\chi^2 = 74.2$, df = 3, $p < 0.001$) (Figure 3.3a). Spring had the highest predicted fatalities per nest (2.25; 95% CI: 0.81–6.23), followed by summer (0.68; 95% CI: 0.25–1.89), autumn (0.35; 95% CI: 0.13–0.97), and winter, which had the lowest fatalities (0.18; 95% CI: 0.06–0.50). Spring had significantly higher fatalities than Autumn, Summer, and Winter (all $p < 0.001$). Summer also showed significantly higher fatalities than Winter ($p < 0.001$).

The cumulative model, which aggregated fatalities per year across the entire site rather than individual nests, showed a similar temporal pattern to our individual nest site analysis (Figure 3.3b). There was a marginally significant negative effect of year on total fatalities ($\beta = -0.10$, $z = -2.05$, $p = 0.04$), indicating the number of tortoise shells across the entire study area has decreased by 9.6% annually, since 2016. Even after excluding the first three years, an annual decline of 15.7% was still apparent ($\beta = -0.17$, $z = -4.20$, $p < 0.001$).

3.4.2 Pied Crow abundance in relation to the powerline

A total of 112 Pied Crows were recorded across 179 counts from 53 different point count locations over four months. This corresponded to a mean abundance of 0.63 ± 1.47 crows (range = 0–10) per point count.

The best-fitting model included distance to powerlines and month as significant predictors (Suppl. Table S8). Pied Crow abundance declined significantly with increasing distance from powerlines ($\beta = -0.30$, $z = -2.62$, $p = 0.009$; Figure 3.4a). For every 1 km increase in distance from a powerline, crow abundance decreased by approximately 26%. The model's fixed effects explained 31% of variance in crow numbers (marginal $R^2 = 0.31$). Although the transect-level random effect explained negligible variance, it was kept to account for repeated sampling within point counts. As expected, given the low random-effect variance, marginal and conditional R^2 values were nearly identical, indicating that most explained variation was attributable to fixed effects.

Month also explained variation in Pied Crow abundance ($\chi^2 = 11.64$, DF = 3, $p = 0.009$; Figure 3.4). Pied Crow abundance was lowest in December (0.28 estimated Pied Crows per survey; 95% CI: 0.13–0.62) and February (0.34; 95% CI: 0.17–0.67), and highest in October (0.80; 95%

CI: 0.48–1.35) and September (0.92; 95% CI: 0.55–1.54) (Figure 3.4b). September had significantly higher Pied Crow abundance than December ($p = 0.038$). No other terms were significant, therefore distance to other infrastructure, hours since sunrise, and temperature were dropped from the final model. A polynomial term for distance was tested but did not improve model performance. No spatial autocorrelation was observed in the residuals.

3.4.3 Tortoise abundance in relation to the powerline

During surveys, we recorded 52 living and 185 dead Angulate Tortoises (dead: live ratio of 3.6:1), across 283 walked transects from 95 transect locations. This corresponded to encounter rates of 0.2 live individuals per km and 0.7 dead individuals per km. Living tortoises had a mean carapace length of 18.12 ± 3.29 cm, while dead tortoises had a mean carapace length of 16.61 ± 4.06 cm (range = 5–24.5 cm). Living juveniles (tortoises with a carapace < 12 cm) made up approximately 4% of the total population, with the rest being larger adults (Figure 3.5a). In comparison, dead juveniles made up approximately 18% of the population of dead tortoises. This scarcity appears to be driven by high juvenile mortality, with the smallest size class (5–10 cm) consisting entirely of dead tortoises, with no living individuals (Figure 3.5b). Sex could be determined for 18 females and 24 males, with the rest being juveniles, and therefore were not sexable.

The best fitting model for Angulate Tortoise abundance included the non-linear relationship with distance from powerlines and temperature (Suppl. Table S9). Tortoise abundance changed little through the first 4 km from the powerline but increased sharply beyond 4 km from the powerline (linear term: $\beta = 0.80$, $z = 0.30$, $p = 0.70$; quadratic term: $\beta = 7.01$, $z = 3.16$, $p < 0.005$) suggesting suppression close to the powerlines and then a marked recovery in abundance at a threshold distance from the powerline (Figure 3.6a). Tortoise abundance was significantly negatively associated with temperature ($\beta = -0.064$, $z = -2.31$, $p = 0.021$), with abundance decreasing as temperature increased (Figure 3.6b). The model's fixed effects explained only 10% of the variance in tortoise abundance (Marginal $R^2 = 0.106$), indicating substantial unexplained variation. No other variables (distance to other infrastructure, hours since sunrise, % vegetation cover, average maximum height, or month) improved model AIC scores and were dropped from the final model. No spatial autocorrelation was detected in the residuals.

The spatial analysis of live tortoise size revealed no significant relationship between SCL and proximity to the powerline. Distance from the powerline did not significantly predict tortoise size (β = -0.39, SE = 0.25, t = -1.53, p = 0.131).

