



The impact of climate change on the distribution patterns of *Schistosoma* transmitting snails in South Africa

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PREFACE

Embarking on my PhD marked a shift from focusing on severe weather to investigating how climate change affects the distribution of *Schistosoma*-transmitting snails, placing me at the vanguard of this research area. My work aimed to predict where these snails might be found in SA. The common thread, climate change, piqued my interest during my master's studies and now guided me to a field where my work would be cutting-edge. I was driven by the ambition to connect the dots between climate change and the distribution of schistosomiasis. South Africa's varied landscapes are the perfect backdrop for my innovative research. Being among the first to model the future distribution of *Schistosoma*-transmitting snails in South Africa came with enthusiasm, as my findings could lay the groundwork for future studies. Little did I know it would come with months of headaches or, should I say, "snail-aches"!

Attending COP 28 enriched my PhD experience, providing a global perspective on the urgency of addressing climate change, which is central to my current research. The insights gained from the conference reinforced the importance of my work in predicting the distribution of these disease vectors in the context of a changing climate. The discussions and knowledge shared at COP 28 highlighted the relevance of my efforts to bridge the gap between climate change impacts and public health.



I attended COP 28, which was hosted in the UAE in 2023.

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- Last but not least, I would like to thank myself for the dedication, perseverance, and resilience I have shown throughout this journey. This PhD has been a challenging and rewarding experience, and I am proud of the hard work and determination I have put into reaching this milestone.

This research is the author's original work and was not previously submitted for a degree at any university. I was engaged in the study presented in this document from January 2021 to February 2024 and was involved in formulating, conducting, and writing.

ABSTRACT

Schistosomiasis is a vector-borne disease transmitted by trematode worms. Two schistosome species, *Schistosoma mansoni* and *Schistosoma haematobium*, cause human schistosomiasis in South Africa (SA). This neglected tropical disease is transmitted by three gastropod intermediate host species, *Bulinus africanus*, *Bulinus globosus* and *Biomphalaria pfeifferi*. Temperature and rainfall can affect *Schistosoma* species' distribution by altering their prevalence and geographical distribution. Examining projected changes in rainfall, temperature shifts, and other climatic factors is imperative to understand how climate change may affect schistosomiasis transmission dynamics. The impacts of climate change on schistosomiasis distribution in SA remain unclear. This thesis aims to investigate the current and future impacts of climate change on the spatial distribution patterns of schistosomiasis intermediate host snails in SA. It combined ecological niche modelling with bioclimatic data from downscaled climate projections to predict future changes. Three ecological models and three General Circulation Models (GCMs) under two emission scenarios (RCP4.5 and RCP8.5) for two future periods (2040-2070) and (2070-2100) were used. The climate projection data for future periods (2040-2070) and (2070-2100) were derived from the Coupled Model Intercomparison Project (CMIP5) provided by the Copernicus Climate Change Service. A highly correlated variable (>0.85) was excluded from the analysis to reduce multicollinearity.

The results showed that the historical distribution of *Schistosoma*-transmitting snails in SA has been influenced by temperature and rainfall, with the Random Forest (RF) model proving most effective in mapping the habitats of these intermediate hosts. The ensemble model, which combines various Ecological Niche Models (ENMs), demonstrated a greater performance in identifying suitable environments for these snails. *Bulinus africanus*, *B. globosus*, and *B. pfeifferi* have historically thrived in the eastern and coastal regions of South Africa, with *B. pfeifferi* being the most widespread, favouring warmer temperatures and average rainfall. Future projections for the distribution of *Schistosoma*-transmitting snails under climate change scenarios RCP 4.5 and 8.5 suggest a complex landscape of habitat suitability. The ensemble model forecasts a decrease in highly suitable habitats for *B. pfeifferi* in the eastern areas of SA, with potential expansion in the north of Kwa-Zulu Natal. *Bulinus globosus* may find fewer optimal areas but could adapt to warmer and hotter habitats in the interior and east of SA. *Bulinus*

africanus is likely to experience a reduction in suitable regions, with some coastal areas potentially becoming more favourable due to warmer temperatures. The predicted impacts of climate change on *Schistosoma*-transmitting snails in SA indicate a shift in habitat suitability for these intermediate hosts. *Bulinus africanus* may see a reduction in habitats across several provinces but could expand into the southwest coast and central Free State. *Biomphalaria pfeifferi* is expected to encounter decreased suitability in the eastern regions of SA but may find new habitats in the Free State, Northern Cape, and western areas. *Bulinus globosus* is likely to face habitat declines but could adapt to suitable climates in the Free State and Kwa-Zulu-Natal regions. These shifts suggest that warming climates may create new habitats for these snail species at higher elevations and cooler regions. This study established a foundational framework for subsequent research at provincial and municipal levels. This can be a foundation to develop strategies to prevent transmission and range expansion of schistosomiasis into previously unaffected areas.

Key terms: Schistosomiasis, *Bulinus africanus*, *Bulinus globosus*, *Biomphalaria pfeifferi*, Climate change, ENMs, Unsuitable habitats, Suitable habitats

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LIST OF ABBREVIATIONS

°C	Degrees Celsius
AUC	Area Under the Curve
CaCO₃	Calcium Carbonate
CMIP	Coupled Model Intercomparison Project
CTA	Classification Tree Analysis
DEA	Department of Environmental Affairs
ENMs	Ecological Niche Models
GAM	Generalised Additive Models
GCM	Global Circulation Models
GIS	Geographic Information System
GLM	Generalized Linear Model
IPCC	International Panel on Climate Change
km²	Square Kilometres
m³	Meter cube
MARS	Multivariate Adaptive Regression Splines
MaxEnt	Maximum Entropy
mm	Millimeters
ms⁻¹	Meters per second
NFSC	National Freshwater Snail Collection
RCP	Representative Concentration Pathway

RF	Random Forest
ROC	Relative Operating Characteristics
SA	South Africa
SDM	Specie Distribution Models
SRE	Surface Range Envelope
TSS	True Skill Statistic
VIF	Variance Inflation Factor
WHO	World Health Organization

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CHAPTER 1

The introduction gives an extensive overview of schistosomiasis, focusing on its global prevalence with a particular emphasis on Africa, especially Sub-Saharan Africa. It discusses the geographical distribution of the disease and its impact on the region. This chapter examines the potential influence of climate change on the spread and dynamics of schistosomiasis, highlighting the importance of climate models for predicting the future distribution of schistosomiasis. The chapter ends by identifying the research gap related to the impact of climate change on *Schistosoma*-transmitting snails in South Africa.

INTRODUCTION

1.1 Background

Schistosomiasis, or bilharzia, is a vector-borne disease caused by trematode worms. It impacts over 732 million individuals globally in key transmission regions and is classified as a neglected tropical disease in 78 countries (Xu et al., 2017; Tanser et al., 2018). The geographical distribution of the parasitic disease is across the Caribbean, Brazil, Venezuela, Suriname, Indonesia, Philippines, Cambodia, Africa, the Middle East and Southeast Asia to as far as Japan (Figure 1-1). In 2015, approximately 192 million people were reported to be infected with schistosomiasis in 42 countries on the African continent (Adenowo et al. 2015). In 2022, the World Health Organization (WHO, 2022) reported that around 251 million individuals need preventive treatment for schistosomiasis, with the majority of those infected residing in Africa. Schistosomiasis is most prevalent in Africa, particularly in Sub-Saharan Africa, where 90% of cases occur despite Africa only having 13% of the global population. This leads to around 280,000 deaths annually (McManus et al., 2018).

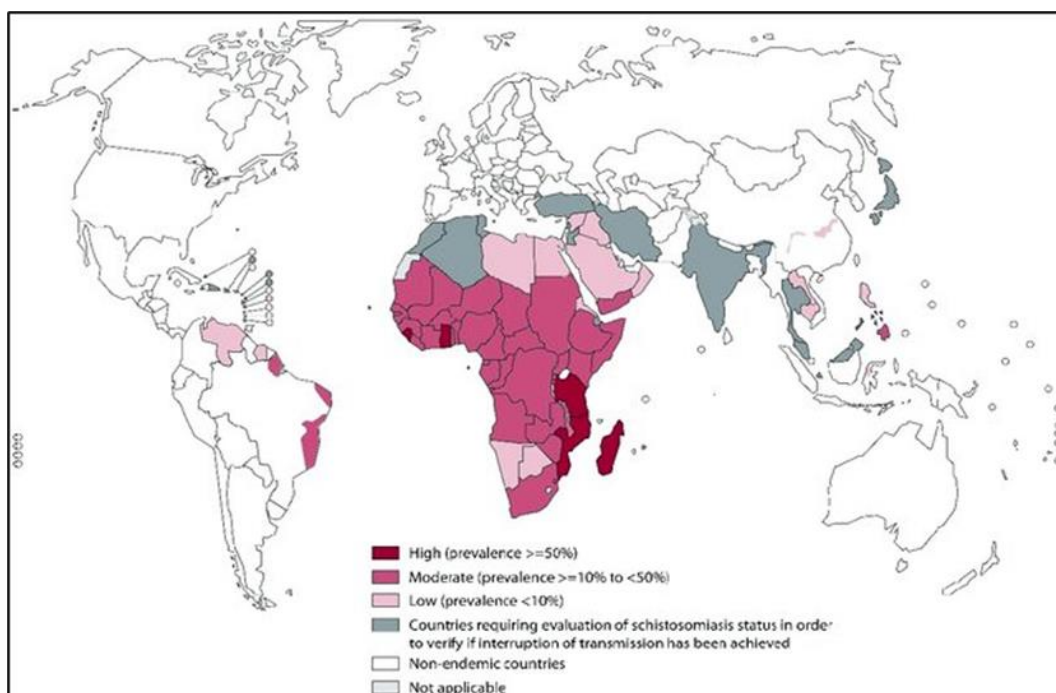


Figure 1-1: Worldwide geographical distribution of schistosomiasis. Adapted from Pal et al. (2022).

Parasitic diseases are more prevalent in areas where the intermediate host snail is in water contaminated by faeces or urine of the infected animals or humans, allowing it to reproduce (WHO, 2021). People who reside in semi-rural and rural areas frequently come into contact with water contaminated by trematode worms (Manyangadze et al., 2016). In communities where people live near one or more bodies of water, the prevalence of schistosomiasis is about 70% due to *S. mansoni* eggs being washed into these waters (Chimbari et al., 2003; Mujumbusi et al., 2023). This may increase the risk of exposure to waterborne diseases in areas due to unsanitary conditions, inadequate sanitation, and a lack of clean water (De Leo et al., 2020). Communities that do not have access to tap water are more likely to contract the disease since they travel to snail-infested water sources for domestic activities such as laundry, bathing, and cooking (WHO, 2021). In addition, in poor rural areas, most cases are linked to agriculture and fishing (WHO, 2021). During their daily activities, fishermen and farmers are in contact with snail-infested water, making them susceptible to schistosomiasis (Sady et al., 2013).

Variations in temperature across seasons in temperate and subtropical regions influence the seasonal abundance of snails and the transmission of schistosomiasis ((McCreesh and Booth, 2013). Water bodies are crucial for transmission, and seasonal rainfall changes are more pronounced on permanent water bodies than on temporary ones (McCreesh and Booth, 2013; Pedersen et al., 2014a). Huang et al. (2020) indicate that seasonal variability hinders endemicity and transmission, making schistosomiasis control measures more feasible in regions with consistent transmission than those with seasonal differences. In addition, temperature and rainfall are major climatic factors contributing to the distribution of *Schistosoma* species (Mangal et al., 2008; Stensgaard et al., 2013; Monde et al., 2016; Yang and Bergquist, 2018). Figure 1-2 illustrates how temperature, rainfall, floods, and droughts can impact the snails' and worms' lifespan and fertility rate during the schistosome life cycle (McCreesh et al., 2015; Adekiya et al., 2019). As a result of temperature changes, chemical reactions in water can increase, aquatic plant photosynthesis and metabolism rates may increase, and parasites may become more active (Mackey et al., 2013). The occurrence and distribution of *Schistosoma*-transmitting snails are closely related to fluctuations in average temperature because their transmission depends on the reproduction and survival of their intermediate hosts (WHO, 2004; Mangal et al., 2008). As intermediate hosts cannot thermoregulate, their survival and reproduction rates greatly depend on the temperature changes that can thus alter schistosomiasis patterns (Kalinda et al., 2017).

In Eastern Africa, studies by McCreesh and Booth (2014), McCreesh et al. (2014) and Adekiya et al. (2019) indicated that increasing temperatures could provide a favourable environment for the proliferation of *S. mansoni* infections. This may result in adverse conditions for intermediate host snails (McCreesh et al., 2014; Adekiya et al., 2019). As a result of a warmer and drier climate, Midzi et al. (2011) and Pedersen et al. (2017) reported that the incidence of schistosomiasis infections in Zimbabwe has decreased over the last three decades. In addition, Zhang et al. (2020) found that snail habitats become larger when ecological conditions become suitable for their growth and reproduction. This is because snail populations can quickly adapt to changing environmental conditions and increase their population size. Schistosomiasis may spread to previously unaffected areas with the spread of *Schistosoma* parasites in warmer locations (Mbabazi et al., 2011; Mutuku et al., 2014).

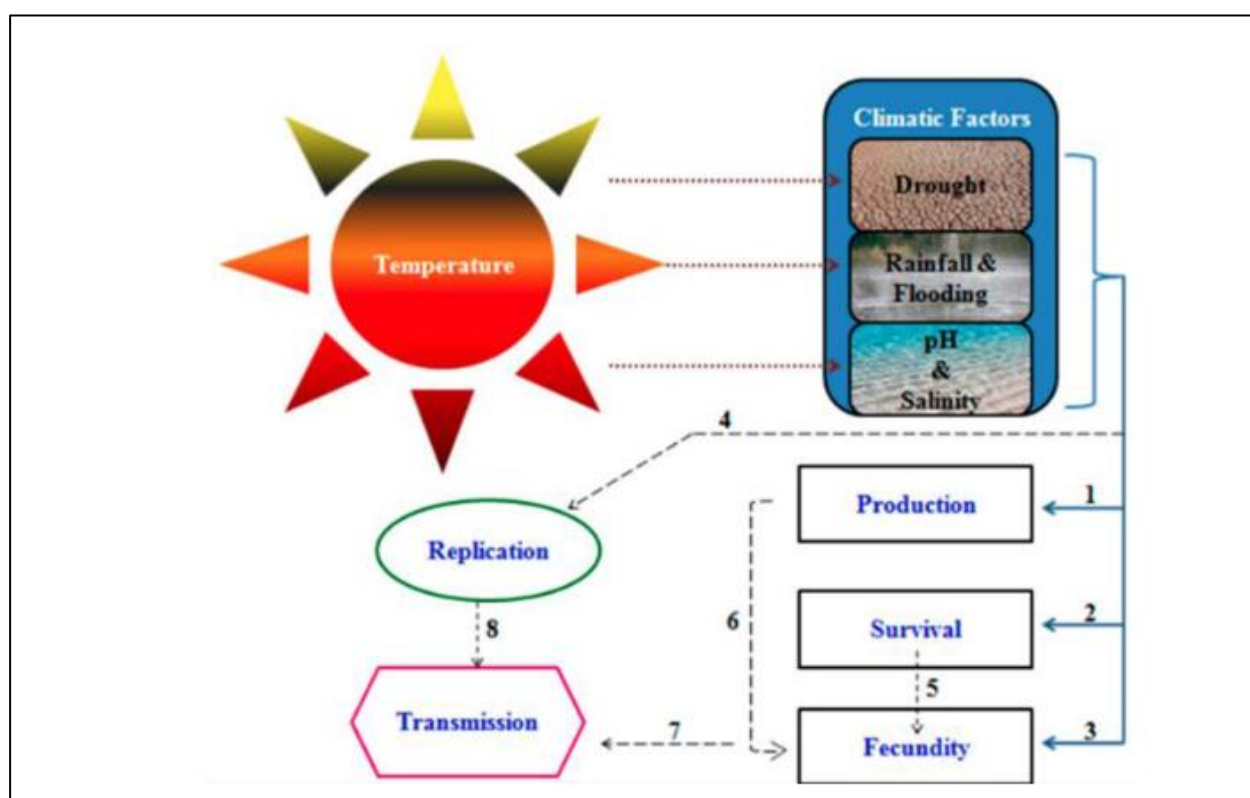


Figure 1-2: The changes in temperature, rainfall, droughts and floods on *Schistosoma* transmission. Source: Adekiya et al., (2019).

Climate change has resulted in changes in precipitation patterns, rising temperatures, and more frequent and severe extreme climate events (such as droughts and floods) (Gulzar et al., 2021). In addition, SA's eastern regions are experiencing severe storms, landslides and flash flooding caused

by changing rainfall patterns (McDonald et al., 2004). Heavy rainfall can result in flooding, reducing water transparency and changing snails' environment. Appleton (1978) found that the speed of water flow plays an important role in the dispersion of snails, as high water velocity during floods makes the host snail vulnerable to movement and food dispersal. De Kock et al. (2004) highlighted how fast-flowing water may limit the distribution of host snails. Snails typically breed in water with laminar flow, and rainfall can fill stagnant water habitats and convert contaminated or unproductive areas into breeding grounds (Suliman et al., 2017). Slow-moving water is preferred over fast-moving water. Hence, the transmission of *Biomphalaria pfeifferi* increases significantly during post-rainy seasons compared to *Bulinus globosus* (Madsen et al., 2011; Guo et al., 2021; Manyangadze et al., 2021). In addition, it has been shown that floods can cause schistosomiasis outbreaks when people are exposed to snail-contaminated water during flooding, increasing their risk of infection with schistosome (Ge, 2004; Hu et al., 2015).

Under moderate climate scenarios, global average surface temperatures will increase between 1.4 and 3.1°C by 2081-2100 (IPCC, 2013). The global hydrological cycle and precipitation patterns will be affected by this warming (IPCC, 2013). These changes will likely impact vector-borne diseases with intermediate invertebrate hosts (Parham et al., 2015). As a result, the likelihood of transmission in any location is influenced partly by abiotic factors that affect free-living organisms and intermediate host organisms such as snails (McCreesh and Booth, 2013). The average yearly temperatures in SA have increased by at least 1.5 times more than the global average of 0.65°C in the last 50 years (Ziervogel et al., 2014; Botai et al., 2018; He et al., 2021). The Department of Environmental Affairs projects a temperature increase of 1°C to 2°C in South Africa's interior and a potential 1°C rise in coastal temperatures between 2015 and 2035. The increase in temperatures creates better conditions for the spread of the parasite and its hosts, increasing the likelihood of schistosomiasis transmission in impacted regions (Stensgaard et al., 2013).

Climate change can be evaluated/quantified using various pathways to predict emission scenarios. In addition to the climate change impacts on the distribution patterns of *Schistosoma*-transmitting snails, the Representative Concentration Pathway (RCP) includes four scenarios that describe greenhouse gas emissions (GHG) and concentrations up to the year 2100, based on assumptions (Meinshausen et al., 2011; van Vuuren et al., 2011). Under the Representative Concentration Pathway, RCP 4.5 and 6 are stabilisation scenarios whereby greenhouse gas concentrations in the atmosphere stabilise by the end of the 21st century due to mitigation efforts. This is added to the thesis RCP 2.6 is a low-emission scenario where GHG emissions peak in 2020 and decline as

populations peak and renewable energy increases (Meinshausen et al., 2011; van Vuuren et al., 2011; Hayhoe et al., 2017). In RCP 8.5, greenhouse gases are expected to increase, creating a 'high emission scenario'. Temperature and precipitation are expected to vary in low and high-emission scenarios, which could affect the geographical distribution of schistosomiasis (Khasnis and Nettleman, 2005).

1.2 Problem Statement

South Africa is located in the sub-Saharan area, which is expected to have the largest number of individuals susceptible to human schistosomiasis due to climate change (WHO, 2021). Historically, schistosomiasis has favoured the northern and northeastern regions of SA. These regions have been classified as humid and subtropical environments where *Schistosoma*-transmitting snails thrive (Magaisa et al., 2015). *Schistosoma* worms can flourish in warmer climates, potentially leading to the emergence of transmission in new areas (De Leo et al., 2020). The rise in temperatures is expanding the habitat suitability for these snails, which may cause the spread of schistosomiasis to areas that were previously unaffected. McCreesh et al. (2015) and Pedersen et al. (2014b) emphasise that climate change will likely impact these worms' distribution and transmission patterns. Climate patterns and projections for SA suggest notable changes, with expected yearly average temperature increases reaching approximately 2°C by 2100 (Engelbrecht et al., 2011; Niang et al., 2014). This temperature increase heightens the vulnerability in SA, which is compounded by poverty, lack of clean drinking water, and unequal access to healthcare (Werakoon et al., 2015). Water and sanitation issues further exacerbate the vulnerability, particularly in South African rural areas where communities lack access to clean water sources. Additionally, rural areas usually lack awareness of this parasitic disease, heightening exposure and susceptibility (Abrams et al., 2021).