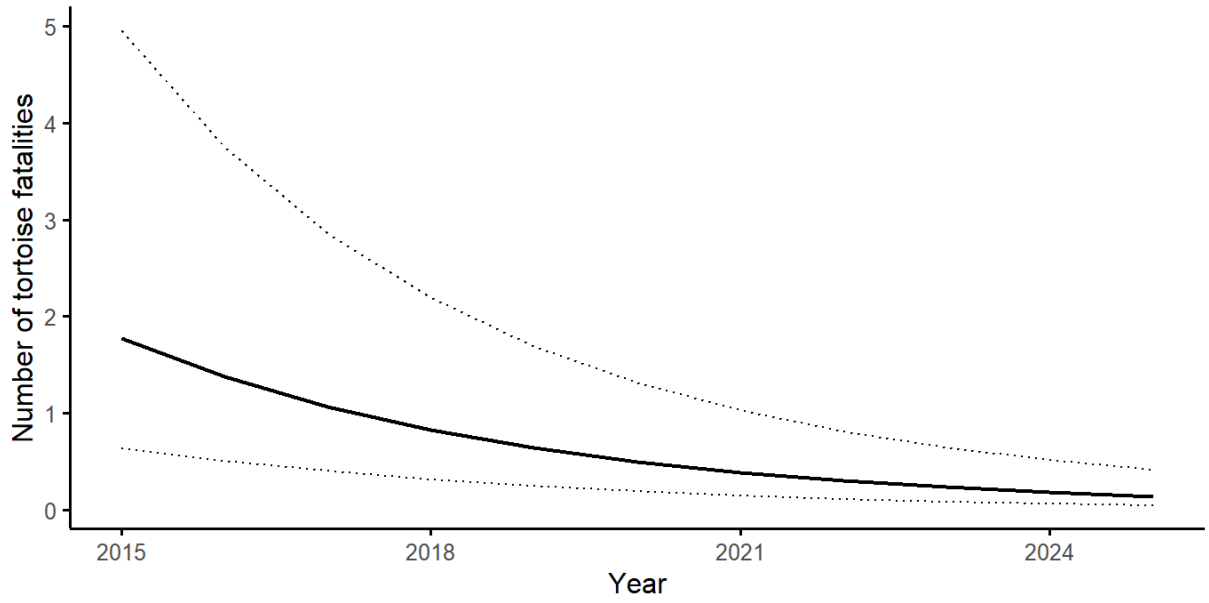

Figure 3.2. The average number of Angulate Tortoise fatalities (shells) found beneath Pied Crow nests over time (2015–2025), derived from model-based marginal effects using the *allEffects()* function. Estimates are standardised to the average survey effort (i.e., the log(+1) number of days between each survey). Dotted lines represent confidence intervals.

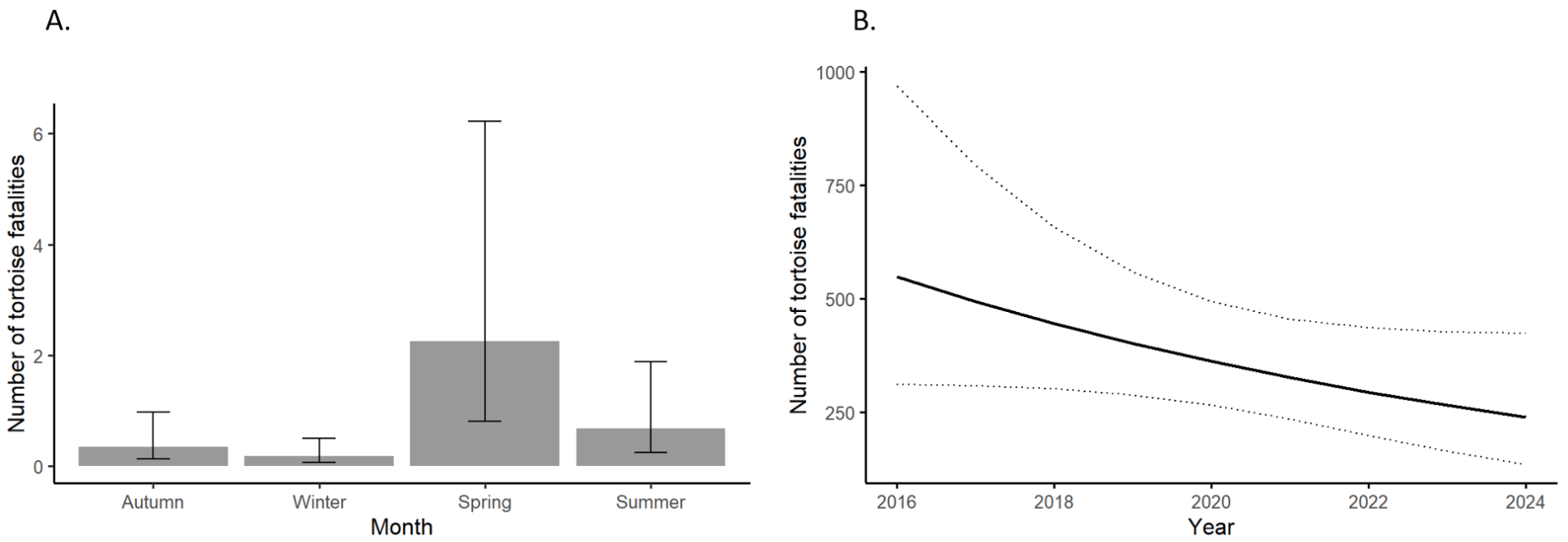

Figure 3.3. (a) The average number of Angulate Tortoise fatalities (shells) beneath Pied Crow nests within each season, derived from model-based marginal effects using the *allEffects()* function. (b) The estimated number of Angulate Tortoise fatalities beneath Pied Crow nests between 2016 and 2024, situated atop pylons at the Sere Wind Farm, derived from model-based marginal effects using the *allEffects()* function. Dotted lines represent confidence intervals.

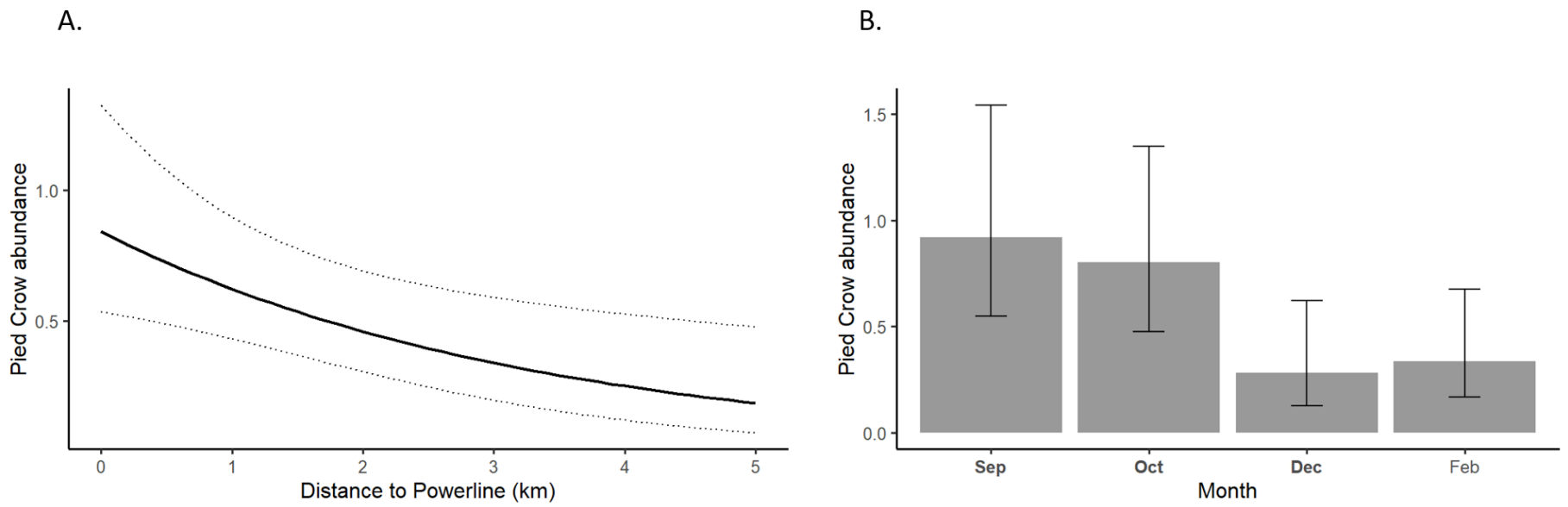

Figure 3.4. (a) Modelled Pied Crow abundance at different distances to the main Sere Wind Farm powerline, derived from model-based marginal effects using the *allEffects()* function. The dotted lines represent confidence intervals; (b) Modelled Pied Crow abundance by month, derived from model-based marginal effects using the *allEffects()* function. Months are abbreviated by acronyms (Feb: February, Sep: September, Oct: October, and Dec: December). Pied Crow breeding months are indicated in bold along the x-axis.

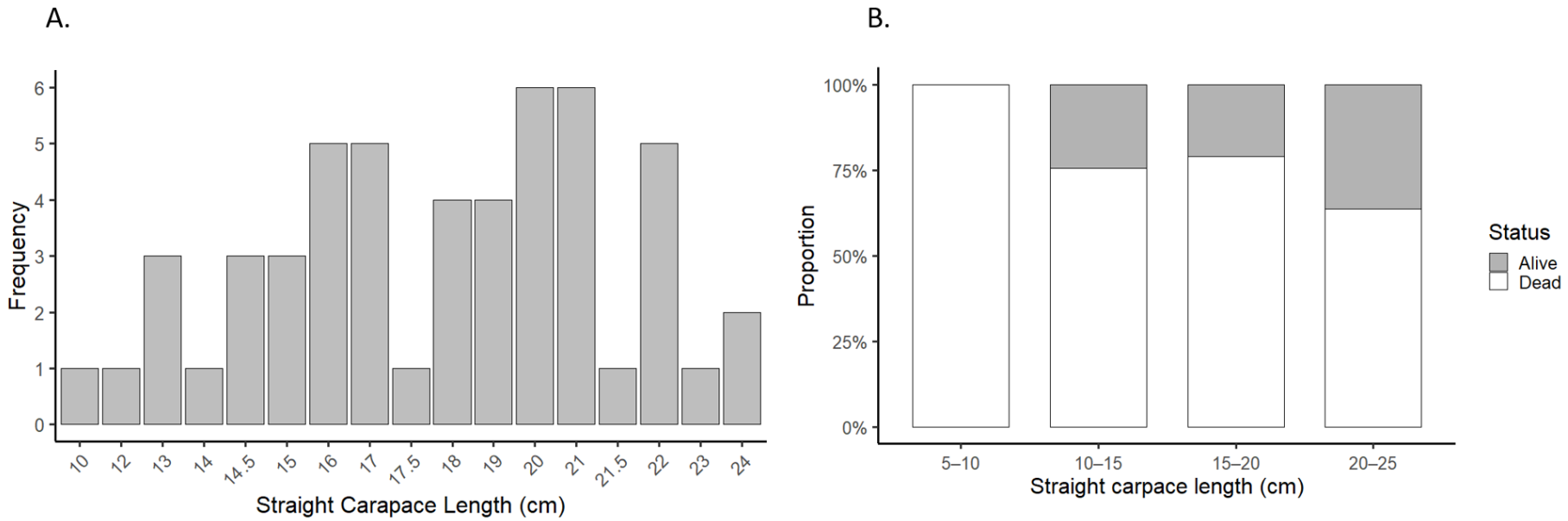

Figure 3.5. (a) Frequency of straight carapace length of living Angulate Tortoises recorded along walked transects at the Sere Wind Farm; (b) The proportion of live versus dead Angulate Tortoises across four size classes based on Straight Carapace Length. White bars indicate dead individuals, and grey bars indicate live individuals.