The majority of research on the impact of climate change on schistosomiasis is centred on China, even though Africa faces a more significant public health challenge with the disease. Africa's vulnerability to climate change and its limited ability to adapt to its effects exacerbate the situation (Stensgaard et al., 2019). Stensgaard et al. (2019) found that the relationship between climate change and schistosomiasis does not distinguish between parasite species; instead, they focus on the overall impact of the disease. Most of these studies were conducted in China, emphasising *Schistosoma japonicum* and its snail host, *Oncomelania hupensis*. In addition, global studies have examined the impact of climate change on *S. mansoni*, focusing on snail species like *B. pfeifferi*

and *B. glabrata*. However, more research is needed on *S. haematobium* and its host, *Bulinus* species. (Stensgaard et al., 2019). Only two out of twenty modelling studies addressed *S. haematobium*, with one predicting increased potential in Europe and the other noting a decrease in prevalence in Zimbabwe over three decades amidst drier and warmer conditions (Pedersen et al., 2017). In addition, Yang and Bergquist (2018) predicted that between 2021 and 2050, *S. haematobium* will be expanding into central and eastern areas of SA. The lack of focus on *S. haematobium* in past modelling research, along with Yang and Bergquist's (2018) study on its expansion in SA, emphasises the importance of this thesis. Therefore, this study aimed to fill this knowledge gap and improve understanding of the potential impact of climate change on schistosomiasis transmission in South Africa.

1.3 Aim and Objectives

This thesis aimed to investigate the impact of climate change on the spatial distribution patterns of schistosomiasis intermediate host snails in SA. It combines ecological niche modelling with downscaled climate projections to predict future changes. This study used the available data to estimate the historical and predicted future distribution of *Schistosoma*-transmitting snails.

The main objectives of this study were to:

1. Characterise the historical distribution of *Schistosoma*-transmitting snails in South Africa by:
 - a) constructing a digital geospatial database for the intermediate host's historical occurrences,
 - b) identifying key bioclimatic variables that can be used to model the historical and future distribution of *Schistosoma*-transmitting snails, and
 - c) modelling the historical distribution of *Schistosoma*-transmitting snails using ecological niche models.
2. Predict the future distribution of *Schistosoma*-transmitting snails using climate projections by:
 - a) identifying appropriate climate change scenarios,
 - b) building on the existing ecological niche models using the CMIP5 model outputs to refine predictions of snail distribution under future climate scenarios, and

- c) modelling the future distribution of *Schistosoma*-transmitting snails.
3. Examine the impacts of climate change on the predicted distribution of *Schistosoma*-transmitting snails in South Africa by:
- a) calculating the quantitative differences in habitat suitability using the historical and predicted output of *Schistosoma*-transmitting snails,
 - b) creating suitability maps to illustrate the spatial patterns of change in habitat suitability of *Schistosoma*-transmitting snails, and
 - c) evaluating the potential changes of suitable areas of *Schistosoma*-transmitting snails under different climate scenarios.

1.4 Motivation for the study

There are currently no control programmes for schistosomiasis in SA (Appleton and Miranda 2015). Modelling future distributions of *Schistosoma*-transmitting snails is necessary for identifying mitigation and response strategies. Despite this, few efforts have been made to predict how climate change will affect the spread of schistosomiasis, and the results have been inconsistent (Stensgaard et al., 2013). In some studies, transmission rates have been reported to increase in colder areas such as South Africa and the Ethiopian highlands (Martens et al., 1997; Zhou et al., 2008; McCreesh et al., 2015; De Leo et al., 2020). In contrast, Martens et al. (1997) and Stensgaard et al. (2013) found a contraction of transmission and geographical shifts due to climate change. The contradictory results indicate that the link between climate change and schistosomiasis transmission is intricate and can differ based on local environmental factors and other variables. (Mangal et al., 2008). Further research is needed to understand these dynamics better and develop predictive models for the future distribution of *Schistosoma*-transmitting snails.

Examining projected changes in rainfall, temperature shifts, and other climatic factors is important to understand how climate change may affect schistosomiasis. Ecological Niche Models (ENMs) that predict the effects of climate change on the distribution of schistosomiasis may provide insightful information on regions that are likely to become suitable for the transmission of schistosomiasis (McCreesh and Booth, 2013). However, ENMs often do not include future climate predictions, creating a gap in understanding climate change effects on schistosomiasis beyond temperature (McCreesh and Booth, 2013). Even though future climate predictions have been tried and

tested in numerous studies across African countries such as Ethiopia, Uganda, Tanzania and Zimbabwe (Kristensen et al., 2001; Stensgaard et al., 2006; Stensgaard et al., 2013; Pedersen et al., 2014a), few climate studies focused on SA. Identifying the impacts of climate change on the distribution and transmission of schistosomiasis in SA remains unclear, as it has proven to be complex. This study used ENMs with climate projections from GCMs to create high-resolution maps for SA for the first time in this field, indicating areas that will exhibit an increase or decrease in transmission and where new infections may occur.

1.5 Study design and thesis outline

The study was classified as a minimal-risk study. The Faculty of Natural and Agricultural Sciences (FNASREC) Ethics Committee approved on 25 November 2021. The ethics number assigned to this study is NWU-0131321-A9.

This thesis is presented in the traditional format and comprises the following chapters:

Chapter 1 provides an introduction, outlining the background of schistosomiasis, its relationship with climate change, and the study's significance, aims, and objectives.

Chapter 2 reviews existing literature on schistosomiasis prevalence in sub-Saharan and South Africa, factors affecting its distribution, and the influence of climate change on its intermediate host snails and modelling the distribution of schistosomiasis.

Chapter 3 describes the study area in detail. The chapter also explains the data and methodology for each objective.

Chapter 4 presents the findings and discussion on historical distribution modelling of *Schistosoma*-transmitting snails.

Chapter 5 discusses the results of predicting the future distribution of these snails using climate and ecological niche models.

Chapter 6 examines the effects of climate change on the predicted distribution of *Schistosoma*-transmitting snails'.

Chapter 7 summarises the study and its conclusions, as well as the limitations of the study.

CHAPTER 2

This chapter provides a comprehensive review of key elements relevant to the study. It aimed to lay a solid foundation for the research by understanding the distribution of schistosomiasis in Sub-Saharan Africa and SA, the factors governing the distribution of schistosomiasis and the impact of climate change on the distribution of *Schistosoma*-transmitting snails. This is vital because climate change has the potential to change environmental conditions and affect transmission dynamics. The last section of the literature review examines modelling approaches from previous studies, which inform the methodology chosen for this thesis, ensuring it advances existing knowledge.

LITERATURE REVIEW

2.1 Schistosomiasis in Sub Saharan Africa

Schistosomiasis, also known as bilharzia or bilharziasis, is a disease caused by parasitic *Schistosoma* worms transmitted through freshwater snails and it primarily resides in human bloodstreams (Gryseels et al., 2006; Steinmann et al., 2006). The World Health Organisation classifies it as a neglected tropical disease and notes that it represents a significant portion of the tropical disease burden, excluding malaria (Olveda, 2013). There is a lower global prevalence of schistosomiasis because they have relatively restricted geographic ranges, further limiting their geographic distribution. Most studies conducted on schistosomiasis are primarily focused on sub-Saharan Africa, highlighting its prevalence in poor rural communities with inadequate healthcare systems and limited access to clean water (Chipeta et al., 2013; Adenowo et al., 2015; Hudu and Umar, 2019). The most common and severe cases of schistosomiasis are found in children, adolescents, and young adults in sub-Saharan Africa, with the highest rates of infection and death (Hotez and Kamath, 2009). *Schistosoma haematobium* is responsible for about two-thirds of these cases and is a leading cause of serious urinary diseases. Despite treatment efforts, the disease's prevalence remains high in sub-Saharan Africa, with millions suffering from symptoms and chronic complications (Adenowo et al., 2015). *Schistosoma mansoni* is the parasite responsible for intestinal schistosomiasis, infecting approximately 54 million people each year and leading to considerable mortality and morbidity. This trematode is widespread in sub-Saharan Africa and the Middle East, and it spread to South America during the transatlantic slave trade (Anderson and Enabulele, 2021).

The history of schistosomiasis in Africa dates back over 4000 years, with early evidence found in ancient Egyptian writings and *S. haematobium* eggs in mummies from 1250–1000 BC. (Ruffer, 1910; Mahmoud, 2001; Sarant, 2017; Kayuni et al., 2019). Symptoms included various urological issues that could have been mistaken for other illnesses. (Cox, 2002; Di Bella et al., 2018). Notably, there were observations of persistent blood in the urine among Napoleon's troops in Egypt in 1798 and soldiers in the Boer War (Cox, 2002). Theodore Bilharz was the first to officially identify the *Schistosoma* parasite in 1851. The term "Bilharzia" was later coined for these parasites, and the disease was named Bilharzia as a patronymic to honour Dr. Bilharz. (Siebold, 1856; Di Bella

et al., 2018). Sir Patrick Manson proposed the idea of humans being infected by various *Schistosoma* species in 1902. This was later validated in 1915 when *S. mansoni* was identified as a distinct species by Louis Westenra Sambon (Chernin, 1983).

The prevalence of *Schistosoma* infection remains alarmingly high in certain African regions, even though there has been significant progress in decreasing and managing schistosomiasis globally (Adekiya et al., 2019). Schistosomiasis remains a significant health concern, especially in sub-Saharan Africa, where *S. haematobium* is the most common, affecting around 112 million people (WHO, 2021). This region often sees co-infections of *S. haematobium* and *S. mansoni* (Figure 2-1) (WHO, 2021). Nigeria has the world's highest schistosomiasis rates, with both species present since the 19th century (Dawaki et al., 2015). While urogenital schistosomiasis is widespread, *S. mansoni* is less common and more localised (Ezeh et al., 2019). Tanzania ranks second in African schistosomiasis cases, with both species endemic and *S. haematobium* being more dominant, particularly in coastal regions (Brooker and Clements, 2009; Rollinson et al., 2013; Mazigo et al., 2012), whereas *S. mansoni* is concentrated around large water bodies like Lake Victoria (McCullough, 1972; Clements et al., 2006; Brooker and Clements, 2009). The entire population of Tanzania is at risk due to the disease's distribution (Mazigo et al., 2012). The Democratic Republic of Congo and Ghana are tied for the third-highest schistosomiasis cases in Africa, with three endemic species (Hotez and Kamath, 2009). Over the past six decades, the disease has expanded from endemic to new areas in Ghana (Rimon and Hotez, 2013; Madinga et al., 2015).

Around 12.7 million individuals in North Africa and the Middle East are impacted by schistosomiasis, with Egypt experiencing a decrease in cases as a result of control measures (Hotez et al., 2012). In Uganda, the focus has shifted to *S. mansoni* due to its rising prevalence, with *S. haematobium* being less common (Emmanuel and Ekkehard, 2008). Ethiopia has a high prevalence of *S. mansoni*, with recent surveys showing a wide range of prevalence rates (Aula et al., 2021). Mozambique, like Tanzania, has both species but a higher prevalence of *S. haematobium*, whereas *S. mansoni* is more prevalent in Tanzania (Aula, 2021). The invading parasites in Botswana are *S. mansoni* and *S. haematobium*, with prevalence rates fluctuating depending on rainfall. The prevalence of schistosomiasis in Botswana has been as high as 80% or as low as 20% in defined geographical areas (Appleton et al., 2008). While some regions, like Japan and Tunisia, have eradicated the disease, others are working towards control and elimination (Utzinger et al., 2009). Recently, urinary schistosomiasis, caused by *S. haematobium*, has been reported in Corsica, France,

a place not previously affected, presumably brought over by individuals from West Africa (Boissier et al., 2015; Boissier et al., 2016).

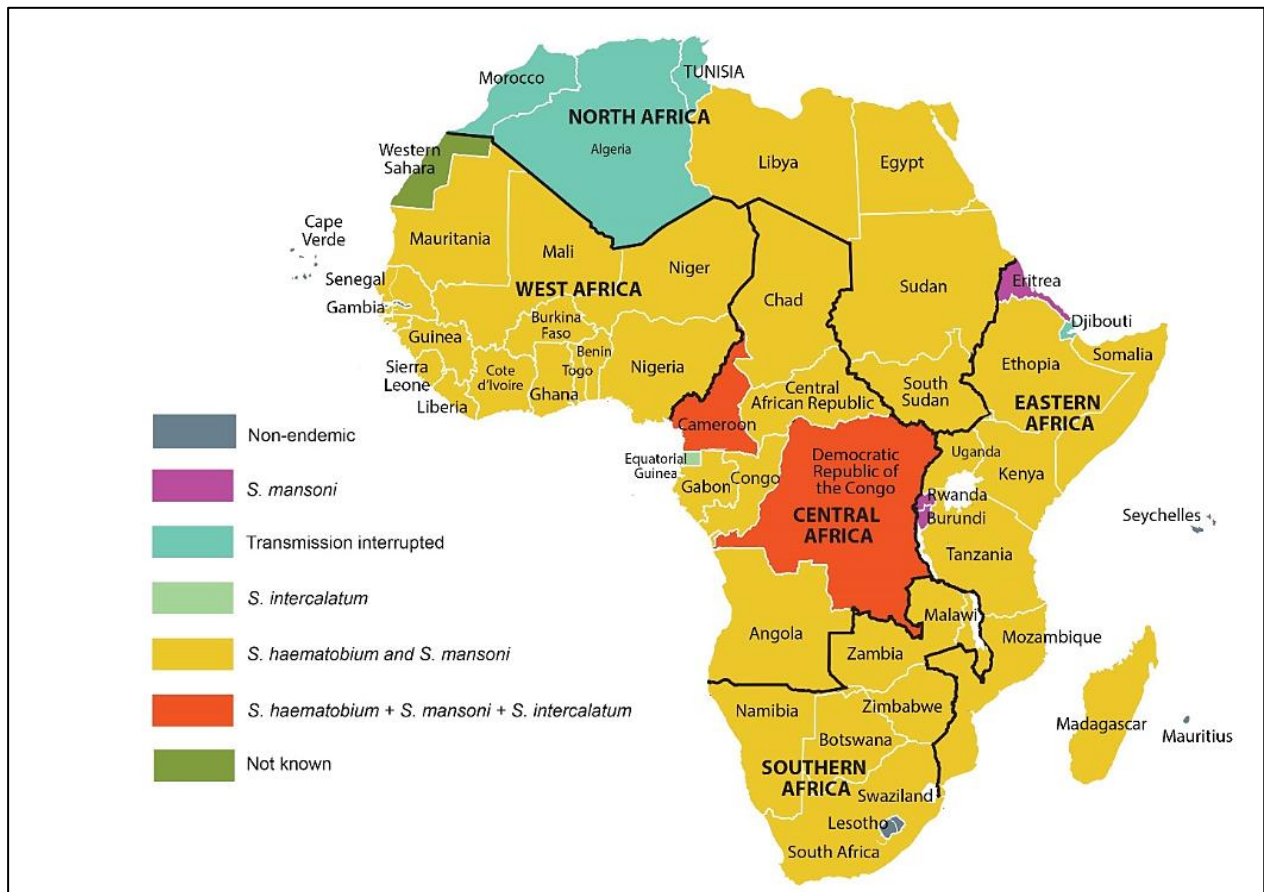


Figure 2-1: Distribution of *Schistosoma* infections in Africa. Source: Aula et al., 2021.

2.1.1 Control measures and mitigation strategies

Praziquantel is widely used to control schistosomiasis (Rollinson et al., 2013). It is administered as preventive chemotherapy to at-risk populations, and given to people who may be infected with *Schistosoma* without confirming the diagnosis through individual testing (McManus et al., 2018). Despite its effectiveness, praziquantel alone is insufficient to eliminate schistosomiasis due to high reinfection rates, potential drug resistance, lack of immunity, and its partial efficacy against immature parasites (McManus et al., 2018). The disease's impact on public health is significant, with estimates of the global burden ranging from 1.7 to 4.5 million disability-adjusted life years, reflecting not only the direct effects of the infection but also associated conditions like undernutrition and anaemia, particularly in children (Utzing and Keiser, 2004). Molluscicides are another way to reduce snail populations, but they rarely eliminate them because the snails return to their habitat

(Zheng et al., 2021). Continuous and long-term application of the chemicals is necessary. It effectively eliminated the disease in Morocco and Japan and was employed in control efforts in Egypt and China (Utzinger et al., 2009). However, its impact on fish and other aquatic organisms is a major ecological and economic risk. Plant-based substances such as Endod and biological methods using snail competitors are considered alternatives to chemical molluscicides (Zheng et al., 2021). Several studies have used mathematical modelling to find effective and cost-efficient strategies for managing schistosomiasis. Zhang et al. (2007) created a partial differential equation model for human schistosomiasis, focusing on treatment strategies based on infection rates in different age groups. In addition, Liang et al. (2007) concentrated on site-specific schistosomiasis transmission in China, emphasising the importance of control strategies such as snail control, chemotherapy, and egg control to reduce population dynamics. Makinde and Okosun (2011) discussed the impact of chemotherapy on controlling malaria dynamics, considering factors like infected immigrants and insecticide use. However, none of these works considered the role of adequate provision of basic amenities on the spread of malaria and the challenge faced due to drug resistance.

2.1.2 Life Cycle of human *Schistosoma* spp

The life cycle of the *Schistosoma* species involves both intermediate and definitive hosts. Eggs are released into the bloodstream and, depending on species, they find their way to the urinary bladder or intestines (where they cause bleeding pathology), from where they are shed into the environment through urine or faeces (Coon, 2005). These eggs reach freshwater bodies, hatching and releasing miracidia (Mawa et al., 2021). The miracidia then infect specific freshwater snail species, acting as intermediate hosts. Inside the snails, the miracidia develop into sporocysts and release numerous cercariae (Coon, 2005). The cercariae are shed into the water, actively seeking human hosts (Lu et al., 2021; Mawa et al., 2021). Once in contact with human skin, the cercariae enter the bloodstream, transforming into *schistosomulae* and migrating to the liver. In the liver, the *schistosomulae* mature into adult male and female worms, which mate and migrate to their final sites in the venous system, as illustrated in (Figure 2-2) (Nelwan, 2019). The female worms produce eggs, completing the life cycle when the eggs are excreted in human urine or faeces (Lu et al., 2021).

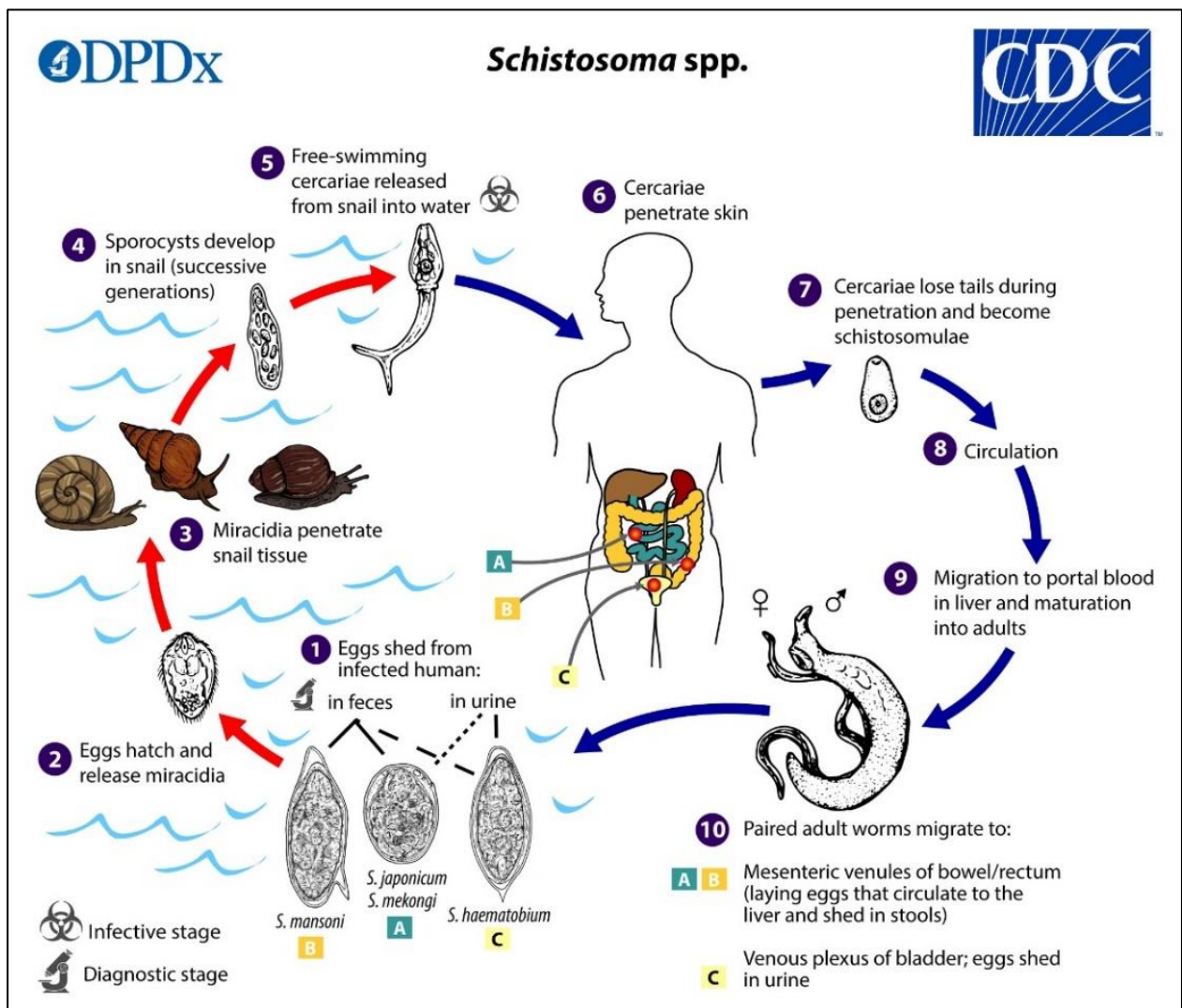


Figure 2-2: The life cycle of *Schistosoma* spp. Source: CDC, Division of Parasitic Diseases and Malaria, 2018.

2.1.3 Prevalence of schistosomiasis in South Africa

Urogenital schistosomiasis in SA was first identified in 1863 by Dr J Harley, a general practitioner in Port Elizabeth. He observed the disease in young males from Uitenhage, Eastern Cape, after the discovery of *S. haematobium* by Bilharz in Egypt in 1851 (Rabello, 1997; Appleton and Naidoo, 2012). Subsequent case studies from 1864 to 1899 highlighted infections predominantly in boys aged 3 to 16 in the Eastern Cape, contracted through activities like swimming in contaminated waters such as open pools, farm dams, and irrigation channels, with blood in urine being a frequent symptom (Appleton and Naidoo, 2012). By 1934, comprehensive data had been compiled, creating the inaugural map detailing the disease's geographical spread in SA, based on information from the 1860s to 1932 and released in 1938 (Porter, 1940). Studies and surveys conducted after the

initial map's release, using data from the 1950s to the late 1970s, led to the creation of the Atlas of Bilharzia in SA by Gear and colleagues. This atlas closely resembled Porter's 1938 map (Porter, 1940; Gear et al., 1980), as illustrated in (Figure 2-3).

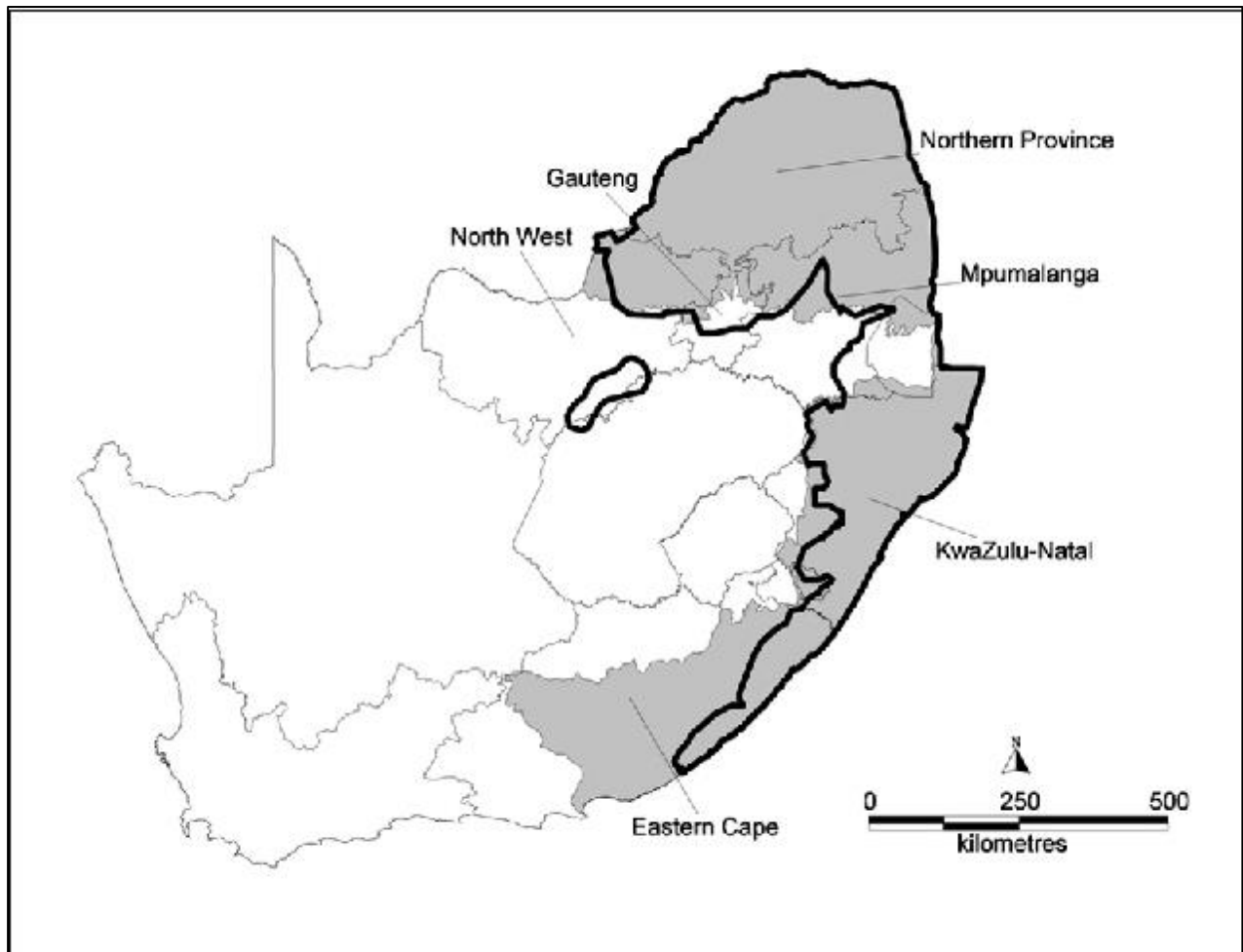


Figure 2-3: A map showing South Africa's areas where schistosomiasis is commonly found. The shaded areas are the places mapped in the 1940s (Porter, 1940), and solid black lines on the map were mapped in the 1980s by Gear et al. (1980).

Schistosomiasis has been well-documented, and five schistosome trematode species infect humans. The three main schistosome species that infect humans are *Schistosoma haematobium*, *Schistosoma japonicum* and *Schistosoma mansoni* (Sady et al., 2015). *Schistosoma haematobium* mainly affects urogenital organs, and the other species are responsible for intestinal schistosomiasis (WHO, 2021). Two of the five *Schistosoma spp* are commonly found in SA. *Biomphalaria pfeifferi* is the vector for *S. mansoni* and is responsible for rectal and intestinal schistosomiasis. *Bulinus africanus* and *Bulinus globosus* are vectors of *S. haematobium*, causing urinary schistosomiasis. These immediate host snails are tropical as they are predominantly found in regions that

are mild to warm (15-25°C) with moderate to high rainfall events (300-900mm/a) (de Kock et al., 2004). Schistosomiasis-transmitting snails are found in areas that provide ideal habitats for intermediate hosts. This includes the warm and tropical northeastern part of SA, such as the eastern and northern regions of the Gauteng and North West provinces, most of Kwa-Zulu Natal, Mpumalanga and Limpopo provinces and parts of the Eastern Cape province (Porter, 1940; Moodley, 2003; Appleton and Naidoo, 2012).

Schistosomiasis is mainly concentrated in the northeastern part of SA, impacting approximately 25% of the population, with *S. haematobium* being the most prevalent type (Appleton and Miranda, 2015). In 2006, Wolmarans et al. (2006) indicated that the parasitic disease was endemic in 3 provinces in SA: Limpopo, KwaZulu-Natal and Mpumalanga, while Kabuyaya et al. (2017) extended its range to the North West, Gauteng, and Eastern Cape provinces, with an estimated prevalence of about 70%. Schistosomiasis is a significant public health issue in SA, with approximately 4 million people infected. An estimated 2 to 3 million children in the country have been affected by the disease, and 40% of the population is vulnerable to contracting it (Appleton and Miranda, 2015).

Schistosomiasis is most common among poor rural populations, especially agricultural communities (WHO, 2021). In rural communities, lack of water is a major contributor to the transmission of waterborne diseases such as bilharzia. An estimated 5 million people in poor rural areas in SA do not have access to clean water (Hove et al., 2019). Hence, these communities are at risk of contracting schistosomiasis and they include agricultural workers, fishermen, miners, women engaging with water during domestic chores, and children playing in the water (Wolmarans and De Kock, 2009; Magaisa et al., 2015; Adenowo et al., 2015). Moreover, domestic activities such as fetching water or washing clothes in infected water put women and children at risk of infection (Adenowo et al., 2015). Females, mostly in rural areas, use water from rivers, dams and lakes nearby to do such domestic activities, and children play in these open water sources, thus putting them at risk of infection (McManus et al., 2018). This is because most infections for schistosomiasis occur when humans come into contact with contaminated water. Lack of access to piped water, adequate health care systems and proper hygiene also make children vulnerable to parasitic diseases (Magaisa et al., 2015). *Schistosoma haematobium* and *S. mansoni* are highly prevalent during heavy rainfall as faecal material is washed down to water bodies through surface runoff (Appleton and Madsen 2012). The infection occurs through direct contact of humans with freshwater bodies

inhabited by infected hosts of the parasites. These parasites, in turn, penetrate the human skin and cause infection (Secor, 2015).

Research conducted in SA, utilising patient urine and stool sample data from the National Health Laboratory Service, between 2011 to 2018 revealed that nearly all patients, 99.8%, had infections caused by *S. haematobium*, while a minor fraction, 0.2%, were affected by *S. mansoni* (De Boni et al., 2021). The study also reported that among 135,272 recorded cases, the highest number was in Kwazulu-Natal with 54,177 cases, followed by Limpopo with 38,822, Mpumalanga with 28,205, and the Eastern Cape with 9,385 (De Boni et al., 2021). A map visually representing these statistics (Figure 2-4) demonstrates the spread of the disease to yet another province (Western Cape).

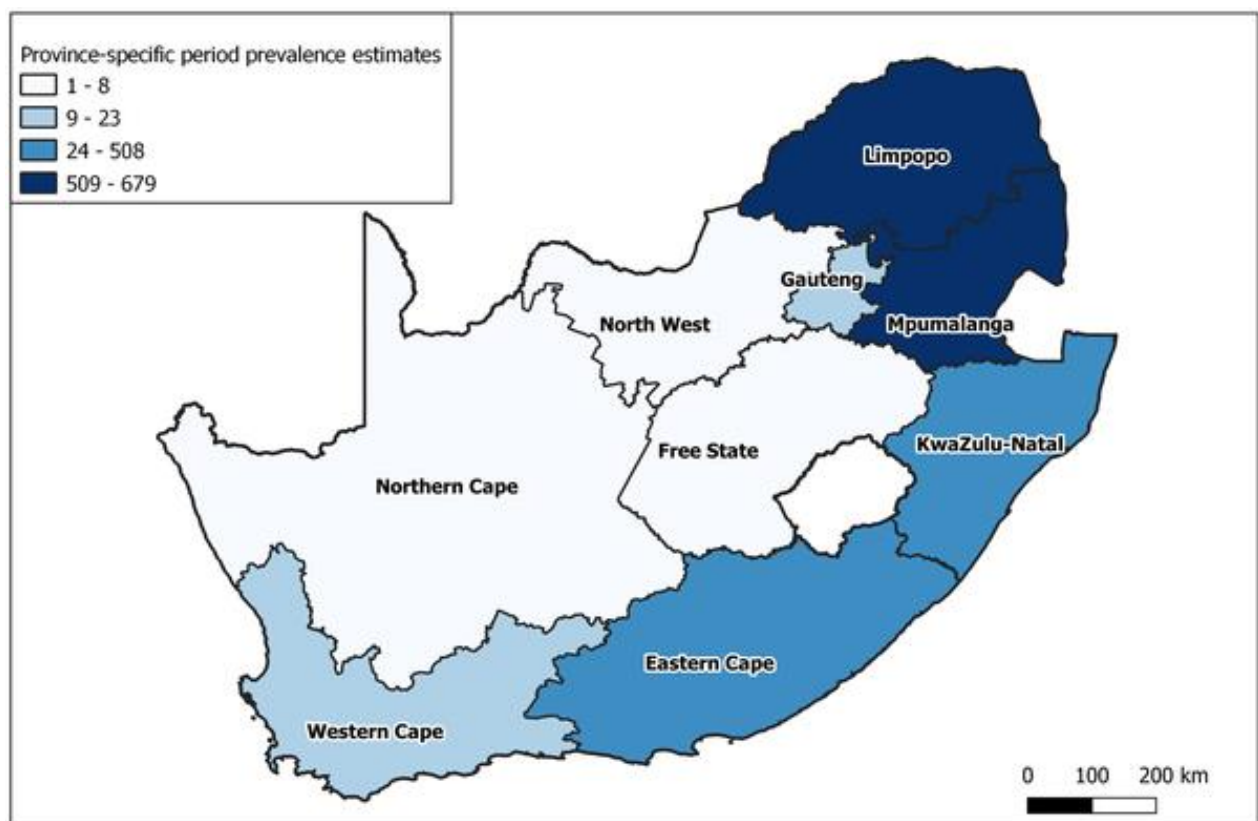


Figure 2-4: The prevalence estimates for each province in South Africa. Source: (De Boni et al., 2021).

2.1.4 The spatial distribution of the intermediate host snails in South Africa

Spatial and temporal spreading or distribution of intermediate host snails is essential in identifying the distribution of schistosomiasis (Manyangadze et al., 2016). This means that the distribution or movement of the intermediate host snail species across a geographical area over some time can be

used to determine the distribution pattern of schistosomiasis. Pedersen et al. (2014a), in a study that was conducted in Zimbabwe, also agreed that the distribution of parasitic infections is reliant on the presence of the respective intermediate host and that the distribution of the snail species is crucial because it provides information on the distribution of the disease. This means that the snail can provide information on the type of blood fluke species and how it may be geographically distributed. Therefore, to understand and explain the distribution patterns of some of the mentioned blood fluke species in SA, it is essential to understand the distribution patterns of the intermediate host snail species in SA.

The intermediate host snails are mainly found in the eastern and northern regions of SA, comprising provinces such as Mpumalanga, Limpopo, and Kwa-Zulu Natal (de Kock et al., 2004). Some isolated species have been observed in Gauteng and the North-West Provinces (de Kock et al., 2004). Tropical conditions and high rainfall influence the distribution pattern of snail species. Two species, *B. africanus* and *B. globosus*, act as intermediate hosts for *S. haematobium*. *Bulinus africanus* is better adapted to temperate and subtropical climates in the southern regions of SA, including the Kromme River in the Eastern Cape, while *B. globosus* thrives in warmer northern and northeastern areas. (Figure 2-5; Appleton and Miranda, 2015). A study by de Kock and Wolmarans (2005) showed that the *B. africanus* distribution is dispersed along Eastern and Southern Africa. Joubert et al. (1984) and Wolmarans et al. (2006) noted that the distribution of *B. africanus* highly depends on minimum or maximum favourable temperature conditions. This further determines the geographical distribution of the *Bulinus spp* group (Joubert et al., 1984).

Bulinus africanus can be found in the highveld regions of the Free State, Gauteng, and North-West Provinces (de Kock and Wolmarans, 2005; Figure 2-5). De Kock and Wolmarans (2005) reported that it is due to the ability of this species to survive in areas with constant low temperatures. The snail species is a good aestivator but struggles due to its temporary habitats and limited ability to reproduce even in ideal conditions (Brown, 1994). This would primarily result in fluctuating population numbers, resulting in species survival depending on rainfall during a particular season and a period without surface water (Brown, 1994). De Kock and Wolmarans (2005) agreed that this rainfall could cause the unstable presence and irregular appearance of *B. africanus* snail populations in the Free State and North West provinces. The existence and survival of *B. africanus* require an area with open-source water bodies and moisture because they are aquatic. Such habitats are where they can survive, reproduce, and carry schistosomes from an early stage in the form of miracidia after being excreted by humans through urine or faeces into open-source water or an

area with moisture. De Kock and Wolmarans (2005) indicated that *B. africanus* has a significant distribution from the western parts of the North West to various provinces in SA and near coastal areas of the Eastern Cape Province. The distribution of snails is also determined by the environmental conditions in which the snails are located. As mentioned previously, temperature and rainfall play a critical part in the determination of the geographical distribution of this group. Around 70% of the habitats of the *Bulinus spp* group can be found in slow-moving water or stagnant water sources in SA (de Kock and Wolmarans, 2005).

Bulinus globosus is confined to the subtropical zones, including Limpopo Province, parts of Mpumalanga, and the northeastern regions of KwaZulu-Natal and Eswatini. According to Joubert et al. (1984), among the two snail species, *B. africanus* can survive at constant low temperatures compared to *B. globosus*, which can survive at constant high temperatures. The optimum temperature conditions of each snail species further support this statement. The ideal or optimum temperature range for *B. africanus* is between 23°- 26°C while *B. globosus* preference ranges from 26°- 29°C (De Kock, 1973). It is also reported that both intermediate host snail species prefer water bodies with low water velocities of 0.3 ms⁻¹, similar to *B. pfeifferi* (Frank, 1966; Appleton, 1975). However, intermediate host snail species can also be found in areas with fast-flowing water. This is due to rivers containing boulders where the bedrock is hard, which shelters the snail species populations from the current velocity above their threshold (Brown, 1994). In addition, recent experimental studies have shown that aquatic environmental factors, which influence snail density and food resources (such as periphyton on surfaces), can affect cercarial production per snail and potentially human exposure risk (Haggerty et al., 2020). Aquatic vegetation offers extensive surface-area snail habitats, supporting periphyton growth (attached algae and biofilms). Therefore, submerged aquatic vegetation may have resource-dependent, bottom-up ecological effects that could impact snail population growth and cercarial production per infected snail (Vivas Muñoz et al., 2018).

Biomphalaria pfeifferi (Figure 2-6) is found in various regions, including the Limpopo Province, the Lowveld and middleveld of Mpumalanga, the north-eastern area of the North West Province, and the eastern half of KwaZulu-Natal (de Kock et al., 2004). The absence of *B. pfeifferi* in the Western Cape and Free State provinces is attributed to the cold winter climate in those regions. (de Kock et al., 2004). The absence of *B. pfeifferi* in the wetlands on the coastal plains of the KwaZulu-Natal is attributed to the high temperatures in those areas (Appleton and Madsen, 2012). Snail species take oxygen from the air rather than the water (Appleton and Miranda, 2015). In

addition, the intermediate host snail species favour various water bodies within the temperature range 20°C and 25°C, areas with a low velocity of about 0.3 ms⁻¹ (de Kock et al., 2004). Appleton and Stiles (1976) state that *B. pfeifferi* can be found in many isolated and small rugged rock outcrops surrounded by large areas of seemingly unsuitable soft rocks. In addition, De Kock et al. (2004) found that *B. pfeifferi* is usually found in various isolated and small hard rock formations, typically surrounded by extensive areas of unsuitable soft rocks. It is suggested that during earlier periods of rainfall, the snail occupied widespread areas that currently survive as the relict population in scattered and suitable habitats (Appleton and Stiles, 1976). One example of the suggestion would be the occurrence or the development of a persistent population of *B. pfeifferi* snail species in Taung, a small town in the North West Province of South Africa. (Appleton and Stiles, 1976). A study in 2010 reported a high prevalence of schistosomiasis among schoolchildren in the Eastern Cape Province, suggesting the need for further research to understand the disease's impact in that area and to predict the future distribution of *B. pfeifferi* in SA (Meents and Boyles, 2010; Appleton and Miranda, 2015).

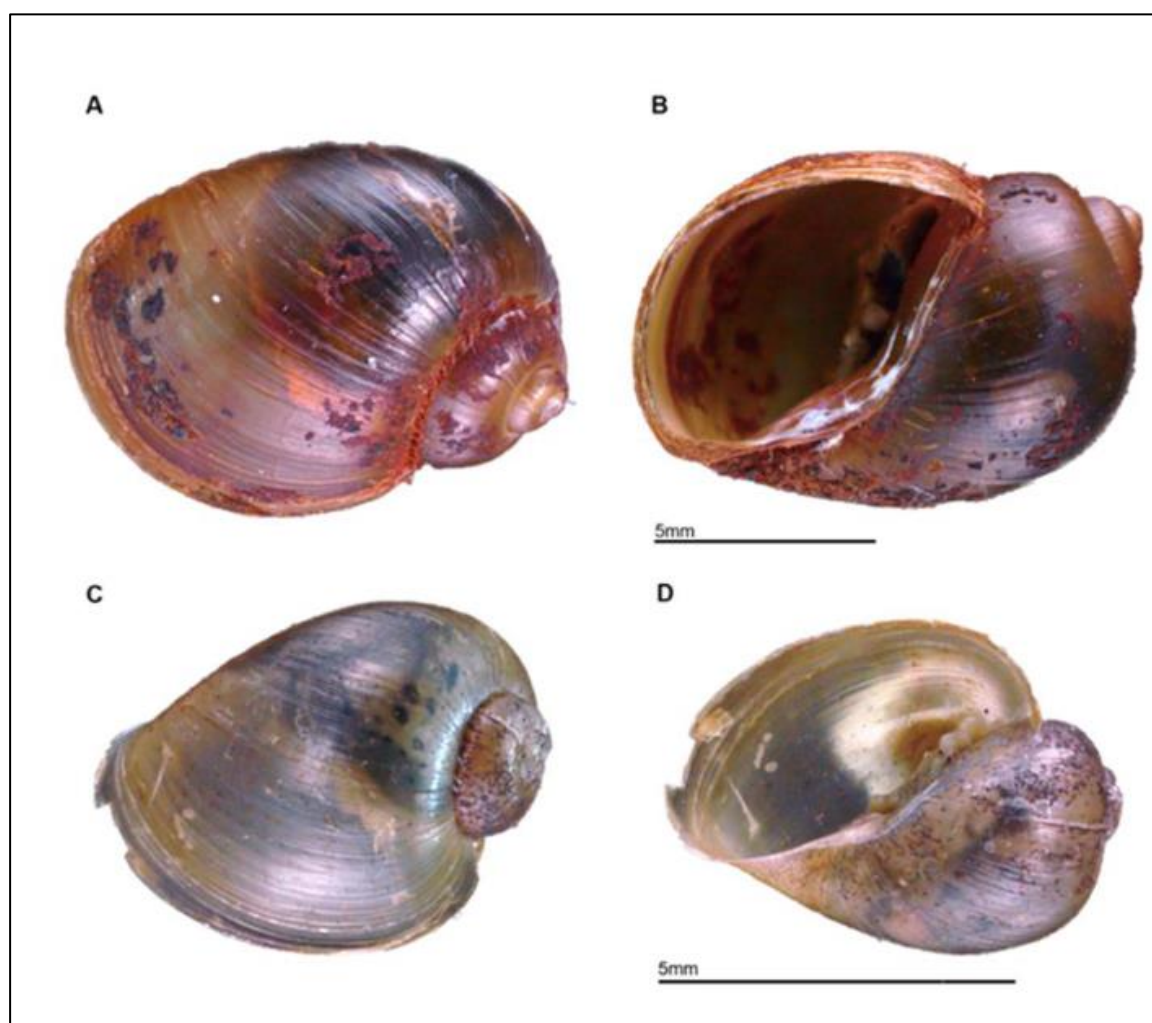


Figure 2-5: Shell morphology of *Bulinus* spp. (Photo Credit: M.H. Le Roux).