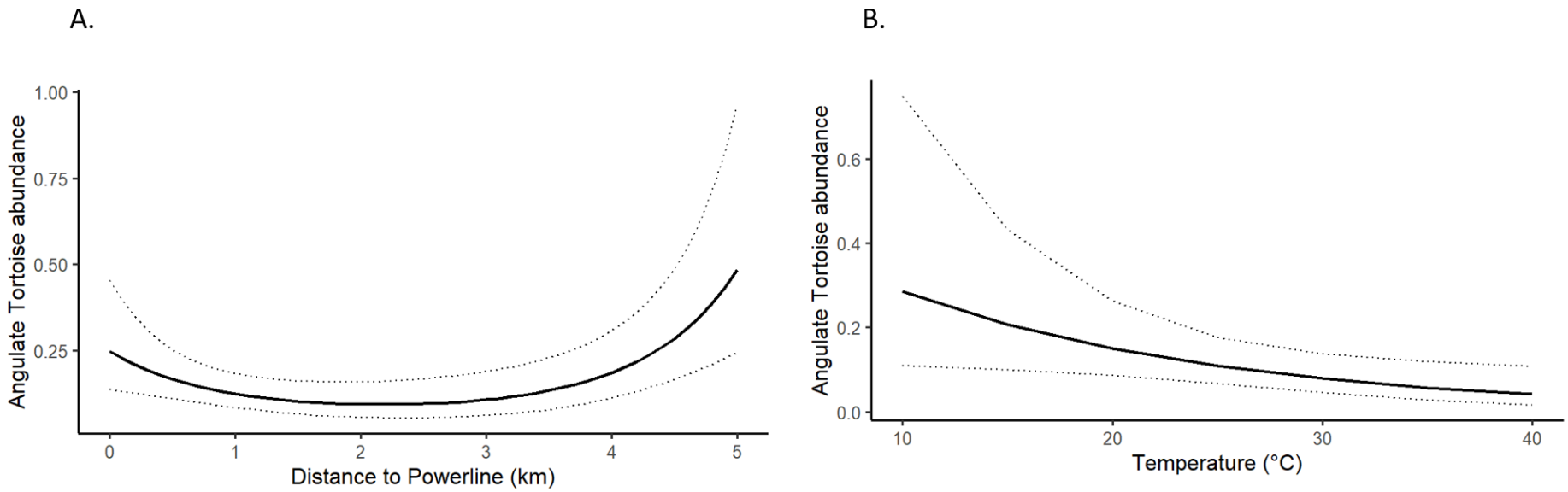

Figure 3.6. (a) Modelled tortoise abundance at different distances to the main Sere Wind Farm powerline, derived from model-based marginal effects using the *allEffects()* function; (b) Modelled tortoise numbers at different temperatures [°C], derived from model-based marginal effects using the *allEffects()* function. In both figures, dotted lines represent confidence intervals.

3.5 Discussion

This study found support for our hypothesis that powerline infrastructure facilitates Pied Crow expansion and creates zones of increased predation pressure on local Angulate Tortoise populations. In keeping with our (temporal) prediction, we found that over the ten-year monitoring period, counts of tortoise shells beneath Pied Crow nests declined significantly both at individual nest sites and cumulatively across all nests. Additionally, matching our (spatial) predictions, we found that Pied Crow abundance was higher near the powerline, decreasing by approximately 26% for every km away from the powerline, and correspondingly there was an increase in the abundance of Angulate Tortoises at distances greater than 4 km away from the powerline, with no significant changes below 3 km. Interestingly, we found 50% of fatalities/dead tortoises beneath just 9% of nest sites, which points to the idea that substantial predation impact may be carried out by a few individuals within the crow population. The powerline development has therefore created a predation hotspot with long-term consequences for local tortoise populations, which may need to be mitigated in order to protect the tortoise population in the region. Our results represent some of the first empirical evidence that Pied Crows may have a negative population-level impact on native Angulate Tortoises.

3.5.1 Temporal declines in tortoise shells beneath Pied Crow nests

The number of tortoise shells found beneath individual nest sites showed a significant decline over time. However, because Pied Crows can build multiple nests, in theory this decline could have occurred through nest abandonment over time rather than reduced predation pressure. However, our additional analysis suggested this was unlikely to explain the observed pattern, because the cumulative number of tortoise shells recorded over the entire study also declined across the study period. Although this could have theoretically been driven by an overall reduction in Pied Crow abundance rather than a decline in available tortoises, this is also thought unlikely based on anecdotal observations (personal communication, Lizel Tolken). The consistency in the temporal decline beneath each nest and across the entire study area suggests a reduction in the availability of tortoises small enough for crows to eat, thereby supporting the idea that Pied Crow predation could be driving a decline in the population. However, using shell counts beneath nests introduces potential biases from scavenging and

other predators. Other scavengers could remove carcasses from beneath the nests, which means tortoise shell counts could be an underrepresentation of the actual number of depredated juvenile tortoises. For example, Durà i Franch (2017) estimated scavenging rates of tortoises and found that 10% of carcasses were removed over a two-week period. In addition, other predators that prey on tortoises may also use the same perches close to the nesting sites, meaning that not all of the accumulated carcasses can be definitively attributed to Pied Crows.

Temporal declines in tortoise shells beneath Pied Crow nest sites could be explained by a potential decline in prey abundance. Pied Crows appear to be selective in their prey choice, targeting individuals within the shell length range 3.5 – 9.8 cm (Durà i Franch, 2017). This size range corresponds primarily to juveniles, up to a maximum age of 2–3 years old (Branch, 1984), which form the recruitment cohort needed to sustain tortoise populations, as demonstrated by population declines observed when juvenile recruitment fails (Loehr, 2017; Durà i Franch, 2017). Angulate Tortoises are long-lived, slow to mature, and produce few young, making them sensitive to losses at early life stages (Hofmeyr, 2004; Branch, 1984). Constant juvenile mortality can therefore lead to long-term population declines, with similar accounts reported for several other chelonian species (Boarman, 1992; Segura et al., 2020; Price et al., 2021). Sustained removal of juveniles over several years may therefore lead to recruitment failure, with fewer individuals surviving to reproductive maturity. Similar population structures have been documented in Desert Tortoise populations exposed to subsidised Common Raven (*Corvus corax*) predation, where long-term recruitment failure preceded population declines (Boarman, 2003; Kristan and Boarman, 2003). Long-term, size-selective predation has also been documented in other birds, including Kelp Gulls (*Larus dominicanus*), where tortoises within a juvenile size range (90–110 mm) were largely absent, consistent with high juvenile mortality due to gull predation (Branch and Eis, 1990).

If constant juvenile mortality is responsible for population decline, we might expect to see a time lag before the number of tortoise fatalities decreases. This is because the adult tortoises in the population continue to reproduce. However, this will also be affected by the fact that tortoise fatalities may span several years (e.g. 1–3-year-olds), and this may influence the rates at which declines are observed due to a shift in sizes classes available (as only 0–1 years olds would be subsequently available). Thus, over time further declines may manifest as breeding

adults die and are not replaced by new recruits. This process may take some time given that Angulate Tortoises are longed lived (over 30 years) (Hofmeyr, 2004) and take a relatively long time to reach sexual maturity (e.g., ca. 10 years to reach a size of 12 cm) (Branch, 1984).

Predation by Pied Crows varied seasonally, with significantly more tortoise shells per nest observed during spring and summer, respectively, which coincides with the peak Pied Crow breeding season. Tortoise predation by Pied Crows has been linked to chick provisioning, with one breeding pair recorded killing a substantial number of tortoises (Fincham & Lambrechts, 2014). Food resources may be limited during this period, and Pied Crows may target largely sedentary and easily captured prey such as tortoises. Adult Pied Crows are likely to increase foraging effort and selectively target juvenile tortoises. Seasonal increases in predation pressure may be especially negative for Angulate Tortoises, as spring and early summer coincide with periods of increased activity and mating behaviours (Branch, 1984). Outside the breeding season, Pied Crows may prey on tortoises less, or use alternative perches and foraging areas, so predation may occur more diffusely, potentially leaving tortoise shells in locations not directly beneath monitored nests, becoming harder to find, and therefore missed in surveys. In addition, Pied Crows may not need to bring back tortoises to their nest during the non-breeding season.