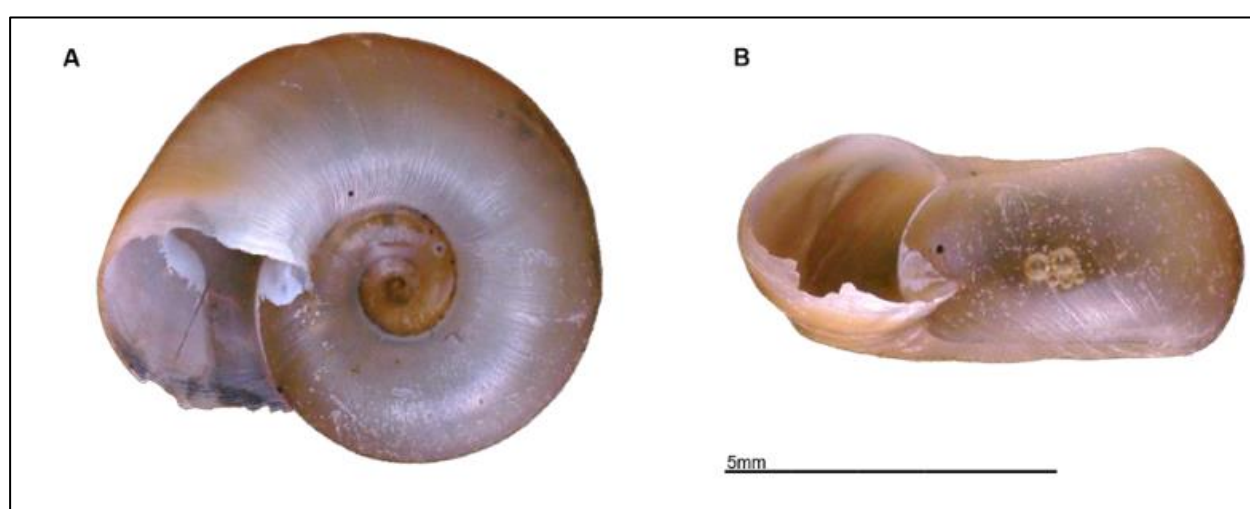


Figure 2-6: Shell morphology for *Biomphalaria pfeifferi* (Photo Credit: M.H. Le Roux).

2.2 Factors governing the distribution of schistosomiasis

The distribution of schistosomiasis is governed by various factors such as climate (e.g. rainfall, temperature, floods and droughts), socioeconomic status, and proximity to water sources (Brooker et al., 2002; Adenowo et al., 2015). Human activities like building irrigation systems, dams, and reservoirs have influenced the habitats of snails, which in turn has impacted the transmission of schistosomiasis in areas where the disease is prevalent (Fenwick et al., 2006; Stensgaard et al., 2013). Dam construction in sub-Saharan countries has been associated with increased urinary schistosomiasis cases (Olveda, 2013). More than 100 million individuals living near large dams or irrigation areas are at risk of schistosomiasis (Steinmann et al., 2006). Additionally, in Zambia, local practices like cassava farming and cattle rearing influence schistosomiasis transmission, with human-induced changes in water chemistry and flow also playing a crucial role (Monde et al., 2016). The population dynamics of snail hosts in SA are mainly influenced by temperature, rainfall, and habitat stability (Appleton, 1978; Sturrock, 1993; Brooker, 2007).

Additionally, certain habitat features, including silt, organic matter breakdown, and vegetation, are linked to the infectivity of snails (Coelho et al., 2021). These aspects are instrumental in forming schistosomiasis hotspots and altering water quality, influencing the habitat suitability for both snails and parasites. Hence, the habitat suitability for the intermediate host snail species, including *B. pfeifferi*, *B. africanus* and *B. globosus* in SA, is determined by climatic and biotic factors that should be considered when determining their distribution.

2.2.1 Environmental Factors

The spread of schistosomiasis is significantly influenced by environmental conditions that impact the snail hosts, such as temperature, rainfall, water pH, vegetation and water velocity. The disease's prevalence and geographic spread are affected by climate change (Adekiya et al., 2019). Climate change impacts aquatic ecosystems, altering the patterns of transmission and distribution of water-related diseases like schistosomiasis (Adenowo et al., 2015). In addition, studies suggest that temperature and precipitation have contributed to changes in water availability (Stocker, 2013; Adekiya et al., 2019). As temperatures increase, the water in waterbodies can become stagnant and provide a breeding ground for the parasites that cause the disease (Stocker, 2013; Stensgaard et al., 2013; Adekiya et al., 2019). Climate variations are anticipated to greatly affect the dynamics between pathogens and their hosts, including increased stress on hosts due to environmental

changes and expanded host ranges that may lead to higher transmission and parasite exposure rates (Cohen et al., 2018). The relevant factors and their optimal conditions for the distribution of the intermediate hosts are shown below in Table 2-1.

Table 2-1: Environmental factors and their optimal conditions influencing the distribution of schistosomiasis.

Environmental Factors	Species	Optimum conditions for snail species	Importance of the related factor to Schistosomiasis	Reference
Water velocity	All three species	Less than 0.3m/s	Water velocity greater than the suggested can sweep and dislodge the intermediate host snail species.	(Appleton and Madsen, 2012; Walz et al. 2005; Sulieman et al., 2017).
Temperature	<i>B. africanus</i> <i>B. globosus</i> <i>B. pfeifferi</i>	19°C - 25°C 23°C - 30°C 20°C - 27°C	Influences the fecundity, growth distribution and survival rate of the snail species.	(Shiff and Husting, 1966; Shiff and Garnett, 1967; de Kock and Van Eeden, 1984; Walz et al. 2015; Sulieman, et al., 2017).
Water chemistry/quality	All three species	Low pH and less concentration of certain ions (e.g. Sodium), less polluted waters.	Low PH in water and refuse from factories may directly harm snails. They are highly abundant in water that is polluted by human excrement.	(Walz et al. 2015; Sulieman, et al., 2017; Letlaila et al., 2024).
Vegetation	All three species	Availability of Marginal, broad-leaved, aquatic, and floating vegetation.	They provide snails with sheltered niches that they favour and provide substratum for intermediate hosts to lay eggs and feed.	(Appleton and Madsen, 2012; Appleton and Miranda, 2005; Walz et al. 2015).
Desiccation/Aestivation	All three species	~30-50 days	It can be described as a survival strategy for dealing with arid conditions, enabling them to survive out of water for weeks, and dry conditions and bury themselves in mud.	(Silveira and Araújo, 2014; Kalinda, Chimbari and Malatji, 2008; Sulieman et al., 2017).
Rainfall	<i>B. africanus</i> <i>B. globosus</i> <i>B. pfeifferi</i>	~600-1200mm/a ~600-1200mm/a ~300-900mm/a	Affects the life cycle and the population density of the snail.	(de Kock and Wolmarans, 2005; Appleton and Madsen, 2012; Sulieman et al., 2017; Adekiya et al., 2020).

Water temperature significantly affects the presence of host snails, with rising temperatures in sub-Saharan Africa potentially impacting their growth, distribution, survival, and reproduction (De Leo et al., 2020). This, in turn, could alter the population dynamics of *Schistosoma* infections, which vary with snail species and schistosome types in the region (McCreesh and Booth, 2014). Air temperature influences water temperature, affecting water quality and river ecosystems (Adekiya, 2018). Extremely low water temperatures can prevent schistosome development in snails, and freezing conditions lead to death (Yang and Bergquist, 2018). Water temperature is essential for developing and reproducing intermediate host snails, with temperature thresholds determining the suitability of water bodies for different snail species. McCreesh and Booth (2014) found that

rising water temperatures significantly influence the transmission dynamics of *S. mansoni* in Eastern Africa. Their research indicated that warmer waters impact both the snails and parasites, with specific outcomes varying based on the water's abiotic characteristics. The study highlighted that *B. pfeifferi* is sensitive to temperature changes, affecting its life cycle. Intermediate hosts remained steady between 15°C and 31°C but declined when water temperatures fell below 14°C or rose above 32°C (McCreesh and Booth, 2014). Furthermore, the highest human infection risk was noted in stagnant water at temperatures of 16°C to 18°C and in flowing water at temperatures of 20°C to 25°C (Adekiya et al., 2020). Climate change-induced temperature shifts could alter the distribution and transmission of schistosomiasis vectors, as modelled by Yang and Bergquist (2018), shown in (Figures 2-7 and 2-8). Additionally, inconsistent rainfall in sub-Saharan Africa could lead to drier conditions and reduced transmission rates.

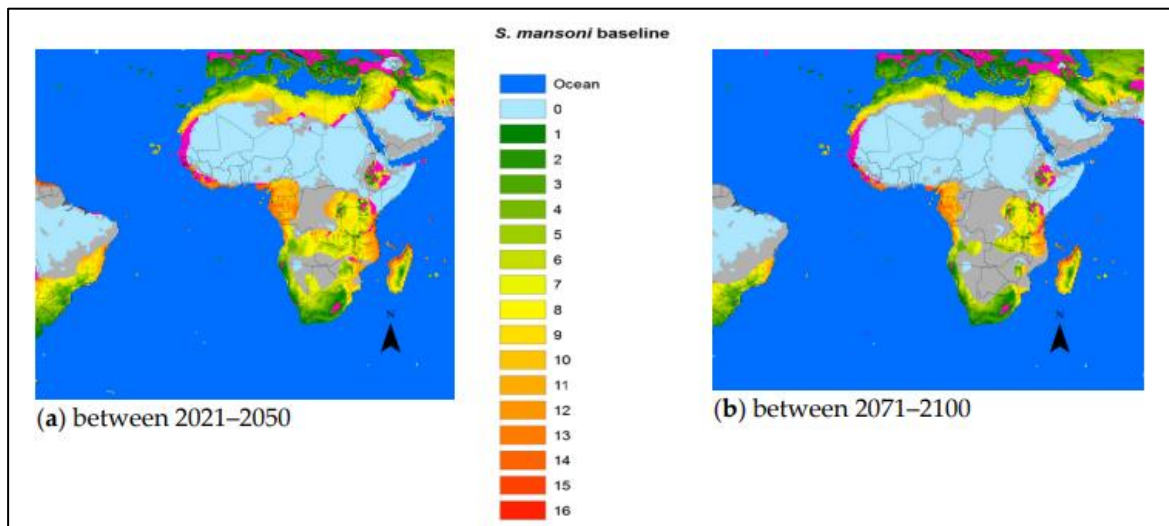


Figure 2-7: Change of risk area for *Schistosoma mansoni* in Africa. Red represents the most suitable conditions for the snails, while grey areas show places where the conditions might not be as good. As the temperature changes, some areas might become less suitable for snails. Source: Yang and Bergquist (2018).

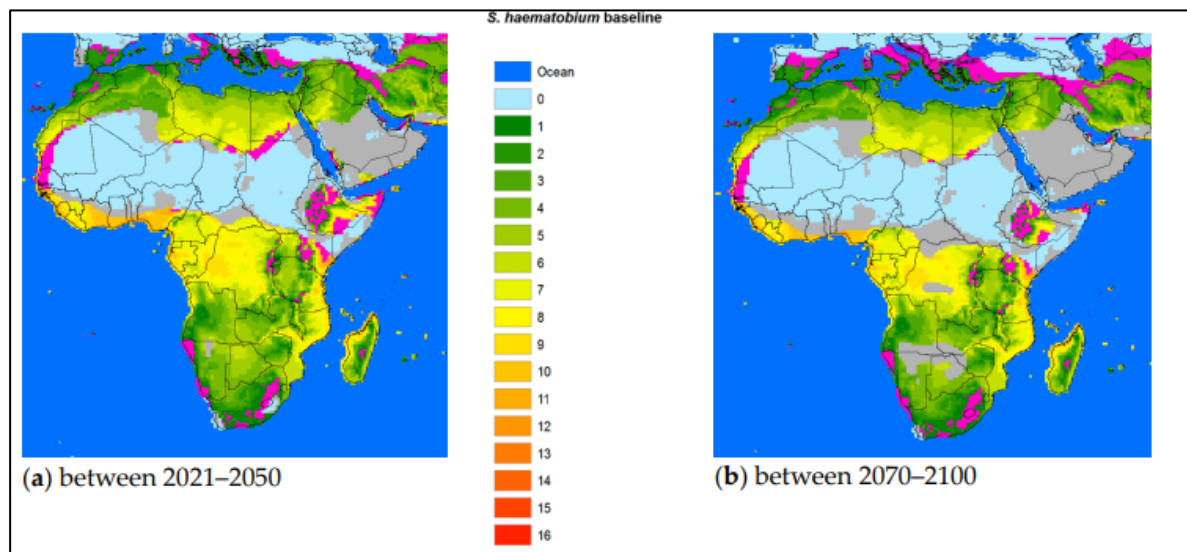


Figure 2-8: Change of risk area for *Schistosoma haematobium* in Africa. Red represents the most suitable conditions for the snails, while grey areas show places where the conditions might not be as good. As the temperature changes, some areas might become less suitable for snails. Source: Yang and Bergquist (2018).

Air temperature is a critical factor in the distribution of intermediate host snail species. Sulieman et al. (2017) observed in Sudan that high temperatures significantly reduced the population of *B. pfeifferi* snail species, indicating temperature's crucial role in the survival and mortality of these snails, particularly in water bodies. McCreesh et al. (2015) noted that intermediate host snails are sensitive to freshwater temperatures, influencing their geographic distribution in tropical and sub-tropical areas. De Kock and Wolmarans (2005) studied *Bulinus* species distribution and habitats in SA using decision trees. They found that temperature is the most crucial factor determining the geographic range of *B. africanus*. Brown (2002) showed that *B. africanus* is associated with cooler weather than *B. globosus*. The adaptability of snail species like *B. pfeifferi* and *B. globosus* to high temperatures and *B. africanus* to lower temperatures affects their survival and reproduction, making knowledge of these temperature ranges vital for identifying suitable habitats and understanding species distribution.

Rainfall is another essential factor in the distribution of host snail species. Rainfall in the dynamics of snail populations and the spread of schistosomiasis is challenging as it varies by location and snail species (Brooker, 2007). Rainfall can cool aquatic ecosystems, affecting the air temperature above the water. Research has shown that snail populations experience significant variation in space and time due to changes in rainfall (de Kock et al., 2004; Brooker, 2007). Rainfall plays a crucial role in spreading schistosomiasis, as evidenced by research conducted near three villages

in the Senegal River's lower delta (Ernould et al., 1999). The findings indicated a surge in *B. pfeifferi* populations during the wet season. Depending on the amount of rainfall, rainfall quantities may positively or negatively influence the intermediate host snail species (Manyangadze et al., 2016).

Increased rainfall can create more snail habitats by adding water to irrigation channels. This can also lead to higher water flow rates, facilitating the interaction between parasites and their snail hosts. This could increase host snail population numbers after the peak rainfall seasons (Suliman et al., 2017). Additionally, higher water levels from heavy rains can cause more turbulence, potentially disrupting snail habitats and reducing the survival of the parasite's larvae (Xue et al., 2011; Adekiya et al., 2019). Conversely, *B. globosus* showed a more restricted distribution in the wet season, leading to increased *S. haematobium* transmission in the dry season (Ernould et al., 1999). The changes in water levels caused by rainfall directly affect the transmission of the disease (Adekiya et al., 2019). In Ghana's Ga District, Codjoe and Larbi (2016) found a direct relationship between rainfall amount, rainy days, and schistosomiasis cases. De Kock et al. (2004) observed that certain annual rainfall ranges, specifically 300 to 600mm and 600 to 900mm, are associated with high snail populations. Stensgaard et al. (2013) noted that lower rainfall years tend to have reduced schistosomiasis cases, whereas years with moderate to high rainfall see increased cases.

It is important to consider four season variations that play a role in how rainfall in central, northern and eastern South Africa can impact the distribution of the intermediate host snail species, which is described as.

1. Post-rainfall season occurs between March to May months.
2. The cold/dry season occurs between June to August.
3. The hot/dry season occurs between September to November.
4. Rainfall season occurs between December to February months.

During the seasons following the rains and throughout the colder, drier times, pools and dams along streams serve as appropriate environments for *B. globosus* and *B. pfeifferi* (Manyangadze et al., 2016). Conversely, during the peak of the dry season, when rivers often run dry, snail populations decline, possibly due to aestivation (Betterton et al., 1988; Rubaba et al., 2016). *Bulinus*

globosus is transmitted during the seasons when rainfall is limited (Ernould et al., 1999). Manyangadze et al. (2021) found similar results where increased rainfall is inversely related to the distribution of *B. globosus*, with greater amounts of rain potentially causing a reduction in their numbers, as shown in (Figure 2-9). Nonetheless, this correlation is only meaningful at a certain threshold for *B. globosus*. This implies that additional elements like the quality of their habitat and the chemical properties of the water might also affect where these snails are found. Due to its sensitivity, *B. pfeifferi* is unlikely to be present in temporary rainy habitats (Manyangadze et al., 2016). These species typically live in still or slow-moving permanent waterbodies. Consequently, while prolonged dry spells, potentially exacerbated by climate change, might reduce snail populations, the surviving snails may have the opportunity to recolonise these areas (Rubaba et al., 2016).

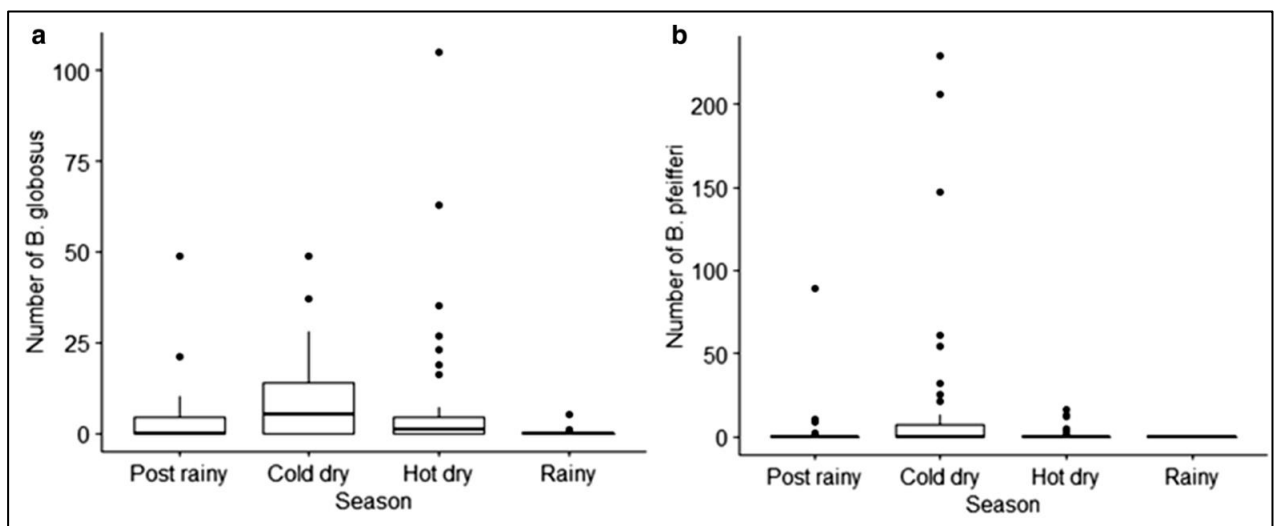


Figure 2-9: Box and whisker plots showing a) the number of *B. globosus* and b) the number of *B. pfeifferi* collected by season. Source: Manyangadze et al. (2021).

Water velocity is also one of the factors that is considered to influence the distribution of intermediate host snail species. The distribution of intermediate host snails in SA is moderately influenced by the water velocity (de Kock and Wolmarans, 2005). Appleton and Madsen (2012) reported that the tolerance of snail species to a narrow range of current velocity is essential for determining the type of wetland the snail species can colonise. Therefore, any wetland or water bodies above the intermediate host snail species threshold could affect the ability of the snail species to survive in that area. Current velocities of less than 0.3 ms^{-1} are essential, ensuring that the intermediate host snail species are not dislodged or swept away by currents (Appleton, 1975). Water speed plays a crucial role in the spatial spread of the *Schistosoma* parasite. Slower water speeds, around 0.1 ms^{-1}

1, facilitate the parasite's wide distribution, enhancing the chances of encountering intermediate host snail species (Walz et al., 2015).