3.5.2 Powerline Infrastructure facilitates Pied Crow Expansion

Spatial patterns in Pied Crow and Angulate Tortoise abundance further support our hypothesis that the newly erected powerline has facilitated Pied Crow expansion into this historically treeless habitat, potentially increasing predation pressure on tortoises and other reptiles. Pied Crow abundance declined with increasing distance from the powerline, while Angulate Tortoise abundance increased further away from the powerline, in a non-linear manner, with abundances increasing rapidly at distances greater than 4 km from the powerline. Linear infrastructure is known to facilitate the expansion of corvid populations by providing nesting and perching structures and predictable foraging opportunities, and Pied Crow abundance has previously been shown to increase in areas with higher powerline densities (Cunningham et al., 2015). The patterns observed are consistent with a combination of hyper-predation and spillover predation (Holcomb et al., 2021). Breeding Pied Crow populations facilitated by the powerline may display heightened predation pressure near

nesting sites (hyper-predation), while non-breeding individuals or dispersing foragers may extend predation impacts several kilometres into the surrounding landscape (spillover predation: Kristan and Boarman, 2003; hyper-predation: Oro et al., 2013). In this context, the powerline likely functions as an initial entry point into the landscape, with prey mortality expected to be highest near the infrastructure and to decrease with distance as predator density declines. Concentration of predators around such structures may therefore elevate local predation pressure, particularly on vulnerable life stages. This interpretation is supported by our observation that all live tortoises recorded across the study area measured between 10 and 24 cm in straight carapace length, and averaging 18.12 cm, sizes that just fall outside the preferred predatory range of Pied Crows (up to 10 cm).

Given that the field surveys for this study were concentrated during the breeding season, with the exception of a final survey carried out in early February, the available data are insufficient to determine whether declining Pied Crow abundance associated with increasing distance to the powerline is a seasonal effect. Resource selection in breeding Common Ravens appears to be centred around nest sites (Howe et al., 2014), whereas non-breeding ravens display more nomadic behaviour when it comes to food selection (Heinrich et al., 1994), relying more on anthropogenic food sources (Jain et al., 2022). Provided that Pied Crow foraging ranges are similarly restricted within a 4 km area of pylon nest sites during the breeding season, and that tortoises constitute a primary dietary component mainly during this period, life stage history could explain the observed increase in tortoise abundance beyond 4 km. More research is therefore needed to determine how Pied Crow abundance changes in relation to powerline infrastructure, in addition to other anthropogenic features, outside of the breeding season.

While tortoise abundance increased with distance from the powerline, there was no significant change in the size of the tortoises recorded. These results indicate that the size distribution of tortoises remained consistent across the study area, regardless of the distance from the powerline. This suggests that individuals smaller than a given threshold are perhaps consumed by Pied Crows, meaning only those who have grown past their preferred range remain in the population and were thus recorded in surveys. For example, Loehr (2017) found a decline in the proportion of Speckled Padloper juvenile tortoises found within the same populations several years apart. The higher abundance of tortoises at distances greater than

4 km likely implies that a higher number of individuals is a result of successful growth to a large enough size due to lower predator density, which could have occurred given that the powerline has been present for around 10 years. It might also suggest that although there is lower predation at these distances, predation is still present. Alternatively, it may be that smaller tortoises are simply much harder to spot and thus are missed by the observer, although in other studies smaller tortoises were observed (Branch and Eis, 1990; van Heezik et al., 1994, Durà i Franch, 2017), suggesting that this may not be the case.

Although the sample size (52 live tortoises) of this study is relatively small, we found that the size distribution of living tortoises was skewed towards larger individuals, with juveniles (< 12 cm) comprising only 4% of the total live population (Figure 3.5a), which is substantially lower than other populations that have been monitored previously. For example, van Heezik et al. (1994) found around 18% of the population sampled were below this size. While not conclusive, this disparity does support the idea that smaller age classes are being impacted in this population. While a skew toward larger animals is normal for Angulate Tortoises because of naturally high juvenile mortality and an asympotic growth rate (Branch, 1984), the disparity observed here is apparent when compared to the dead tortoise data. In contrast to the live population, juveniles of the dead tortoises recorded accounted for 18% of all carcasses.

There may exist an “escape” shell size, after which tortoises become less susceptible to predation because they are too large to be depredated. In Morocco, a study found that Common ravens depredated juvenile Spur-thighed Tortoises (*Testudo graeca*) and all remains collected were < 75 mm (Segura et al., 2020). From a conservation perspective, linking tortoise body size to age would be critical for understanding population-level impacts, as this would indicate how many years’ individuals remain vulnerable before reaching a relative size refuge. Angulate Tortoises generally take six years to reach a total length of 10 cm (Branch, 1984). Although this 'total length' metric includes the gular scute making it slightly larger than the SCL used in our study, there is no major size difference between the TL and SCL of individuals at this age (Branch, 1984).

The lack of live juvenile tortoises recorded in this study may also be partially attributed to the nature of the species. Populations of many reptiles, including tortoises, display a high degree of crypsis; their shell patterns provide effective camouflage, making them difficult to find during encounter surveys (Zylstra et al., 2010). Furthermore, tortoise activity is highly

intermittent and driven by environmental variables such as temperature and rainfall (Zylstra et al., 2010; Díaz-Paniagua et al., 2001). In periods of extreme weather, individuals may remain inactive for extended periods, reducing the probability of detection (Drabik-Hamshare and Downs, 2017; Harju and Camrbin, 2019). This bias is often most pronounced in juvenile age classes, with smaller tortoises being more difficult to spot, and more vulnerable to environmental conditions such as temperature and rainfall (Díaz-Paniagua et al., 2001). The absence of smaller individuals likely reflects a combination of true population suppression through predation and secretive behaviours in juvenile individuals. In addition, the ratio of dead to live tortoises was imbalanced, with more dead than live individuals recorded. This may partly be because dead tortoises were easier to detect than live individuals, meaning the observed number of living tortoises may underestimate the actual abundance present. Despite this, the spatial patterns in abundance suggest that predation pressure on tortoises shapes the population structure. The sustained removal of carcasses over time, coupled with the few juvenile sightings, could point toward a population under some demographic stress due to consistent predation by Pied Crows.

To effectively manage the potential impacts highlighted in this study, especially given the continued increase in Pied Crow numbers across the country (Chapter 2), mitigation cannot rely solely on population control. As highlighted by Underhill (2025), traditional culling is often ineffective due to a population of pre-breeding adults, or “floaters”, waiting to occupy vacant nests. In addition, culling represents a short-term and sometimes unjustified solution (Marzluff et al., 2021). Instead, management should focus on limiting the availability of potential habitat through the taking down of unused linear infrastructure such as telephone poles (Underhill, 2025), which have also been identified as an effective management tool for other corvids (Boarman et al., 2006), and the removal of nests. Furthermore, consideration during Environmental Impact Assessments should be an obligation, especially in areas that provide suitable habitat for tortoises identified as species of conservation concern. Where possible, the viability of burying proposed powerlines should be assessed to prevent the development of even more suitable habitat. If not possible and should powerlines be approved in potentially sensitive areas, standardised Pied Crow and tortoise abundance surveys must be carried out prior to, during, and post-construction to monitor shifting population dynamics of both species. Standardised carcass surveys beneath pylons and nest

sites, similar to the protocols conducted by the Endangered Wildlife Trust at the Sere Wind Farm, should be a mandatory compliance action. If high tortoise mortality triggers culling as a last-resort management option, Pied Crow and tortoise abundance surveys must be conducted both before and after implementation to determine its effectiveness.

The spatial and temporal trends observed indicate that Pied Crow predation, facilitated by the development of powerlines, could be changing Angulate Tortoise population dynamics. This could have implications for global conservation efforts, given the rising evidence of juvenile tortoise mortality as a result of corvid population increases around the world (Boarman, 2003; Berry et al., 2013). While the Angulate Tortoise is currently classified as Least Concern (Hofmeyr and Keswick, 2018), using the tortoise densities determined by Branch (1984) demonstrates that the localised loss of 3,182 juvenile individuals over the study period could be equivalent to depleting the carrying capacity of nearly 83 hectares of optimal habitat. Nationally, it can be expected for juvenile tortoise mortality to be substantially higher, with the potential to increase, given South Africa's existing powerline grid structure of 33,067 km, alongside Eskom's planned development of an additional 14,494 km of transmission lines between 2025 and 2034 (Eskom, 2024). Without management interventions to address predator subsidies, the long-term viability of Angulate Tortoise populations near linear infrastructure may be at risk. These findings also have critical implications for other more threatened tortoise species, such as the Tent Tortoise, Geometric Tortoise (*Psammobates geometricus*), the Karoo Dwarf Tortoise (*Chersobius boulengeri*) (Loehr and Keswick, 2021), and the Speckled Padloper, across the country (Fincham and Lambrechts, 2014; Durà i Franch, 2017; Loehr, 2017). These species reach a considerably smaller size than Angulate Tortoises, with some already having been confirmed as prey for Pied Crows (Loehr et al., 2004; Hofmeyr et al., 2018). The loss of breeding adults could be potentially more damaging than the loss of juveniles, particularly for long-lived chelonians that rely on high adult survivorship to maintain population stability. If powerline infrastructure facilitates the predation of threatened tortoise species, it could drive rapid local extinctions rather than the slow, recruitment-driven declines predicted for Angulate Tortoises. Therefore, the expansion of energy infrastructure into the ranges of these smaller, cryptic species represents a critical conservation threat that requires urgent action.

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Chapter 4: Summary and Conclusion

The goal of this thesis was to provide an updated population status of Pied Crows (*Corvus albus*), in the hopes that the information generated can be used to further our understanding of native invaders and stimulate more research into corvids from an African perspective. I sought to answer questions relating to the spatial drivers of Pied Crow expansion, the role of powerlines as entry points for Pied Crows into historically treeless areas, and the potential consequences of these patterns for native biodiversity, and specifically for Angulate Tortoise populations. Overall, my findings show that Pied Crow abundance continue to increase at a rapid rate across South Africa, and that the development of powerlines may facilitate negative interactions between Pied Crows and Angulate Tortoises (*Chersina angulata*). These findings have major implications for how we might wish to manage this species and represent the first empirical evidence that Pied Crows may be impacting native biodiversity.

4.1 Drivers of Pied Crow population change in South Africa

Pied Crows are a native species in South Africa that has displayed an increase in population abundance in response to climate change, increasing powerline densities, road infrastructure, and human waste products and has therefore been identified as a native invader (Dean and Milton, 2009; Cunningham et al., 2015; Joseph et al., 2017). However, the most recent assessments of its population trends extended only up until 2012 and were explored at a relatively large sampling unit (e.g. quarter degree squares) (Cunningham et al., 2015). In chapter 2, I quantified more recent population changes within each South African province, biome, and in protected versus unprotected areas, and related these changes to three environmental covariates, including temperature [°C], rainfall [mm], and global human modification. Across South Africa, Pied Crow populations showed a proportional ca. 45% increase, which is substantially higher than that found by the previous Cunningham (2015) study. Particularly strong increases were observed in the Free State, Eastern Cape, and Mpumalanga, suggesting a potential eastward and central shift in the epicentre of population growth, compared to previous reports that identified the south-western regions as the area with the most rapid growth (Cunningham et al., 2015). These changes were evident within their dominant biomes, namely grasslands, which historically represent treeless habitats.

Pied Crow population increases were more pronounced in drier, cooler, and more human-modified areas. This suggests that the species is benefiting from both climatic conditions and anthropogenic changes, such as the expansion of linear infrastructure, which provides additional nesting and perching opportunities along with more predictable food resources. The most important variable which had the most explanatory power was temperature, with human modification and rainfall significant, but less important. The observed shifts in abundance and distribution also indicate that Pied Crows are increasingly exploiting habitats that were previously less favoured. While shrubland biomes supported highest abundances at the start of the study period, the greatest increases are now occurring in other areas. I suggest that already high population densities in many areas may have driven this shift, with greater increases now occurring in regions where numbers were previously low.