Water chemistry is essential to consider because it influences the availability of dissolved oxygen and the overall toxicity of the environment for intermediate host snail species (Silveira and Araújo, 2014). Heavy metals, when present in trace amounts, can help maintain a stable pH and provide essential micronutrients, promoting healthier and less toxic conditions. This balanced environment supports the physiological needs of snails, enabling them to thrive (Silveira and Araújo, 2014). However, it is crucial to note that high concentrations of heavy metals can be harmful, making regular monitoring and management of water chemistry vital. Silveira and Araújo (2014) suggested that most of the endemic areas in SA flowed over insoluble old granite and gneiss formations. Implications are that the concentration of bicarbonate was the indication of the buffering capacity of the water (Silveira and Araújo, 2014). Calcium is also an essential chemical in the distribution of intermediate host snail species because calcium carbonate (CaCO_3) is one of the significant components of the snail shells and is an essential reproduction of snail species (Suliman et al., 2017). According to Suliman et al. (2017), intermediate host snail species need calcium to build strong shells soon after emergence. Some extended parental efforts in some species go so far as providing faeces rich in calcium or coating the eggs with a layer of calcium-rich soil (Suliman et al., 2017). Therefore, it is essential for the emerging species of intermediate host snail populations.

Aestivation is regarded as a state of torpor that is explained as a survival strategy for the intermediate host snail species for dealing with arid conditions (Suliman et al., 2017; Walz et al., 2015). During these periods, the host snails are affected by a lack of food availability and the environmental temperature frequency (Suliman et al., 2017). *Bulinus africanus* and *B. globosus* can withstand or survive more periods of desiccation than *B. pfeifferi* (Walz et al., 2015). The intermediate host snail species can withstand prolonged periods of desiccation in sheltered spots, on mud, mud crevices and under vegetation (Walz et al., 2015). Appleton (1985) conducted a study on the Pongola River, where a prolonged drought was reversed by rainfall, refilling the river. This allowed the *B. globosus* species from upstream refugia to repopulate dried pools, facilitating the distribution of *B. globosus*. (Appleton, 1985). The intermediate host snail species' ability to survive under adverse conditions has allowed them to inhabit that area for a longer period. Therefore, aestivation is crucial as it allows the host snail to endure in environments or conditions where their chances

of survival are low. The mentioned factors are essential in determining the suitability of the areas or habitats for intermediate hosts' snail distribution.

2.2.2 Proximity to Water Sources

Schistosomiasis transmission necessitates direct interaction between humans and the intermediate snail host found in open-water bodies (Brooker, 2007). Reitzug et al. (2023) added that swimming, fishing, bathing, washing, or laundry activities play a key role in determining infection likelihood and are highly variable across small spatial scales. Exposure is defined as having water contact in sites with schistosome cercaria (Reitzug et al. (2023). There is variation in water contact duration, frequency, and activities within and across households and villages across different age groups, genders, and occupational groups.

Approximately 76% of people in sub-Saharan Africa reside near snail-infested water sources, which spreads the disease (Adenowo et al., 2015; Woldegerima et al., 2019). The intensity of schistosomiasis is associated with infected individuals and their proximity to natural water sources such as lakes, rivers, and ponds (Clennon et al., 2006; Kapito-Tembo et al., 2009). A study in the Blantyre district of Malawi revealed that schools situated near open water bodies corresponded with a higher infection risk among children (Clennon et al., 2006). This could be due to children swimming in open water bodies during hot summers. Another reason is that children usually need to cross shallow water bodies to get to school. Additionally, fishing, farming, and domestic and recreational activities involving contact with infected water are significant risk factors for disease transmission (Adenowo et al., 2015). In South Africa, recreational activities at dams pose a risk of infection, with many participants unaware of the danger. Rapid population growth and inadequate basic services have led to slum living near water bodies, exacerbating the risk of schistosomiasis in these communities (Wolmarans et al., 2006).

Poverty, inadequate living conditions, poor sanitation, and the absence of clean water are factors contributing to the persistent spread of schistosomiasis in sub-Saharan Africa. (Gryseels et al., 2006). The World Bank has noted that most people in this region live on \$1.25 to \$2 a day (Hotez and Kamath 2009). Poverty leads to using contaminated water, causing illness and preventing individuals from working, thus perpetuating poverty (King, 2010; Adenowo et al., 2015). In a study conducted in Nigeria, Ugbomoiko et al. (2010) identified a 62% prevalence of schistosomiasis among more than a thousand individuals living near water bodies. Esrey et al. (1991) emphasised

the significance of clean water and sanitation in decreasing the spread of diseases. Access to clean water and sanitation is crucial in eliminating schistosomiasis transmission. Areas with limited water access often rely on open water sources, increasing exposure to the disease. Studies by Tanser et al. (2018) and Sacolo-Gwebu et al. (2019) show a clear link between water access and schistosomiasis infections. Lack of piped water and toilets in a household is associated with higher infection rates, emphasising the importance of improved water and sanitation infrastructure in combating schistosomiasis. In northern Nigeria, a study highlighted the correlation between access to safe water and the severity of urinary schistosomiasis, which had a much higher infection rate in a community relying on a pond than a borehole (Kanwai et al., 2011).

2.2.3 Agricultural Impacts

The spread of schistosomiasis is associated with agricultural activities, which provides more habitats for the snails that host the disease and impacts the distribution of their natural predators (Steinmann et al., 2006; Sokolow et al., 2015). Agricultural chemicals can disrupt ecosystems in ways that benefit these snails, harm their predators, or directly influence the schistosomes themselves (Hoover et al., 2020). There has been a lack of comprehensive research into how agrochemicals affect *Schistosoma* transmission (Rohr et al., 2019). In sub-Saharan Africa, where most schistosomiasis cases are found, the use of agrochemicals has been minimal due to the prevalence of small-scale farming (Hoover et al., 2020). The rise in industrialisation has led to a rapid increase in the use of agrochemicals due to their growing accessibility and the shift towards less labour-intensive farming practices (Ciceri and Allanore, 2019). Historically, the limited local production of agrochemicals has restricted their use in regions of sub-Saharan Africa affected by schistosomiasis.

Agrochemicals affect the transmission of non-human trematodes by directly impacting the parasites and their snail hosts and indirectly altering food web dynamics (Rohr et al., 2008; Blaustein et al., 2011; Halstead et al., 2018). Fertilisers and herbicides initiate bottom-up food chain reactions by modifying algal populations, which benefits the algae that snails feed on (Perez et al., 2007; Rohr et al., 2008). Conversely, insecticides prompt top-down food chain reactions by reducing predation on snails due to their harmful effects on aquatic insects that prey on snails (Hoover et al., 2020). Moreover, these agrochemicals directly impact snail health and reproduction and the viability and survival of various schistosome life stages (Halstead et al., 2018). A comprehensive analysis has yet to be done to understand how agrochemicals impact the transmission of human

schistosomiasis, despite suggestions that certain agrochemicals could increase the risk of this disease (Rohr et al., 2019).

2.3 Impact of climate change on the distribution of intermediate host snails

The Intergovernmental Panel on Climate Change (IPCC) forecasts that global surface temperature increase will exceed 1.5°C by 2040, even under low greenhouse gas emissions (IPCC, 2023). Climate change involves changes in precipitation patterns, rising temperatures, and an increase in extreme weather events such as droughts and floods (Stensgaard et al., 2019). These environmental changes impact food security, air quality, and disease distribution. Climate change threatens freshwater ecosystems, especially in areas already impacted by human activities (De Necker, 2020). In SA, different regions will experience varying temperature and rainfall changes, with some areas becoming hotter and wetter while others become hotter and drier (Engelbrecht and Engelbrecht, 2015). Climate change heightens certain regions' susceptibility to infectious diseases like schistosomiasis. These climatic shifts significantly affect their interactions with hosts, altering the transmission dynamics of schistosomiasis, which has evolved rapidly in recent years. Climatic factors like rainfall, temperature, flooding, and drought are essential factors in the spread of tropical diseases, as shown in (Figure 2-10).

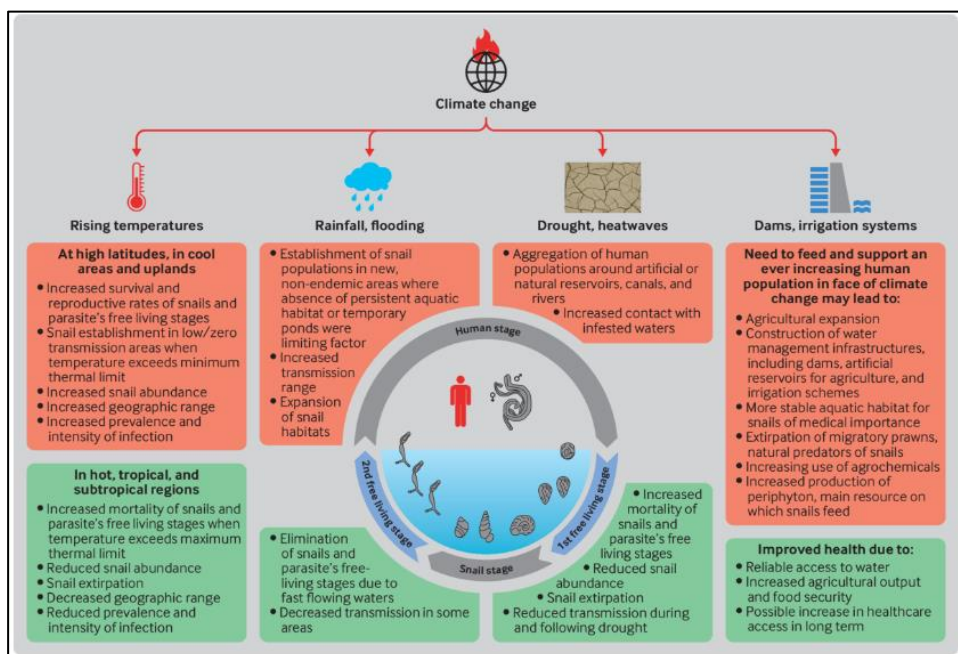


Figure 2-10: Climate change, land use change, agricultural expansion, and water management infrastructure development can influence schistosomiasis transmission and human health. These factors can increase the risk of schistosomiasis (red panels) or decrease transmission risk (green panels). Source: De Leo et al. (2020).

McCreesh et al. (2015) suggest that climate change may shift the distribution of bilharzia by impacting the populations of intermediate host snails and freshwater ecosystems. Pedersen et al. (2014b) concur, noting that climate variations could alter the spatial distribution of suitable habitats for these snails in Zimbabwe. Joubert et al. (1984) found that *B. pfeifferi*, *B. africanus*, and *B. globosus* could not survive at temperatures above 36°C, with *B. globosus* showing greater resilience at high temperatures. Pedersen et al. (2014a) predict that climate change may shrink the habitat range for intermediate host snails. Still, it could also expand suitable areas for the *B. pfeifferi* species due to their tolerance to high temperatures. This could lead to new regions becoming suitable for the snails, altering the distribution of schistosomiasis. McCreesh et al. (2015) found that rising African temperatures could exacerbate parasitic diseases and undermine control efforts, potentially allowing *S. mansoni* to spread to new areas.

Conversely, in some regions, higher temperatures might create conditions unsuitable for the parasites and their hosts, potentially reducing infections (Adekiya et al., 2019). In Zimbabwe, a decline in schistosomiasis cases over thirty years has been linked to warmer, drier weather, although mass drug administration and changes in behaviour might have contributed.

A study around a high-altitude crater in Western Uganda found that rising temperatures could be changing the geographical spread of schistosomiasis, with areas above 1400 meters that were once too cool now seeing disease transmission due to climate change (Kabatereine et al., 2004; John et al., 2008). In Ethiopia, *S. haematobium* transmission is likely below 800 meters, while *S. mansoni* is more prevalent between 1300 and 2000 meters above sea level (Mekonnen et al., 2013).

2.4 Modelling schistosomiasis

Schistosomiasis is a significant health issue in Africa, with spatial modelling improving our comprehension of the disease (French et al., 2018). In the 1960s, the distribution of the disease across Africa was extensively documented through historical sources and hospital data (Doumenge et al., 1987). However, these traditional maps are static and do not capture present epidemiological shifts caused by changes in the environment, such as building dams and healthcare initiatives (Fenwick et al., 2006). Therefore, satellite data has been utilised in global studies to predict disease and vector distribution, including malaria and schistosomiasis (Hay et al., 2000; Malone et al., 2001; Brooker et al., 2002; Rogers et al., 2002; Moodley et al., 2003; Kabatereine et al., 2004).

Predictive modelling is useful for creating strategies to manage schistosomiasis effectively in endemic regions. Vegetation, temperature, elevation, and precipitation are dependable factors for identifying snail habitats and can provide more precise mapping of schistosomiasis distribution compared to prevalence surveys. (Simoonga et al., 2009; Walz et al., 2015; Sato et al., 2018). These environmental factors can be collected through Remote Sensing (RS) and Geographic Information Systems (GIS) (Simoonga et al., 2009; Schur et al., 2011; Walz et al., 2015; Kulinkina et al., 2018). A Ghanaian study (Wrable et al., 2019) used environmental metrics like land surface temperatures, the normalised difference vegetation index, and accumulated precipitation to study disease trends over broad areas with different spatial and temporal detail levels. The study found lower schistosomiasis rates, identified seasonal trends, and linked infection rates to time zones, aiding in understanding disease dynamics.

2.4.1 Climate Modelling

Martens et al. (1995, 1997) were among the first to use a global modelling approach to study how climate change affects schistosomiasis. Initially, they connected climate change scenarios with a model linking climate variables to the parasite's reproduction rate, predicting a potential increase in the population at risk by 0.7–3.3% (Martens et al., 1997). However, a subsequent study projected a decrease in schistosomiasis transmission potential of 11–17% by 2050, globally. Boissier et al. (2015) highlighted that countries with previously limited transmission might experience an increase, as seen with the urogenital schistosomiasis outbreak in Corsica in 2015. Yang et al. (2005) found that the shift in the historical isotherm in China expanded the potential transmission area of *S. japonicum* and increased the population at risk of schistosomiasis. It also introduces a Growing Degree Day (GDD) modelling approach to predict increased *S. japonicum* parasite generations due to longer growing seasons. The study further suggests that the distribution of organisms correlates with Annual Growing Degree Days AGDD, which measures heat energy accumulation. Zhou et al. (2008) also predicted further expansion of schistosomiasis transmission in northern China by 2050.

Stensgaard et al. (2013) introduced statistical modelling in Africa by combining GDD models for *S. mansoni* with habitat suitability models for intermediate host snail species. The study suggests that under future climate change scenarios, suitable conditions may be reduced for most snails that act as intermediate hosts for *S. mansoni* in Africa (Stensgaard et al., 2013). It emphasised the significance of considering additional environmental factors like environmental changes, land use,

and water availability in snail habitats. Previous studies mainly focused on temperature as the sole influencing factor, neglecting other potential variables and lacking specificity, especially concerning intermediate host snails (Mangal et al., 2008).

Two main methods for predicting the impact of climate change on vector-borne diseases, including schistosomiasis, are distinguished: empirical-statistical approaches using statistical models and process-based approaches simulating detailed biophysical/epidemiological processes (Stensgaard et al., 2016). The former examines the connection between the distribution of snails and parasites with environmental factors. In contrast, the latter explores the relationships between environmental conditions and the performance of organisms (Stensgaard et al., 2016). Stensgaard et al. (2019) compared the climatic niche space of two African schistosome species by analysing their thermophysiological thresholds against temperature data from areas with known schistosomiasis transmission. The study used bioclimatic temperature data and georeferenced prevalence locations to depict the present temperature conditions encountered by the schistosomes (Figure 2-11).

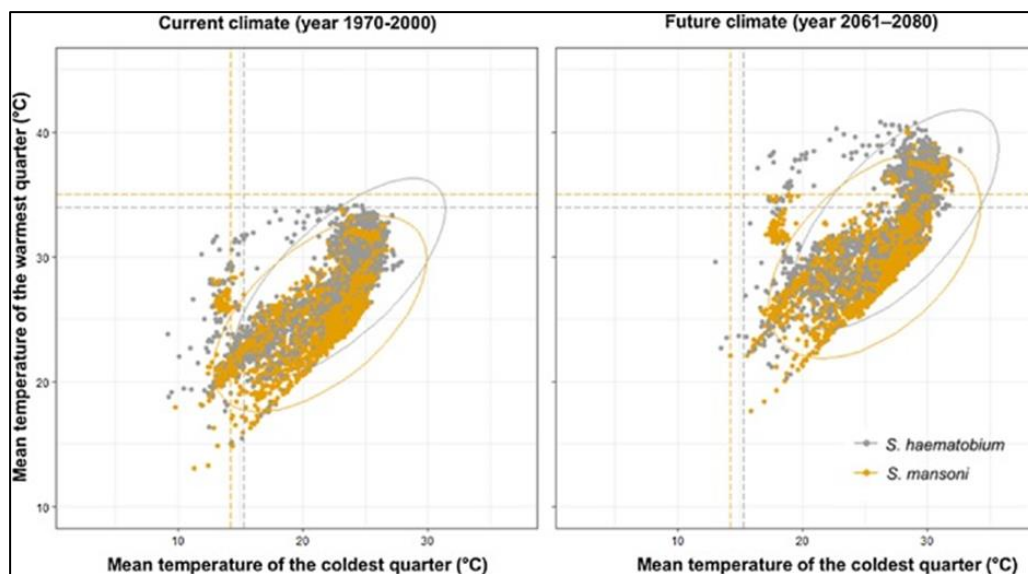


Figure 2-11: Climatic temperature windows for *Schistosoma mansoni* (orange) and *Schistosoma haematobium* (grey) in Africa. It compares the mean temperature of each parasite's warmest and coldest quarters under current and future climatic conditions (predicted for 2070). Physiological thermal thresholds for parasite development in intermediate snail hosts indicate the potential thermotolerance range. Both species are near their upper thermal threshold under current temperatures, with *S. haematobium* in slightly warmer areas. The data in ellipses represent 95% of the presence data for each parasite species. Source: Stensgaard et al. (2019).

A study by McCreesh et al. (2015) predicted the effects of climate change on *S. mansoni* transmissions using three varying levels of climate warming projections—low, moderate, and high. To

assess the robustness of their forecasts, they applied eight distinct model scenarios that accounted for variations in the correlation between air and water temperatures and divergent snail mortality rates. In most parts of eastern Africa, infection risk can rise by around 20% over the next 20 to 50 years (McCreesh et al., 2015). Specifically, areas like Rwanda, Burundi, southwest Kenya, and eastern Zambia may experience increases in infection risk. Additionally, there is a concern that *S. mansoni* could become newly endemic in certain regions (McCreesh et al., 2015). McCreesh et al. (2015) found that the 20-year projections remain consistent despite simulated snail habitat conditions variations. However, there is more uncertainty regarding how different habitats will impact risk changes over 50 years, as shown in (Figure 2-12).

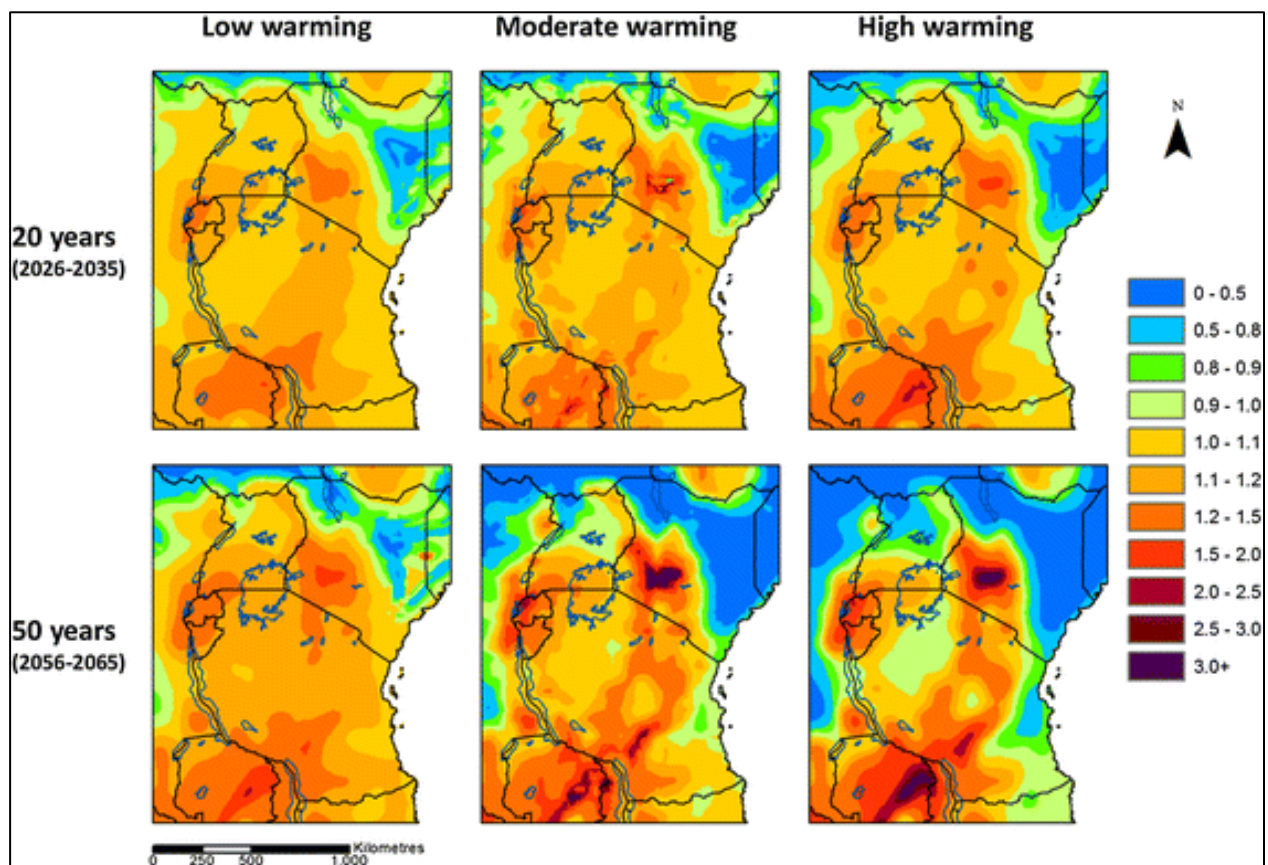


Figure 2-12: The predicted change is presented for two time periods: 2026-2035 and 2056-2065, both relative to the baseline period of 2006-2015. The median values are calculated across eight model scenarios for each map, providing a comprehensive overview of the predicted changes in *S. mansoni* risk over time in eastern Africa. Source: McCreesh et al. (2015).