4.2 Powerlines facilitate population expansion

Across the globe, anthropogenic change has driven the expansion of many native generalists, which are able to exploit increasing habitat availability and more predictable foraging opportunities (Boarman, 2003; Gibson, 2011). In South Africa, rising densities of telephone poles, windpumps, and powerline infrastructure in treeless shrubland biomes provide nesting and perching substrate, with increased powerline densities having been linked to changes in Pied Crow populations (Cunningham et al., 2015). However, these open, treeless habitats also host populations of many tortoise species, some of which are endangered (Drabik-Hamshare and Downs, 2017), making them particularly vulnerable to predation. Much like other corvids (Segura et al., 2020; Marzluff et al., 2021), increases in Pied Crow abundance in many areas have been associated with elevated predation pressure on tortoise populations (Durà i Franch, 2017; Loehr, 2017; Tolley et al., 2019). The broader biodiversity impacts on tortoises have remained poorly understood, highlighting the need for further research, especially given that other avifaunal species have been identified as predators of tortoises (Loehr and Keswick, 2022; Branch and Eis, 1990)

In chapter 3, I explored the hypothesis that the facilitated expansion of Pied Crows into a historically treeless habitat, facilitated by a newly erected powerline, is impacting Angulate Tortoise populations. To test this, I made two predictions. First, I predicted that the number of tortoise shells recorded beneath Pied Crow nesting sites has declined since 2015, indicating

a shrinking population of Angulate Tortoises in the surrounding area. Secondly, I predicted that the number of Pied Crows will show a decline with increasing distance to the main powerline, and that Angulate Tortoises will be higher where Pied Crows are lower. I found support for this hypothesis. Tortoise shells found beneath Pied Crow nesting sites and across the entire study area showed an annual decline, indicating a potential reduction in prey availability. Pied Crow abundance was highest near the powerline, whereas Angulate Tortoise abundance increased sharply at distances greater than 4 km away from the powerline, potentially reflecting a recovery in abundance where Pied Crow numbers are lower.

These patterns indicate that powerlines act as an anthropogenic subsidy for Pied Crows, potentially concentrating predation near nesting sites. The decline in tortoise shells beneath Pied Crow nests, combined with higher tortoise abundance further away, suggests that powerline development may create areas with a higher predation risk for Angulate Tortoises, particularly for juveniles. I suggest that the consistent removal of juveniles has likely skewed the population toward older individuals that have grown beyond the Pied Crows' preferred prey size. Higher tortoise numbers further from the powerline may reflect that juveniles in these areas are able to survive and reach safer sizes.

4.3 Future recommendations

The knowledge generated in my thesis contributes to the existing knowledge on the drivers of population trends and the potential impacts of Pied Crows on Angulate Tortoises. Together, this information can help to understand how Pied Crows utilise powerlines (with the potential to exploit other infrastructure) as gateways into previously uninhabitable areas and prey on vulnerable species such as tortoises. Further field studies are likely required before any definitive claims about the long-term influence of Pied Crows on tortoise abundance and their population structure.

In a different analysis that I have not reported on, I did attempt to quantify the influence of climate change (not just average climate conditions) on changes in Pied Crow reporting probabilities, by examining temperature and rainfall trends across the study area. However, there were limited significant changes across South Africa during the study period, limiting the ability to detect climate-driven impacts on Pied Crow populations. Future studies focusing on climate trends would therefore be valuable.

Concentration of tortoise fatalities at just a few nest sites indicates that predation pressure is not uniformly distributed but is likely to be carried out by a few individuals, backing up the conclusions of Durà i Franch (2017). This could support the hypothesis that tortoise predation may be a learned behaviour displayed by "problem individuals" or pairs, rather than a trait of the entire Pied Crow population. If predation is indeed driven by a few pairs, broad-scale management interventions, such as widespread culling, may be inefficient, logistically unfeasible, and unjustified from an ethical perspective. Instead, targeted control of these specific breeding pairs might be worth exploring.

It has been suggested that further field studies aimed solely at demonstrating the biodiversity impacts of Pied Crows are no longer necessary, as they are “entirely negative” (Underhill, 2025). Underhill (2025) suggests that the only viable option to reduce Pied Crow abundance is to remove unused telephone poles, which act as nesting substrates. Studying Pied Crow abundance and associated tortoise population dynamics before and after telephone pole removal would therefore provide a valuable test of management interventions and their effectiveness in mitigating predation of native fauna. Despite growing evidence of negative impacts, key knowledge gaps remain regarding Pied Crow survival rates, age at first breeding, clutch size, breeding productivity, and dispersal (Underhill, 2025), highlighting the need for further research into their behaviour and ecology.

The findings demonstrated in this study should be applied to rarer and more threatened tortoise species. While this study used the Angulate Tortoise as a model species, the evidence provided here is directly applicable to more threatened species, such as the Speckled Padloper (*Homopus signatus*) or the Geometric Tortoise (*Psammobates geometricus*). Given that these species fall within the small size classes vulnerable to Pied Crow predation identified in this study, they are likely subject to similar or even more severe predation pressures from Pied Crows. Conservation efforts should prioritise risk assessments for these species in areas where powerline infrastructure is expanding.

Future research should aim to replicate similar studies across multiple powerlines and other types of linear infrastructure to determine whether the observed patterns are consistent in different regions. Long-term monitoring of Pied Crow and tortoise populations would also help clarify temporal trends and quantify cumulative impacts on recruitment and population structure. In addition, research into the age or size at which tortoises become less vulnerable

to predation would provide valuable information for understanding population resilience. Finally, while Pied Crows display clear negative impacts, in some respects they may also fulfil ecological roles such as scavenging; therefore, management interventions should be carefully evaluated to avoid unintended consequences.