Liu et al. (2021) predicted the suitable habitats for *Sapindus delavayi* for the years 2050-2100 using the Beijing Climate Centre (BCC) Climate System Model (BCC-CSM2-MR). The results showed that the habitat range might not change significantly; the edges of the suitable habitat will

experience unstable changes due to a reduction in habitat area (Liu et al., 2021). This implies that the overall distribution of the suitable habitat for *S. delavayi* may remain relatively constant, but the specific boundaries and areas within that habitat may undergo significant shifts and instability.

As shown above, numerous studies have utilised various climate models to explore the possible global spread of schistosome species, considering elements like temperature and precipitation (De Leo et al., 2020). These studies explain how temperature and rainfall affect the spread of schistosomiasis through seasonal and monthly changes (Tabo et al., 2024). Nonetheless, predicting the impact of climate change on the transmission of schistosomiasis requires detailed simulations that account for uncertainties in future climate scenarios (Adekiya et al., 2019; De Leo et al., 2020). Future projections should account for climate factors beyond just temperature, including rainfall variability, floods, and droughts, which are anticipated to influence schistosomiasis rates (McCreesh et al., 2015). Consequently, future research should enhance precipitation and water availability models to thoroughly evaluate climate change's potential effects on schistosomiasis (Yang and Bergquist, 2019). Moreover, the interaction between climate change and schistosomiasis transmission highlights the necessity for efficient control strategies and public health initiatives to counter the expected consequences of climate change on this disease (Yang and Bergquist, 2019).

2.4.2 Ecological Niche Models

Correlative ENMs are utilised to understand organisms' niches and potential distribution by analysing the relationship between environmental data and occurrence records. (Feng et al., 2019). While ENMs focus on ecological niche parameters, Species Distribution Modelling (SDM) emphasises species' geographic ranges. Widely used in ecology and evolution, ENMs aid in land use and conservation decision-making. The process involves using biodiversity and environmental data to create spatial predictions through correlative or machine-learning methods. This workflow, including data acquisition, model calibration, transfer, and evaluation, is commonly used in various disciplines relying on statistical models (Araújo et al., 2018). The expansion of ENMs studies in the last decade has been driven by the necessity to address future scenarios. While these models are valuable, their predictive accuracy can vary depending on the algorithm used (Dolci and Peruzzi, 2022).

Conventional ecological niche modelling methods use presence-only data to estimate the discrepancy between realised and fundamental ENMs niches or actual and potential distributions in SDM (Peterson et al., 2011). The proposed model aims to accurately estimate fundamental niches by considering accessible climates for species to correct for biased presence samples. It is essential to differentiate between fundamental and realised niches to correctly interpret the results of correlative statistical models in ENM/SDM (Hutchinson (1957). The fundamental niche is the range of conditions where a species can grow independently of other species. In contrast, the realised niche is a smaller subset influenced by abiotic factors, interactions with other organisms, and dispersal limitations (Peterson et al., 2011). Estimating the fundamental niche is vital for predicting species distributions under different conditions, like climate change impacts or invasive species spread. However, accurately determining the complete fundamental niche is more challenging than estimating the realised niche (Qiao et al., 2018)

In recent years, ENMs have become increasingly popular (Phillips et al., 2006; Guo et al., 2013; Carlson et al., 2016). In addition to predicting distributional ranges, the model can identify which climatic and environmental variables shape species distribution (Carlson et al., 2016). Ecological niche models are empirical or mathematical representations of a species' ecological niche (Barbosa et al., 2012). These models use statistical methods or response surfaces based on theory to link data about a species' physiology or locations to environmental factors to describe, understand, or predict where species might live (Franklin, 2010; Sillero, 2011; Barbosa et al., 2012; Guisan et al., 2017). Ecological Niche Models can produce a mathematical equation that connects the expected species distribution (the dependent variable) to various environmental predictors (Olivera-Gomez and Mellink, 2005), or they can generate response curves that show the relationship between each environmental predictor and the dependent variable (Chapman et al., 2019). These models can then be converted into maps that show the suitability of habitats, the likelihood of species presence, or the favourability for a species to occur (Acevedo et al., 2012; Ørsted and Ørsted, 2019). Ecological Niche Models are thus created in an environmental context and then applied to a geographical one. Ponpetch et al. (2021) used 8 ENMs to model the potential distribution of *S. mansonii* in Ethiopia. They found that Generalized Linear Models (GLMs), Random Forest (RF), and Maximum Entropy (MaxEnt) were ranked in the top 5 for high performance in modelling the distribution of ENMs. Another study found that RF and MaxEnt outperformed other ENMs (Kaky et al., 2020). Based on this, the next section will focus on the models used in this thesis, such as GLM, RF and MaxEnt.

The Maximum Entropy approach applied to vector-borne diseases, was selected as this study's primary model. Shannon (1948) defined entropy as a metric for the amount of 'choice' in selecting an event, indicating that higher entropy involves more choices and fewer constraints. The Maximum Entropy model predicts species distribution in a study area and has been widely used in various environmental studies since its publication in 2006 (Elith et al., 2011; Merow et al., 2013). It incorporates different climatic and environmental factors to enhance the reliability and accuracy of the data (Elith et al., 2011). The model compares observed species distribution with sampled climatic factors to make predictions. Stensgaard et al. (2016) explain that MaxEnt estimates species distribution by determining the maximum entropy, or broadest spread of a species' geographical presence relative to various climatic and environmental factors. The model requires only presence-absence data, such as snail occurrences and environmental details of the study area, to predict effectively (Phillips and Dudik, 2008; Phillips and Elith, 2011). MaxEnt is widely used in machine learning to estimate the probability distribution of species based on maximum entropy principles, taking into account limited information about their distribution and the environment (Phillips et al., 2006; Araújo et al., 2018). Maximum Entropy uses this incomplete information to forecast the most dispersed or uniform distribution possible, given certain constraints that represent the limited knowledge of the target distribution (Jaynes, 1957). 'Features' are variables that hold information about the target distribution, and constraints are the expected values for these features, which should align with the empirical average from sample points of the species distribution. Environmental and climatic variables, such as soil type, vegetation, and rainfall, are examples of features. The pixels in the sample points have known species occurrences, and the MaxEnt probability distribution is established across the pixels within the study area (Phillips et al., 2006; Tang et al., 2021). Pedersen et al. (2014b) conducted a study in Zimbabwe utilising the MaxEnt model to assess how climate change could alter the geographical distribution of freshwater snails. The outcome of the MaxEnt model was depicted as a probability map, indicating the potential presence of snails, with values from 0 representing unsuitable habitats to 1 indicating ideal habitats (Figure 2-13).

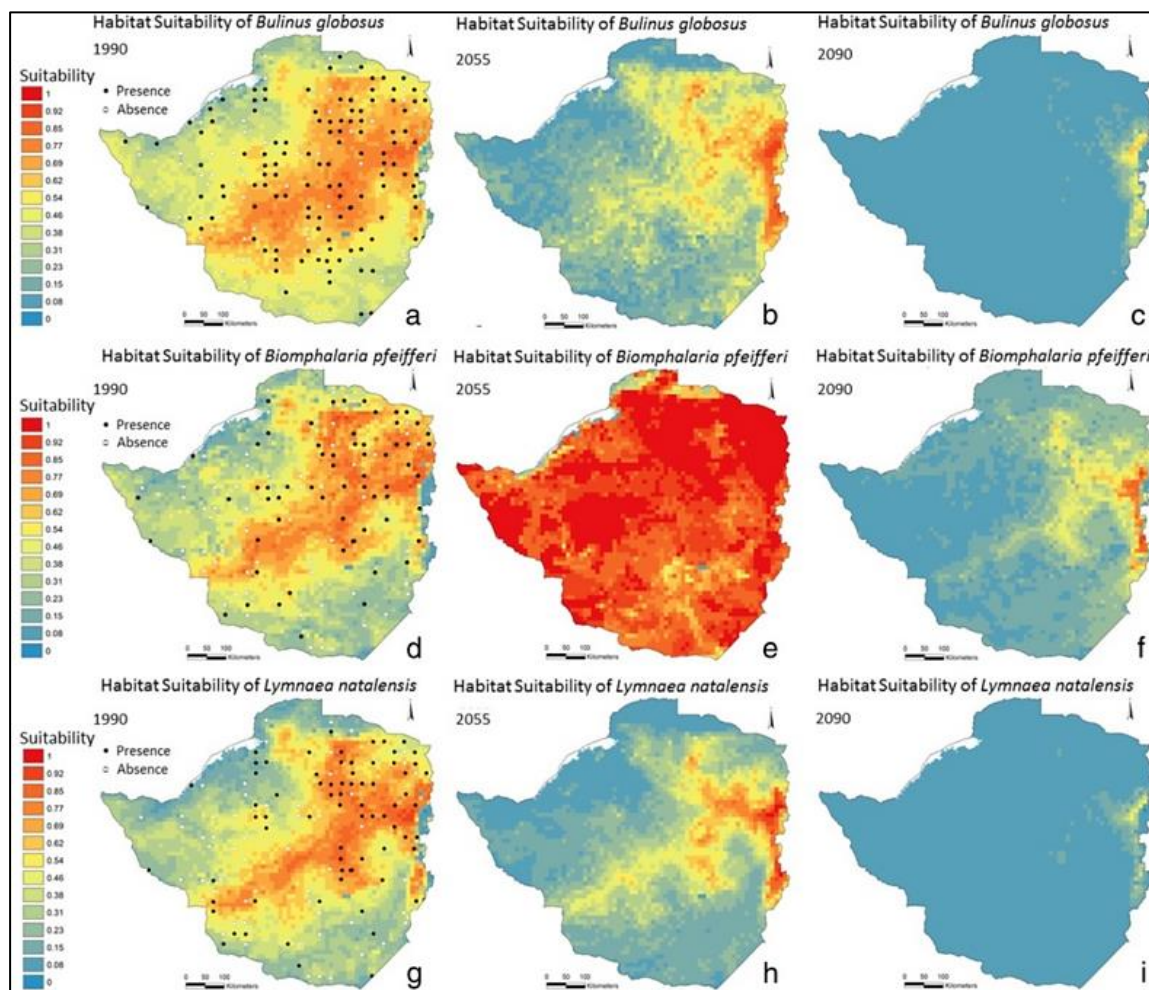


Figure 2-13: *Bulinus globosus*, *Biomphalaria pfeifferi* and *Lymnaea natalensis* habitat suitability for three periods in Zimbabwe. Source: Pederson et al. (2017).

Applying MaxEnt to the habitats of host snails can enhance the understanding and management of schistosomiasis risk over time and space (Simoonga et al., 2009; Manyangadze et al., 2016). However, the MaxEnt model has some uncertainties, including a tendency for overfitting, which can reduce its predictive accuracy on new data (Arnold et al., 2014). To mitigate this, a 'regularisation multiplier' simplifies the model, producing broader predictions. Additionally, biases in the data on where occurrences are recorded can affect the model's precision (Guillera-Arroita et al., 2014). Unlike other algorithms, MaxEnt provides a measure of environmental suitability instead of a direct prediction of occurrence, and its logistic output is based on assumed rather than estimated prevalence rates (Yackulic et al., 2012).

Generalised linear models are an advancement of linear models that accommodate data variability and non-linear relationships without distorting the data's natural scale (Hastie, 2017). Smith (2019)

describes GLMs as comprising three key components: (i) a predictor function that utilises covariates to estimate the response variable, (ii) a link function that establishes a linear connection between the covariates and the average of the response variable, and (iii) the distribution of error terms. Extence et al. (1999) emphasised that GLMs assume the data observations are independent, a condition that can be enhanced through meticulous sampling. These models utilise a link function to connect a linear combination of predictor variables with the average of the outcome variable. Guisan et al. (2002) highlighted that GLMs can handle data from various probability distributions, such as gamma, negative binomial, Poisson, normal, and binomial. This versatility makes GLMs particularly useful for analysing ecological associations between intermediate host snails and environmental factors. However, McCullagh and Nelder (2019) pointed out that GLMs might overestimate the presence of species in certain areas due to their tendency to extrapolate.

Ponpetch et al. (2021) used Generalised Additive Models (GAM), Multivariate Adaptive Regression Splines (MARS), Classification Tree Analysis (CTA), RF, Gradient Boosting Machine (GBM), Surface Range Envelope (SRE), MaxEnt and GLMs, to assess the potential spread of *Schistosoma mansoni* in Ethiopia's endemic regions. The study found that GLMs predicted a more extensive distribution of the disease, in contrast to the narrower ranges forecasted by the RF and MaxEnt models, as shown in (Figure 2-13).

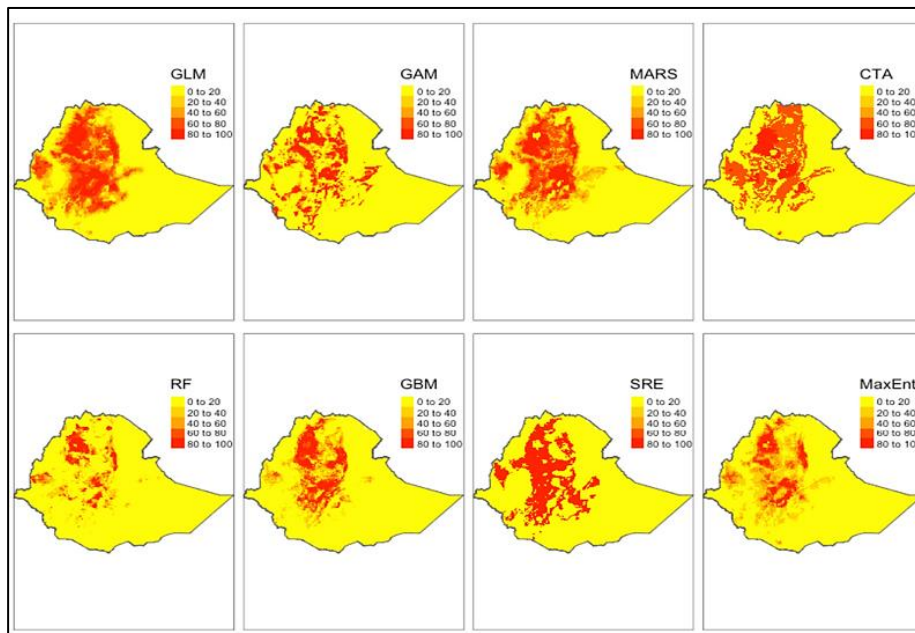


Figure 2-14: The spread of *Schistosoma mansoni* in Ethiopia's endemic regions using various species distribution models. It presents a probability scale from 0 to 100 to indicate environmental suitability, where areas with low suitability are marked in yellow and those with high suitability are in red. Source: Ponpetch et al. (2021).

Random Forest is a machine learning method for predicting species distribution, such as the snail hosts of *Schistosoma*, and for classification and regression problems. Random Forest builds numerous decision trees during training and predicts by aggregating the results using the most common outcome for classification or the mean for regression (Strobl et al., 2009; Valavi et al., 2021). Each tree is created from a random data subset and feature set, enhancing tree diversity and reducing overfitting (Breiman, 2001). Each tree gives an outcome in prediction, and the random forest algorithm combines these outcomes to produce a final prediction.

The use of RF has enhanced the precision of schistosomiasis risk predictions by incorporating the distribution of snail hosts and environmental variables. Zhang et al. (2021) conducted a study in the Yangtze River Basin and applied a spatially weighted random forest model to forecast the risk of *Schistosoma japonicum*'s intermediate snail host. The results helped refine the accuracy of national schistosomiasis control efforts. Kulinkina et al. (2018) utilised RF to analyse the predictive power of data on *S. haematobium* prevalence from 73 schools in rural Ghana. The results highlighted how using RF could enhance the spatial forecasting of *S. haematobium*, aiding in comprehending the disease's geographical spread (Kulinkina et al., 2018). Random Forests are known for their strong performance, yet there are instances where RF has been ineffective in predicting species distributions. This inadequacy is commonly associated with applying presence-only species data, which is inaccurately treated as binary by incorporating background samples as an alternative class (Valavi et al., 2021).

2.5 Chapter Conclusion

The literature review delved into how climate change affects snail hosts' distribution and schistosomiasis transmission. Climate change, with its temperature shifts and extreme climate events, challenges freshwater ecosystems and impacts the suitability of snail habitats for the disease. Literature showed the intricate link between climate factors and schistosomiasis distribution, highlighting temperature and rainfall's role in shaping transmission patterns. Changes in snail habitats due to climate change can either expand or shrink host species' range, thus influencing the spread of the disease. Ecological niche and species distribution models are important tools for understanding and predicting the distribution of schistosomiasis and its snail hosts. MaxEnt, GLM and RF algorithms are commonly used to assess the environmental suitability of snails and predict disease risk in various regions. These models help understand species' ecological needs and plan targeted control measures for schistosomiasis. However, challenges such as model accuracy, data biases,

and uncertainties in future climate scenarios must be carefully addressed to ensure reliable interpretation of model predictions and effective disease management strategies. *Chapter 3* will focus on the data and methods used in this thesis.

CHAPTER 3

The chapter discusses the methodology employed to study the impacts of climate change on the distribution of schistosomiasis in SA. It starts by outlining the study area, emphasising the country's varied geography and climate, making it susceptible to fluctuations. The chapter explains the modelling techniques, data origins, and environmental factors the research considers. Limitations imposed on the study are also mentioned when applicable.

METHODOLOGY

3.1 Study Area

South Africa's surface area covers approximately 1,200,000 km². It extends along latitudes from 22°S to 35°S as well as along the longitudinal axis from 17°E to 33°E (Tibane, 2016; Climate Risk Profile, 2021). The landscape of SA transitions from arid deserts to semi-humid areas. The country experiences a range of climates, from sub-tropical to temperate, influenced by the surrounding oceans, resulting in diverse weather patterns across different regions (Climate Risk Profile, 2021). Historically, schistosomiasis thrived in sub-tropical and humid areas. This was evident in the eastern and northeastern areas extending to the east coast of SA (Figure 3-1; Moodley, 2003).

South Africa faces vulnerability to climate variability and change due to its reliance on rain-fed agriculture, high poverty levels in rural areas, and limited adaptive capacity (Climate Risk Profile, 2021). Approximately 3 million individuals in SA do not have safe drinking water, and 14 million lack adequate sanitation facilities in informal urban areas and rural regions Academy of Science of South Africa (ASSAF, 2023). Schistosomiasis is transmitted through contact with fresh water contaminated by the waste of infected individuals, which contains snails acting as intermediate hosts for the parasite. A study in rural SA revealed that access to piped water could significantly lower the likelihood of children contracting urogenital schistosomiasis by a factor of eight (Tanser et al., 2018). The life cycle of schistosomes suggests that the spread of this disease could be curtailed with the provision of clean water and sufficient sanitation facilities (Mogeni et al., 2020). Consequently, the absence of these amenities in some areas of SA contributes to greater contact with contaminated water and heightened schistosomiasis transmission risks.

Rainfall patterns are changing, resulting in severe storms, landslides, and flash flooding in the eastern regions of SA. Studies have shown that floods can lead to schistosomiasis outbreaks (Ge et al., 2004; Longxing et al., 2014). During floods, people are exposed to contaminated water, increasing their risk of schistosome infection. In addition, temperature in SA varies significantly, with summer temperatures ranging from 15°C to 36°C and winter temperatures from -2°C to 26°C (Ziervogel et al., 2014; Tibane, 2016; DEA, 2018). Temperatures in SA have increased steadily over the last 60 years, impacting the survival and distribution of intermediate host snails (Ziervogel et al., 2014; McCreesh et al., 2014; McCreesh et al., 2015). A study conducted in Limpopo Province found that winters are becoming wetter and warmer, and summers are getting drier and

warmer (Tshiala et al., 2011). This acts as an ideal environment for *Schistosoma*-transmitting snails. These ideal habitats where the snail vectors thrive are tropical, humid, and aquatic environments such as dams and rivers (de Kock et al., 2004).

From the 1950s to 2006, snails infected with parasites were sampled from rivers and dams in SA. In addition, the presence of intermediate host snails that transmit schistosomiasis to humans is associated with water bodies and their physical and chemical properties (Nwoko et al., 2022). Nwoko et al. (2022) found that irrigated agriculture is associated with expanding schistosomiasis in SA. A study highlighted how irrigated farming affects the spread of schistosomiasis, suggesting that the development of water resources and growth in agriculture can influence how widespread the disease is (Lund et al., 2021).

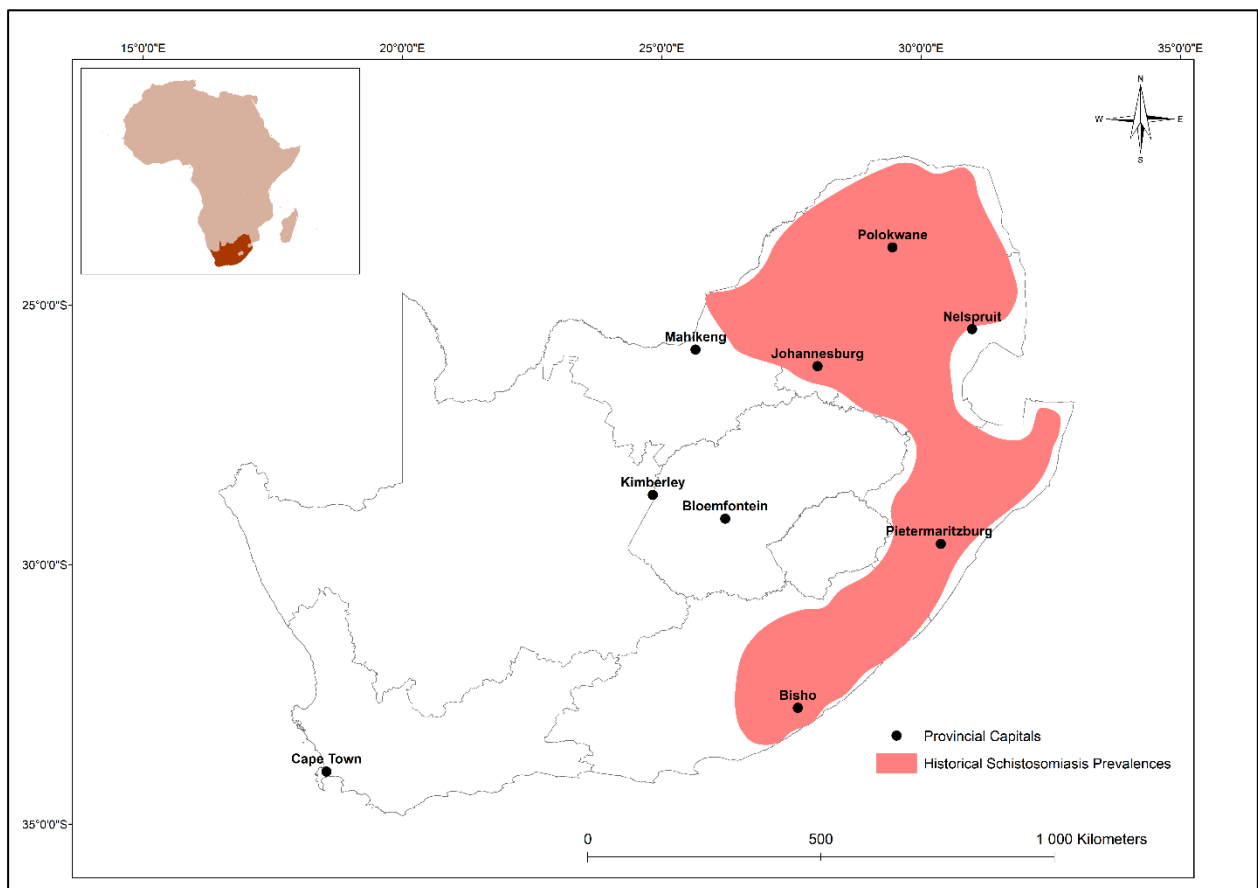


Figure 3-1: Map of South Africa showing the provincial capitals. The red-shaded areas show the historical prevalence of schistosomiasis.

3.2 Characterising the historical distribution of *Schistosoma*-transmitting snails in South Africa

3.2.1 Constructing a digital geospatial database for the intermediate host's historical occurrences.

To model the historical distribution of *Schistosoma*-transmitting snails in SA, a geospatial database was created for the historical intermediate hosts in SA over 50 years. The occurrence data were obtained from the National Snail Freshwater Collection (NFSC) from 1950 to 2006. The National Freshwater Snail Collection is managed by the Unit for Environmental Sciences and Management at North-West University, Potchefstroom, South Africa. This collection was in a CSV format; however, the occurrence dataset was stored in quarter-degree grids. Records that included *B. africanus*, *B. globosus* and *B. pfeifferi* were extracted from the dataset, and 15370 records were digitised (Table 3-1). In addition, the 15370 records did not have an exact location; hence, they were manually digitised based on the location descriptions of points, creating precise point features. A 1:50000 topographical map was used to digitise the occurrence point to ensure spatial accuracy. Based on the descriptions of the points, the locations were digitised close to waterbodies (dams, rivers, reservoirs, lakes, and wetlands). The approach was motivated by ecological factors, focusing on the importance of water bodies as crucial habitats for snails, impacting where they are found and their abundance. Each point's corresponding latitude and longitude coordinates were stored in decimal degrees using a Geographical Coordinate System (WGS1984). Figure 3-2 shows the process of creating the geodatabase.

Table 3-1 shows the number of historical occurrence points for snail vectors of schistosomiasis species found in South Africa from 1950 to 2006.

Species	Occurrence Points
<i>Bulinus africanus</i>	3051
<i>Bulinus globosus</i>	3153
<i>Biomphalaria pfeifferi</i>	9166

The digitised points were checked for errors, inconsistencies, and duplicates to ensure data quality control. Lastly, a geodatabase was constructed to create feature classes for each snail species. The results are shown in *Chapter 4*.

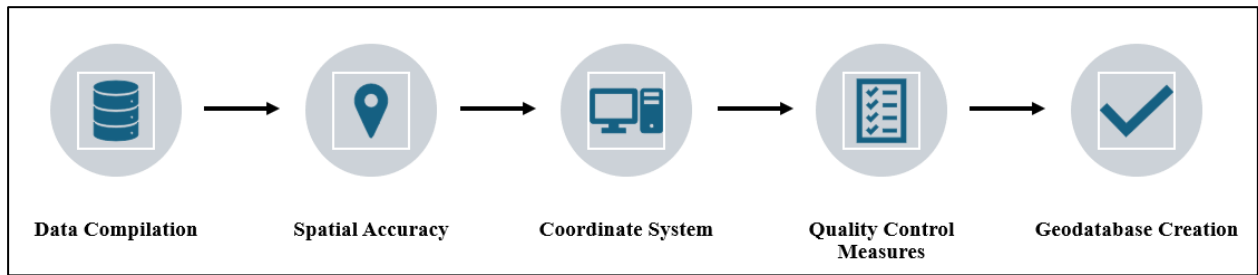


Figure 3-2: A diagram showing the processes taken to create the digital database.

3.2.2 Historical bioclimatic data

As discussed in (Section 3.2.1), to model the historical distribution of *Schistosoma*-transmitting snails accurately, it is essential to have information on the locations where snails have been found. The snail occurrence data must be combined with environmental data to create a comprehensive model of the historical distribution. This section discusses the relevant data needed for modelling the historical distribution of *Schistosoma*-transmitting snails.

The thesis concentrated on Bioclimatic Variables (BCVs) and soil water content due to their perceived importance in the distribution of intermediate host snails (Appleton and Eriksson, 1984; Stensgaard et al., 2013; Fuss et al., 2020). The BIOCLIM program, starting in 1984, introduced 12 BCVs based on temperature and precipitation data. In 1996, the BCVs expanded to 19 variables, incorporating annual factors like minimum temperatures and precipitation levels. Further enhancements in 1999 added more variables, totalling 35 BCVs, including complex water balance interactions (Booth, 2018).

Bioclimatic variables are mostly used in SDM to analyse niche evolution, delineate protected areas, define ecological limits, and assess the habitat suitability of invasive species (Warren et al., 2010; Cunze et al., 2016; Koch et al., 2016; Fourcade et al., 2018). Booth et al. (2014) observed that over 76% of studies on MaxEnt models incorporate at least one BCV, with 55% using all BCVs. Similarly, Fourcade et al. (2018) found that in their review of 190 studies focusing on terrestrial organisms, more than 87% utilised at least one BCV, and 20% used all BCVs. Bioclimatic variables offer data on temperature and precipitation at different time scales, which are more important than monthly climate data for species distributions due to their physiological relevance (Deblauwe et al., 2016).

ERA originates from the European Centre for Medium-Range Weather Forecasts (ECMWF) Reanalysis. Therefore, ERA refers to datasets produced by ECMWF through reanalysis processes, which involve integrating observational data with numerical weather prediction models to generate consistent global atmospheric datasets. Given the extensive time series of historical occurrence points over 50 years, ERA 5, which is gridded and contains a comprehensive historical global reconstruction of bioclimatic indicators, was used in this thesis (Copernicus Climate Change Service). The ERA 5 dataset was considered due to the spatial resolution of $0.5^\circ \times 0.5^\circ$ and a temporal resolution of hourly intervals, enabling in-depth analysis of environmental factors essential for ecological modelling (Hans, 2024; Copernicus Climate Change Service). Secondly, ERA 5 has global coverage, providing data for marine and terrestrial environments. Thirdly, ERA 5 provides data from 1979 to the present, offering a long-time series for ecological modelling (Hans, 2024). Bioclimatic variables were selected due to their ability to represent yearly trends, seasonal variations, and extreme environmental conditions. These variables are frequently utilised in modelling ecological niches and species' potential distributions. (Guo et al., 2013; Mainali et al., 2015; Yang et al., 2018). Lastly, using ERA 5 for future bioclimatic data from Coupled Model Intercomparison Project Phase 5 (CMIP5) outputs ensures consistency in spatial resolution between historical and future datasets. This approach maintains the integrity of ecological modelling by keeping spatial scales consistent across different periods.

From 1979 to 2018, bioclimatic variables were extracted using ERA 5 reanalysis data provided by the Copernicus Climate Change Service. This study used 19 bioclimatic and 4 soil indicators from 1979 to 2006. The soil indicators included volumetric soil water layer in the coldest, wettest, driest and warmest quarter. The soil indicators were included in the modelling process because *S. haematobium* can survive in soil/mud and endure long periods in cold temperatures, showcasing its adaptability to various climates, including heat waves (Kalinda et al., 2018). The temporal aggregation for the bioclimatic and soil indicators was the mean climatological period pre-calculated over the 40-year reference period 1979-2018 with a spatial resolution of $0.5^\circ \times 0.5^\circ$.

3.2.3 Identifying key bioclimatic variables that can be used to model the historical and future distribution of *Schistosoma*-transmitting snails.

The distribution of species is strongly influenced by climate. Advances in modelling techniques like MaxEnt using BCVs make results comparable across studies (Merkenschlager et al., 2023). However, using BCVs has drawbacks due to high correlations between some variables, which

most SDM techniques cannot handle. To address this, it is crucial to preselect relevant predictors based on species-specific key limiting factors identified through expert knowledge or statistical methods (Merkenschlager et al., 2023).

A group of variables was chosen based on bioclimatic and soil factors to minimise collinearity in the dataset (Table 3-2). The *USDM* R package calculated the Variance Inflation Factor Core (VIF). This analysis measures the strength of the relationship between each predictor and the rest (Naimi and Araújo, 2016). In VIFs, the multiple correlation coefficients (R^2) are obtained by performing a regression analysis of each predictor variable against the other variables in the model. If the VIF is >10 , it indicates a collinearity problem (Chatterjee and Hadi 2015). All the variables >10 were removed from the dataset using a threshold (th) of 0.85. The VIF is calculated by excluding highly correlated variables through a stepwise procedure (Table 3-3). During the VIF calculation process, the algorithm looks for variables with a linear correlation exceeding the predefined th value (Naimi and Araújo, 2016). The process was repeated until none of the variables had a high correlation coefficient (r). To determine VIF, a linear regression model was employed, where the numerical variable of interest was utilised as the response variable Eq (1). It must be noted that, due to the nature and distribution of the species, each species has a unique set of bioclimatic variables.

$$VIF = \frac{1}{1 - R_i^2}$$

Where R^2 represents the linear model's regression coefficient.

Table 3-2: The selection of bioclimatic variables for the ecological models based on their VIF values.

Species	Variable	Description	VIF
<i>B. africanus</i>	Bio 3	Isothermality	9.1
	Bio 5	Max temperature of the warmest	4.0
	Bio 8	month	4.1
	Bio 13	Precipitation of the wettest month	5.5
	Bio 15	Precipitation seasonality	6.6
	Bio 16	Precipitation of the wettest quarter	7.4
	Soil water volume for the wettest quarter		9.0
	Soil water volume for the coldest quarter		6.3
	Soil water for the warmest quarter		5.5
<i>B. globosus</i>	Bio 4	Temperature seasonality	3.9
	Bio 7	Temperature Annual Range	3.1
	Bio 8	The mean temperature of the wettest quarter	3.8
	Bio 15	Precipitation seasonality	3.2
	Bio 16	Precipitation of the wettest quarter	5.8
	Bio 17	Precipitation of the driest quarter	5.7
	Soil water for the warmest quarter		1.7
<i>B. pfeifferi</i>	Bio 4	Temperature seasonality	6.9
	Bio 8	The mean temperature of the wettest quarter	3.2
	Bio 12	Annual precipitation	7.3
	Bio 16	Precipitation of the wettest quarter	9.2
	Bio 18	Precipitation of the warmest quarter	3.1

3.2.4 Ecological Niche: the fundamental niche

The ecological niche of a species is the set of environmental conditions that enable the species to flourish without requiring migration (Peterson et al., 2011). Ecological niche modelling is used in public health to understand the ecology of vector-borne diseases by identifying areas and conditions that support disease agents (Ponpetch et al., 2021). Various techniques like GARP, MaxEnt, RF, GLM, and GAM are used to estimate species' spatial distributions (Blackburn, 2010; Scholte et al., 2012). However, selecting the most suitable technique for a specific application is challenging due to different data requirements and factors influencing performance. One potential solution to this problem involves merging various niche modelling methods into an ensemble model (Valavi et al., 2022). An ensemble model in machine learning is used to enhance predictive accuracy. (Section 3.2.5) explains the use of ensemble models in this thesis.

This thesis utilised two kinds of data to estimate fundamental niches: (1) precise species occurrence data with errors removed and (2) environmental layers tailored to the study area to extract relevant environmental data linked to occurrences and sites within the area. Using *S. mansonii* and *S. haematobium* occurrences in the models helps determine if the estimated niche accurately represents the true fundamental niche by assessing if it includes the areas these species have been able to invade under future climate projections and scenarios.

3.2.5 Ecological Niche Models

Correlative models play a vital role in evaluating how climate change affects species distribution using GCM data (Rougier et al., 2015). These models may over- or under-predict potential distributions based on the algorithm used. Various algorithms estimate species' ecological niches based on environmental variables (Karger et al., 2017). Presence-absence, presence-background, and presence-only methods are various types of biological input data. Presence-absence methods analyse species observations and absences to assess habitat conditions, while presence-background methods compare environmental conditions to species requirements (Franklin, 2010). Presence-only methods often use pseudoabsence data due to absence data scarcity. Strategies have been proposed to enhance pseudoabsence dataset selection (Sillero, 2011).

Model and measurement uncertainty are the two main types of uncertainty in SDMs. Uncertainty stems from simplifications or assumptions in the model, like in climate projections, while measurement uncertainty arises from imprecise data, like incorrect geographic coordinates (Elith et al., 2002). Studies have explored uncertainty by comparing different modelling algorithms or altering predictor variables while keeping species and algorithms constant. Some research combines these factors to analyse uncertainty comprehensively (Watling et al. 2012). For instance, a study focusing on a particular species discovered that the algorithm played a significant role in causing uncertainty, with the occurrence data and predictor variable co-linearity closely following (Dormann et al., 2007).

In addition, three ecological niche models were utilised in this thesis to enhance prediction accuracy by reducing the uncertainty associated with a single model: GLM, MaxEnt and RF, as illustrated in (Table 3-3; Petersen et al., 2014; Manyangadze et al., 2016; Kulinkina et al., 2018; Ponpetch et al., 2021; Zhang et al., 2021).

Linear regression is frequently used in environmental modelling for its simplicity, interpretability, and effectiveness in predicting binary outcomes (Valavi et al., 2022). This study employs GLM to understand how environmental factors impact the presence or absence of specific species or phenomena. By estimating the likelihood of occurrence using environmental variables, GLM aids in recognising the key factors influencing the observed trends (Valavi et al., 2022). In addition, MaxEnt is a valuable tool for modelling species distribution, especially with presence-only data (Hastie et al., 2009). Unlike GLM, MaxEnt assumes no specific relationship between predictors and the response variable. It maximises entropy within the study area based on available data constraints, enabling it to handle complex patterns and predict effectively with limited information (Phillips et al., 2006). Random Forest, a machine learning technique, is recognised for its strength in managing intricate relationships between predictor variables. It builds numerous decision trees, each utilising a random sample of data and features. By combining the predictions of these trees, RF reduces overfitting and enhances overall predictive accuracy (Valavi et al., 2021). Random Forest is appreciated for capturing nonlinear connections and interactions among environmental factors, proving valuable for complex systems where conventional linear models may be inadequate (Strobl et al., 2009; Valavi et al., 2021). In essence, the choice of logistic regression, MaxEnt, and RF in this study is a strategic approach to environmental modelling, utilising the strengths of each method to understand the influences on species distribution. More information on ENMs can be found in (Section 2.4.2).

Table 3-3: The characteristics of the ecological niche models used in this thesis.

ENM	Method	Format	Reference
GLM	Regression analysis	Presence/Pseudo-absence	(Valavi et al., 2021)
RF	Regression analysis	Presence/Pseudo-absence	(Strobl et al., 2009).
MaxEnt	Maximum Entropy	Presence/ Pseudo-absence	(Phillips et al., 2006).

This thesis is based on a multi-model SDM approach (Naimi and Araújo, 2016) implemented in the SDM package, and *dismo* was used to examine and model species distribution. This R package unifies different implementations of SDM into one object-oriented framework that is reproducible and extensible. Based on the methodology of Zuza et al. (2021), the occurrence data were divided

into two groups: training and testing. Ecological niche models were evaluated using 75% training and 25% test data (Tan et al., 2020; Gong et al., 2022; Nwoko et al., 2023a). A logistic output format was used based on environmental variables in grid cells, ranging from 0 (unsuitable habitat) to 1 (suitable habitat) (Niu et al., 2019). While presence-only models are commonly used, ENM model evaluations show that presence-background techniques are more efficacious (Merow et al., 2013). A limitation is using pseudo-absence data due to the lack of disease-absence data. To address this, the analysis was conducted with 10000 random pseudo-absence points (Jarnevich et al., 2017).

To evaluate the stability and accuracy of the models, the number of maximum iterations was increased to 5,000 iterations using subsets to reduce underestimations and overestimations (Daba et al., 2021). By doing so, the model will have adequate time to converge. This ensured better data distribution (Barbosa et al., 2016). Regularisation is used in machine learning and ecological modelling to prevent overfitting by penalising large parameter values, encouraging smaller weights, and maintaining model simplicity (Kolluri et al., 2020). The regularisation parameter is typically set to 1 in models such as logistic regression to find a middle ground between accurately fitting the training data and avoiding unnecessary complexity that might not work well with new data. This approach helps reduce overfitting and enhances the model's generalisation capability to unseen data (Kolluri et al., 2020). Therefore, it was decided that the regularisation remained at 1 to reduce model overfitting (Young et al., 2011; Merow et al., 2013).

Ensemble modelling combines various models to make predictions, which can be different types or trained on different data subsets. Each model may capture specific data aspects or offer distinct insights. Based on the results of three ENMs, an ensemble model was developed to model the distribution of schistosomiasis in SA. Ensemble models combine all algorithms, which improves performance (Allouche et al., 2006; Mushi et al., 2022). The weights for each model are decided using different criteria, such as the True Skill Statistic (TSS), to assess model performance. Models with higher TSS values, signifying better performance, are prioritised in the averaging process. This method guarantees that more precise models contribute more to the final prediction. All three raw models were combined using "Weighted averaging" by using the TSS that was > 0.75 to create an ensemble (Mushi et al., 2022). Predictions from different models are combined by calculating a weighted average in weighted averaging. Each model's prediction impacts the outcome, with varying degrees of influence based on assigned weights reflecting their performance or accuracy (Mushi et al., 2022). Weighted averaging was preferred over simple averaging as it enhances the

ensemble's performance by emphasising the best-performing models' strengths. This results in better predictions compared to using a single model.

All analyses were done in R version 4.2.1, utilising various packages for data processing, analysis, and visualisation. These packages include ggplot2, ks, raster, rgdal, rgeos, scales, and sf, each serving different functions in our research (Wickham, 2016; Hijmans, 2020; Bivand and Rundel, 2019).

3.2.6 Ecological niche model evaluation

TSS and the Area Under the Curve (AUC) metrics were employed to assess the model performance in evaluating ecological niche models. TSS and AUC metrics were used to comprehensively evaluate the model's predictive capability, considering both accuracy and discriminant power. Higher values in the area under the curve (AUC), Relative Operating Characteristics (ROC) and TSS indicate better performance in evaluating the model's predictions (Allouche et al., 2006). Known as the Hanssen Kuipers Discriminator, TSS compares the number of actual positive forecasts to the number of correct hypothetical projections. It is pertinent to note that TSS includes omissions and commissions. A value of +1 indicates accurate classification. In contrast, a value of -1 indicates no better performance than random. AUC can be used to calculate ROC values. Random predictions are represented by 0.5, and predictions > 0.5 are better than the random model (Anderson et al., 1979; Wouyou et al., 2022). The AUC values analyse the presence and absence of data across a range of thresholds. An AUC value ranges from 0 to 1, 1 representing perfect discrimination, while values ≤ 0.5 show no difference from random prediction (Allouche et al., 2006; Phillips and Duidik, 2008; Nwoko et al., 2023a). The closer the AUC value is to 1, the better the model's discriminant power. An AUC above 0.75 signifies sufficient discrimination and usefulness. The subsequent section focuses on the contribution of bioclimatic variables from the models' outputs.