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Supplementary Material

Appendix A: Statistical results for Chapter 2 analyses

Table S1. Correlation coefficients (r) for the variables used in the SABAP2 statistical analysis

Variables	(1)	(2)	(3)	(4)	(5)
(1) T_{avg} [°C]	1.00				
(2) T_{min} [°C]	—	1.00			
(3) T_{max} [°C]	—	—	1.00		
(4) P_{avg} [mm]	-0.04	-0.06	-0.01	1.00	
(5) gHM	-0.03	-0.09	-0.08	0.36	1.00

Table S2. Statistical results for generalised linear mixed model predicting Pied Crow presence over time across South African provinces; significance is indicated by asterisks: ***p < 0.001, **p < 0.01, *p < 0.05

Province	Estimate (β)	SE	z-value	p-value	CI (Lower)	CI (Upper)
Eastern Cape ***	0.07	0.01	14.93	<.0001	0.06	0.08
Free State ***	0.14	0.01	20.73	<.0001	0.13	0.15
Gauteng ***	0.06	0.00	18.67	<.0001	0.06	0.07
KwaZulu-Natal ***	–0.03	0.004	–7.73	<.0001	–0.04	–0.02
Limpopo	0.01	0.01	1.79	0.065	–0.00	0.02
Mpumalanga ***	0.05	0.01	7.78	<.0001	0.03	0.05
North West ***	0.07	0.01	13.40	<.0001	0.06	0.08
Northern Cape ***	0.04	0.01	4.52	<.0001	0.02	0.06
Western Cape ***	0.03	0.00	7.31	<.0001	0.02	0.03

Table S3. Statistical results for generalised linear mixed model predicting Pied Crow presence over time across the ten South African biomes; significance is indicated by asterisks: ***p < 0.001, **p < 0.01, *p < 0.05

Biome	Estimate (β)	SE	z-value	p-value	CI (Lower)	CI (Upper)
Albany Thicket***	0.09	0.01	13.61	< 0.0001	0.078	0.10
Azonal Vegetation	0.02	0.01	1.77	0.077	-0.00	0.05
Desert	0.08	0.04	1.99	0.047	0.00	0.16
Forests	-0.01	0.02	-0.42	0.674	-0.04	0.03
Fynbos***	0.03	0.00	8.099	< 0.0001	0.02	0.04
Grassland***	0.07	0.00	21.99	< 0.0001	0.06	0.08
Indian Ocean Coastal Belt***	-0.05	0.01	-8.29	< 0.0001	-0.06	-0.04
Nama-Karoo***	0.06	0.01	6.57	< 0.0001	0.04	0.08
Savanna***	0.03	0.00	9.90	< 0.0001	0.02	0.04
Succulent Karoo*	0.03	0.01	2.59	0.01	0.01	0.06

Table S4. Statistical results of generalised linear mixed model predicting Pied Crow presence over time in protected and non-protected areas; significance is indicated by asterisks: ***p < 0.001, **p < 0.01, *p < 0.05

Variable	Estimate (β)	SE	p-value	CI (Lower)	CI (Upper)
Protected	0.01	0.00	0.155	0.04	0.05
Non-protected	0.05	0.00	< 0.0001	-0.00	0.01

Appendix B: Statistical results for Chapter 3 analyses

Table S5. Summary of linear regression model used to impute missing field data using ERA5-Land temperature [℃] variable. Field measurements were used as the response variable and ERA5-Land data as the predictor.

Variable	n	Regression Equation	r^2	p-value
Temperature [°C]	176	y = 0.98x + 4.55	0.68	< 0.001

Table S6. Correlation coefficients (r) for the variables used in the Pied Crow analysis.

Variables	(1)	(2)	(3)	(4)
(1) Dist. Powerline [km]	1.00			
(2) Dist. Other Infra [km]	0.50	1.00		
(3) Temperature [°C]	-0.11	-0.16	1.00	
(4) Time since sunrise [h]	-0.23	-0.21	0.49	1.00

Table S7. Correlation coefficients (r) for the variables used in the Angulate Tortoise analysis.

Variables	(1)	(2)	(3)	(4)	(5)
(1) Dist. powerline [km]	1.00				
(2) Dist. other infra [km]	0.50	1.00			
(3) Temperature [°C]	-0.19	-0.27	1.00		
(4) Time since sunrise [h]	-0.22	-0.17	0.41	1.00	
(5) Avg. vegetation cover [%]	-0.19	-0.13	-0.08	-0.05	1.00

Table S8. The influences of distance to powerline, nearest infrastructure, and environmental variables on Pied Crow abundance. Adjusted R2 for the best model = 0.31; df = 172. AIC = Akaike's information criterion; Estimate = variable coefficient; SE = standard error of the estimate

	Estimate (β)	SE	z-value	p-value
Best model (AIC = 354.4)				
Intercept	-0.73	0.41	-1.78	0.08

Powerline	-0.30	0.11	-2.62	0.009
Month: February	0.18	0.50	0.36	0.72
Month: October	1.04	0.45	2.34	0.02
Month: September	1.18	0.44	2.67	0.008
Full model (AIC = 358.00)				
Intercept	0.08	0.88	0.10	0.92
Dist. Powerline [km]	-0.27	0.13	-2.18	0.03
Dist. other infra [km]	-0.13	0.15	-0.88	0.38
Temperature [°C]	-0.01	0.03	-0.34	0.73
Time since sunrise [h]				
Month: February	0.11	0.51	0.22	0.83
Month: October	1.11	0.45	2.45	0.01
Month: September	1.23	0.48	2.55	0.01

Table S9. The influences of distance to powerline, nearest infrastructure, and environmental variables on Angulate Tortoise abundance. Adjusted R2 for the best model = 0.106; df = 276. AIC = Akaike's information criterion; Estimate = variable coefficient; SE = standard error of the estimate

	Estimate (β)	**SE**	**z-value**	**p-value**
Best model (AIC = 274.7)				
Intercept	-0.84	0.71	-1.20	0.23
Poly (dist. powerline, 1) [km]	0.80	2.08	0.39	0.70
Poly (dist. powerline, 2) [km]	7.03	2.22	3.16	0.002
Temperature [°C]	-0.06	0.03	-2.31	0.02
Full model (AIC = 286.7)				
Intercept	-2.78	1.28	-2.17	0.03
Poly (dist. powerline, 1)	0.20	2.79	0.07	0.94
Poly (dist. powerline, 2)	5.25	2.37	2.22	0.03
Dist. other infra [km]	0.15	0.18	0.82	0.41

Average maximum height [cm]	0.01	0.01	0.96	0.34
Average vegetation cover [%]	0.02	0.02	1.28	0.20
Temperature [°C]	-0.06	0.04	-1.39	0.17
Time since sunrise [h]	-0.00	0.08	-0.01	0.99
Month: September	0.05	0.54	0.09	0.93
Month: October	-0.08	0.65	-0.13	0.90
Month: December	-0.22	0.66	-0.33	0.74
Month: February	-0.21	0.59	-0.35	0.73