3.2.7 The contribution of bioclimatic variables

Variable importance and response curve – determining the role of predictor variables in explaining the species distribution is of practical relevance to researchers concerned with interpreting the outputs of the models (Naimi and Araújo, 2016). In this thesis, the importance of each variable was analysed using the model's output to understand the influence of bioclimatic variables. The impact of bioclimatic variables on the model's predictions helped identify which factors will have a greater influence on shaping the future distribution patterns of *Schistosoma*-transmitting snails.

For instance, if specific bioclimatic variables are associated with fluctuations in temperature or rainfall levels, it showed greater significance in the model results. This implies that climate change could considerably affect the future spread of schistosomiasis. *Section 3.3* will discuss the methodologies employed for Objective 2: Characterising the future distribution of *Schistosoma*-transmitting snails using climate projections

3.3 Characterising the future distribution of *Schistosoma*-transmitting snails using climate projections

The model built on historical data (discussed in *Section 3.2*: Objective 1) was expanded to address the second objective. The historical ENMs were applied to future bioclimatic data from climate models representing different scenarios. This approach led to new ENMs to predict potential shifts in habitat suitability and distribution patterns due to climate change.

3.3.1 Climate change projections

The International Panel on Climate Change (IPCC) uses the Coupled Model Intercomparison Project (CMIP) experiments, which are ongoing experiments designed to improve our understanding of Global Circulation Models (GCMs; Change, 2023). The IPCC uses Representative Concentration Pathways (RCPs) to project future climates to 2085 based on greenhouse gas emissions (Nwoko et al., 2023a). The Representative Concentration Pathways outline four distinct pathways for greenhouse gas emissions, atmospheric concentrations, air pollutant emissions, and land use in the 21st century. Integrated Assessment Models (IAMs) were utilised to create the RCPs, which serve as inputs for various climate model simulations to predict their effects on the climate system. These climate projections evaluate impacts and plan adaptation strategies (Change, 2023). RCP 2.6 signifies low emissions, while RCP 4.5 and RCP 6.0 are moderate scenarios, and RCP 8.5 indicates high emissions (Change, 2023). If additional efforts are not made to reduce emissions, the pathway will range between RCP 6.0 and 8.5. Meanwhile, RCP 2.6 represents a scenario where all efforts to reduce emissions successfully keep global warming below 2°C (Nwoko et al., 2023a). However, since achieving RCP 2.6 is deemed nearly impossible, the study uses RCP 4.5 and an extreme case of RCP 8.5 to predict the distribution for schistosomiasis intermediate host snails.

Global Circulation Models are vital for projecting the climate for the next 80 years through complex mathematical representations of the Earth's energy balance across the atmosphere, land, sea,

and ice cover (Yang and Bergquist, 2018). These models consider the interactions of these components as a coupled system, with equations based on dynamic climate variables like temperature and winds across the globe. The chosen GCMs for this study were Access 1-0 (Yang and Bergquist, 2018), Bcc-csm-1-m and Hadgem2-cc; these models were chosen due to satisfactory performance over the African continent (McSweeney, 2014; Table 3-4).

Table 3-4: The three Global Circulation Models used in this thesis.

Global Circulation Model	Characteristics	Developing Center
access1-0	The models employed include the UM atmosphere model from the UK Met Office, the MOM4p1 ocean model from GFDL, the CICE4.1 sea-ice model from LANL, and the MOSES2 land surface model (Yang and Bergquist, 2018).	CSIRO & Bureau of Meteorology, Australia
bcc-csm-1-m	The model combines the BCC-AGCM2.0, CLM3 land surface process, POP global ocean circulation, and CISM global dynamic/thermodynamic sea ice models (Balderama et al., 2017).	Beijing Climate Center Climate System Model
hadgem2-cc	The Hadgem2cc model setup includes an atmospheric simulation where input from additional files replaces other component interfaces (Yang and Bergquist, 2018).	UK Met Office Hadley Centre

3.3.2 Future bioclimatic data

The same bioclimatic variables and soil indicators as those selected for the first objective were used to predict the future distribution of *Schistosoma*-transmitting snails. Maintaining consistency in the variables used for historical and predicted distribution patterns of snails helps compare them accurately. This consistency is important for understanding how climate change may affect their habitat suitability. In addition, it ensures the reliability of the results by reducing variations that could arise from using different sets of variables for different purposes.

The chosen GCMs for this study were access 1-0, bcc-csm-1-m and hadgem2-cc. The future periods (2040-2070) and (2070-2100) were derived from CMIP5 climate projections provided by the Copernicus Climate Change Service (McSweeney, 2014). The predicted bioclimatic data were obtained from three GCMs created in a grid format of 0.5° x 0.5°. The data obtained from Copernicus was pre-adjusted for bias against ERA5 reanalysis data (Wouters et al., 2021). This means

that GCM outputs are compared with observations from ERA5, a high-resolution dataset by ECMWF. This process aims to correct systematic errors in GCM predictions by aligning them with ERA5 data, enhancing the models' accuracy and reliability by better matching real-world climate conditions. The bioclimatic indicators had different temporal resolutions, ranging from monthly, annual, and multiannual averages.

3.3.3 Visual and statistical analyses of future suitable habitat patterns

Threshold selection methods vary, such as using the default threshold of 0.5 commonly seen in ecology, opting for a particular sensitivity or specificity level like 95%, or selecting thresholds to enhance the agreement between observed and predicted distributions (Pearson et al., 2002). In addition, this thesis used a classification system based on Gong et al. (2022) to create thresholds for ecological model outputs. The threshold was based on the AUC values; these thresholds are as follows: non-suitable habitats (0.00 to 0.33), low suitability habitats (0.33-0.66), moderate suitability habitats (0.66-0.90), and high suitability habitats (0.90-1.00; Niu et al., 2019; Gong et al., 2022).

3.3.4 Predicted Ecological Niche Model Evaluation

This section is similar to (Section 3.2.6), which evaluates the ENMs' performance using bioclimatic data from GCMs for different emission scenarios. Commonly used metrics like the AUC and TSS are employed to evaluate predictive models for species distribution. These metrics are assessed through cross-validation, a method that rigorously tests the models' predictive performance without requiring a standard train-test data split. Cross-validation is a method used to evaluate predictive models when traditional train/test splits are unavailable due to the absence of known records for future periods (Roberts et al., 2016). The following steps were employed to conduct cross-validation for the models' performances.

- I. Data partitioning - The future bioclimatic data and presence background records (section 3.2.5) were split into 10 folds using the k-fold cross-validation method (Kuhn and Johnson, 2013).
- II. Model training and testing - During each iteration for cross-validation, the ecological niche model was trained on the first fold, treated as a validation set, and the method was fit on

the remaining $k - 1$ folds and tested on the remaining $10 k - \text{fold}$. This cycle was repeated 5 times, ensuring each fold served as the test set exactly once (James et al., 2013).

- III. Performance evaluation - The model's performance was assessed after each iteration by calculating metrics like AUC and TSS based on test set predictions. These metrics were combined across all iterations to determine the overall model performance.

Area Under the Curve and TSS were employed to understand how well the models could predict changes in habitat suitability and distribution patterns under various climate change scenarios. These metrics provided important insights into the models' reliability in the absence of known occurrences for future periods. *Section 3.4* will discuss the methodologies employed for objective 3: Examine the impacts of climate change on the predicted distribution of *Schistosoma*-transmitting snails in SA.

3.4 Examine the impacts of climate change on the predicted distribution of *Schistosoma*-transmitting snails in South Africa

In the third objective, the thesis assesses habitat suitability maps, a common focus in studies predicting future distribution under climate change scenarios. This was done by obtaining the difference between the baseline output (historical model output) and climate projection for each emission scenario and climate model. This methodology provides insights into the potential impact of climate change on the geographic range and prevalence of schistosomiasis.

3.4.1 Potential changes of suitable areas for *Schistosoma*-transmitting snails under different climate scenarios

Understanding the potential changes in suitable habitats for *Schistosoma*-transmitting snails under different climate scenarios is crucial for predicting future disease transmission dynamics. The change in climate and habitat suitability need to be calculated to examine the impacts of climate change on the predicted distribution of *Schistosoma*-transmitting snails.

The change in climate suitability was calculated using the difference between the predicted ensemble and historical ensemble model because it showed the highest performance accuracy (Pedersen, 2014b). The comparison involved assessing how well suitability change maps aligned with projections of areas expected to increase, decrease, or remain unchanged over the next 77

years. To quantify the changes in suitability, the study area was divided into grid cells to assess changes in habitat suitability for *B. africanus*, *B. globosus* and *B. pfeifferi*. Each cell was classified as having increased, decreased, or unchanged suitability compared to the historical period. This classification was determined using the model outputs, which define suitable habitat conditions for the snails based on bioclimatic variables. The calculated area (km²) for the suitable habitats was expressed as a percentage of the total habitat for each model, as well as different year periods and emission scenarios.

To create suitability change and composite maps, the calculated differences were evaluated to determine the changes in the distribution of *B. africanus*, *B. globosus* and *B. pfeifferi*. The composite maps were created by reclassifying the outputs of suitability change to show how habitat suitability has shifted for each species and the magnitude of these changes. The reclass tool was used in ArcGIS 10.8.2 to reclassify suitability change outputs for each climate model and period (Pedersen et al., 2014a). The reclassified values ranging from -0.5 to 0.5 were utilised to indicate the extent and direction of changes compared to the historical distribution of schistosomiasis intermediate hosts. A value of -0.5 signifies reduced suitability, showing a negative shift. The value of 0 denotes unchanged suitability, indicating no difference. A value of 0.5 indicates improved suitability, reflecting a positive change. The suitability change maps show the potential future distribution of *Schistosoma*-transmitting snails and the associated risk of schistosomiasis under various climate scenarios. This is essential for public health planning and disease control strategies, aiding in understanding and predicting the impact of climate change on snail distribution in SA. It assists in evaluating how environmental changes could influence the transmission risk of schistosomiasis in the country.

3.5 Chapter Conclusion

This chapter gave a detailed explanation of the methods used in the study, covering data collection, selection of environmental variables, modelling techniques, and evaluation of the model performance. The next chapter discusses the results for *Objective 1*: Characterise the historical distribution of *Schistosoma*-transmitting snails in South Africa using ENMs.

CHAPTER 4

The following chapter presents the results for Objective 1: ‘*Characterise the historical distribution of Schistosoma-transmitting snails in South Africa using ENMs.*’ Understanding the historical distribution of *Schistosoma*-transmitting snails is important in assessing schistosomiasis transmission risk. This chapter presents the historical locations of *Schistosoma*-transmitting snails. The intermediate hosts' historical suitable habitats and environmental conditions are also shown.

THE HISTORICAL DISTRIBUTION OF *SCHISTOSOMA*-TRANSMITTING SNAILS IN SOUTH AFRICA

4.1 A digital geospatial database for the intermediate host's historical occurrences

Species occurrences and distribution play a crucial role in ecological modelling by providing essential data for understanding species distribution and habitat suitability. Past species observations can help model their distribution over time and space and evaluate habitat suitability. In this thesis, a geospatial database was created for 15370 historical snail occurrences from 1950 to 2006 to model the past and future distribution of *Schistosoma*-transmitting snails. Figure 4-1 shows a map of all the historical snail occurrences that have been digitised.

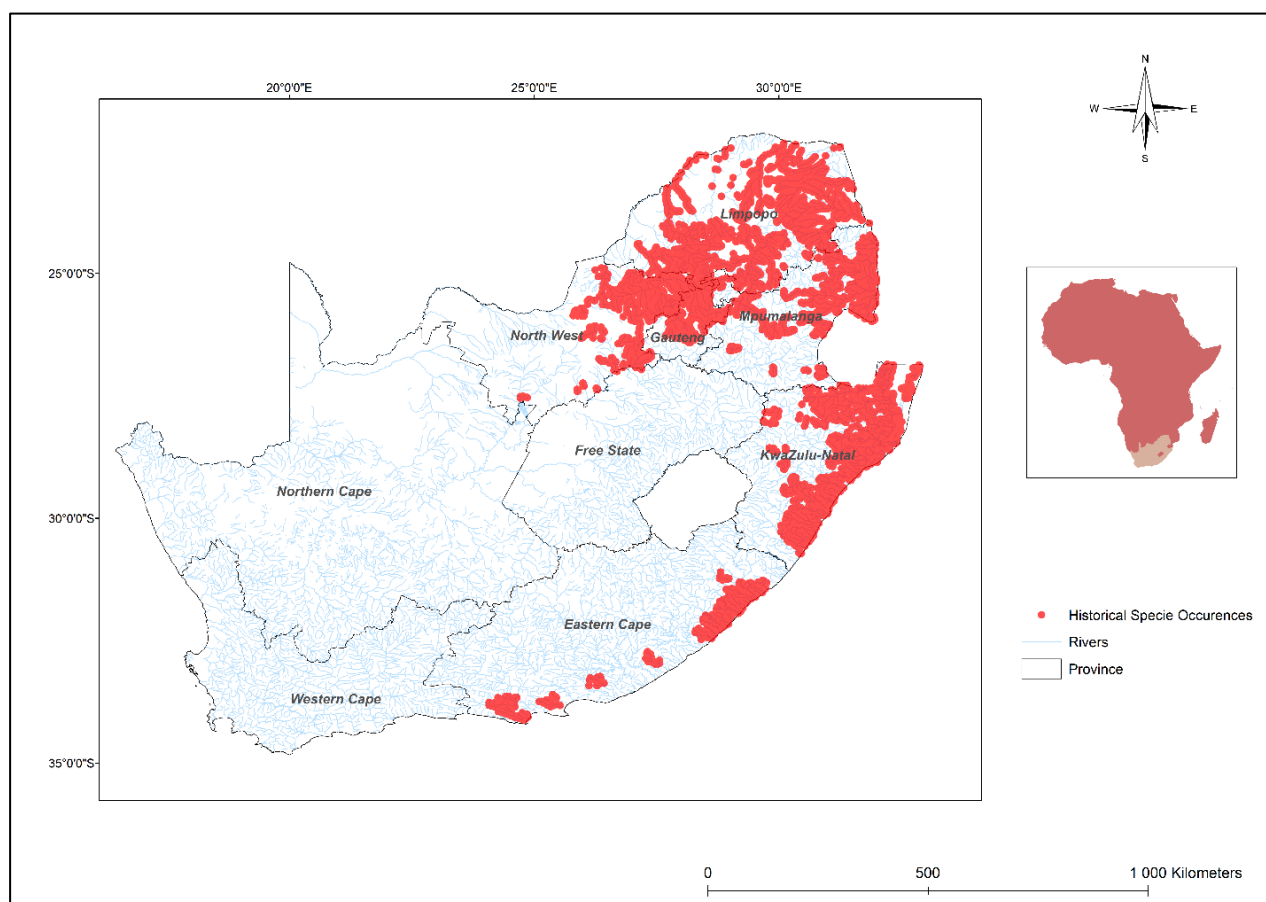


Figure 4-1: Digitised historical occurrences in red for *Bulinus africanus*, *Bulinus globosus* and *Biomphalaria pfeifferi* in South Africa.

4.2 Modelling the historical distribution of *Schistosoma*-transmitting snails

This section will include the results of the performance of the ENMs, the suitable historical bioclimatic habitats, and the spatial distribution of *Schistosoma*-transmitting snails in SA.

Table 4-1 illustrates the AUC and TSS values for the different models and species. All three models had significant AUC and TSS values, demonstrating excellent performance. The RF outperformed the other models in terms of model performance across different species, followed by MaxEnt and GLM. The results showed that the ensemble models achieved the highest AUC scores (0.99) among the three ENM models. Evaluation of the model showed that it was based on competence rather than chance in modelling the historical distribution of schistosomiasis. It must be noted that the high AUC value provides confidence that the ensemble model can be used to examine schistosomiasis-prone areas under current and future climates.

Table 4-1: AUC and TSS for *Bulinus africanus*, *Bulinus globosus* and *Biomphalaria pfeifferi* for the different ENMs used in this thesis.

Species	Model	AUC	TSS
<i>Bulinus africanus</i>	GLM	0.87	0.70
	MaxEnt	0.95	0.77
	RF	0.95	0.93
	Ensemble	0.99	0.95
<i>Bulinus globosus</i>	GLM	0.94	0.78
	MaxEnt	0.95	0.79
	RF	0.98	0.89
	Ensemble	0.99	0.94
<i>Biomphalaria pfeifferi</i>	GLM	0.92	0.73
	MaxEnt	0.93	0.75
	RF	0.97	0.83
	Ensemble	0.99	0.94

Figures 4-2 to 4-4 illustrate ROC plot graphs for *B. africanus*, *B. globosus* and *B. pfeifferi*. These figures show a range of threshold probability values for the True Positive Rate (sensitivity) and False Positive Rate (1-specificity) on the Y-axis. The closer ROC follows sensitivity, the more AUC will have a larger area. With an ROC curve that follows the Y-axis closely, the AUC is larger. Thus, the model will be more accurate. A random model or guess will result in a point along the grey-dotted diagonal line. The results showed that the average ROC scores for GLM, MaxEnt

and RF performed well, with all the models averaging an ROC score ≥ 0.89 . For all three models, RF performed the most accurately (1), followed by MaxEnt (0.93) and GLM (0.9). This indicates that RF is the most accurate model for predicting species occurrence. Furthermore, the high AUC scores suggested that the models can be used to predict species occurrence with a high degree of confidence.

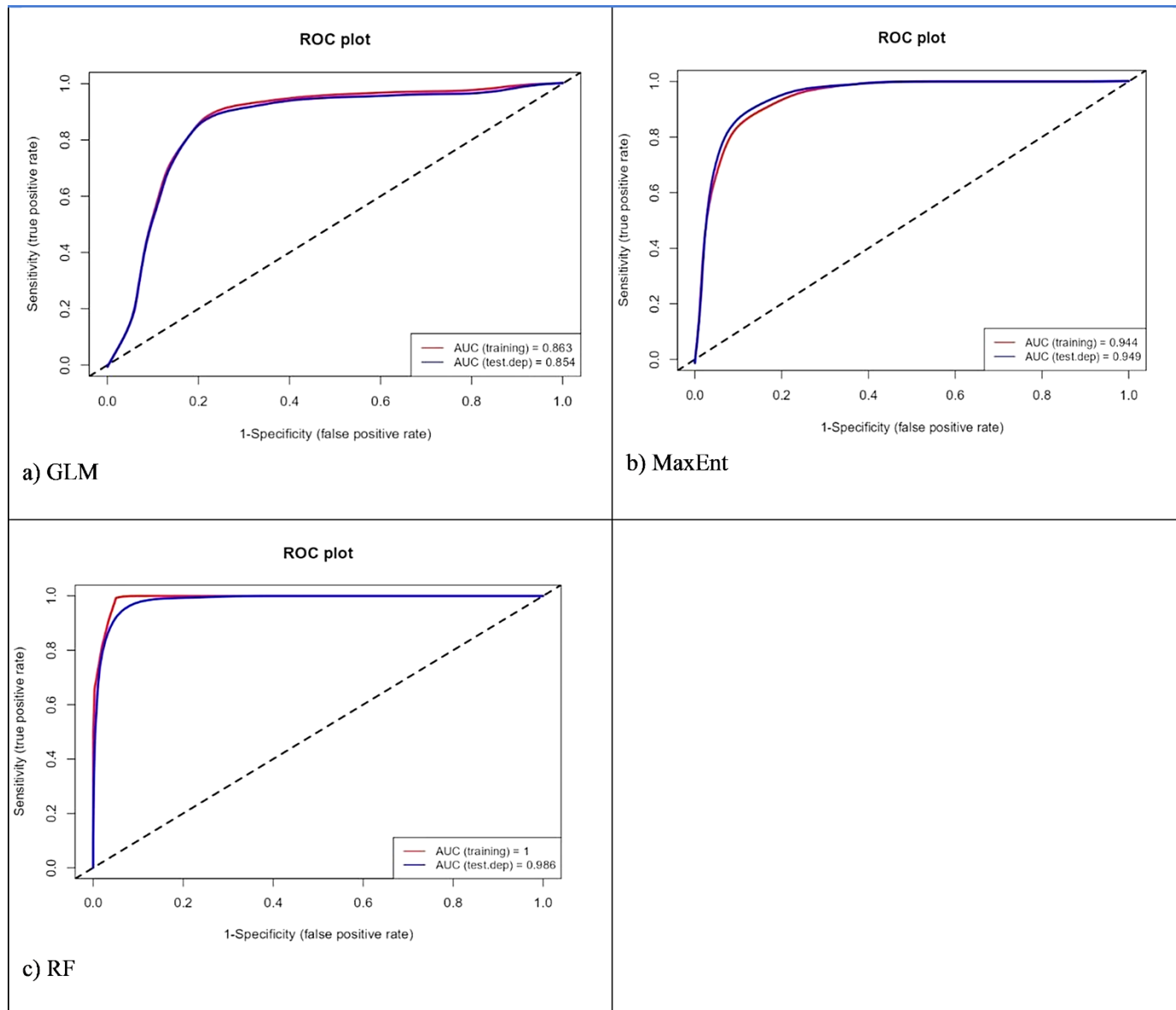


Figure 4-2: Area under the curve and Relative Operating Characteristics for *Bulinus africanus* using three different models, namely (A) GLM, (B) MaxEnt, and (C) RF.

THE HISTORICAL DISTRIBUTION OF SCHISTOSOMA-TRANSMITTING SNAILS IN SOUTH AFRICA

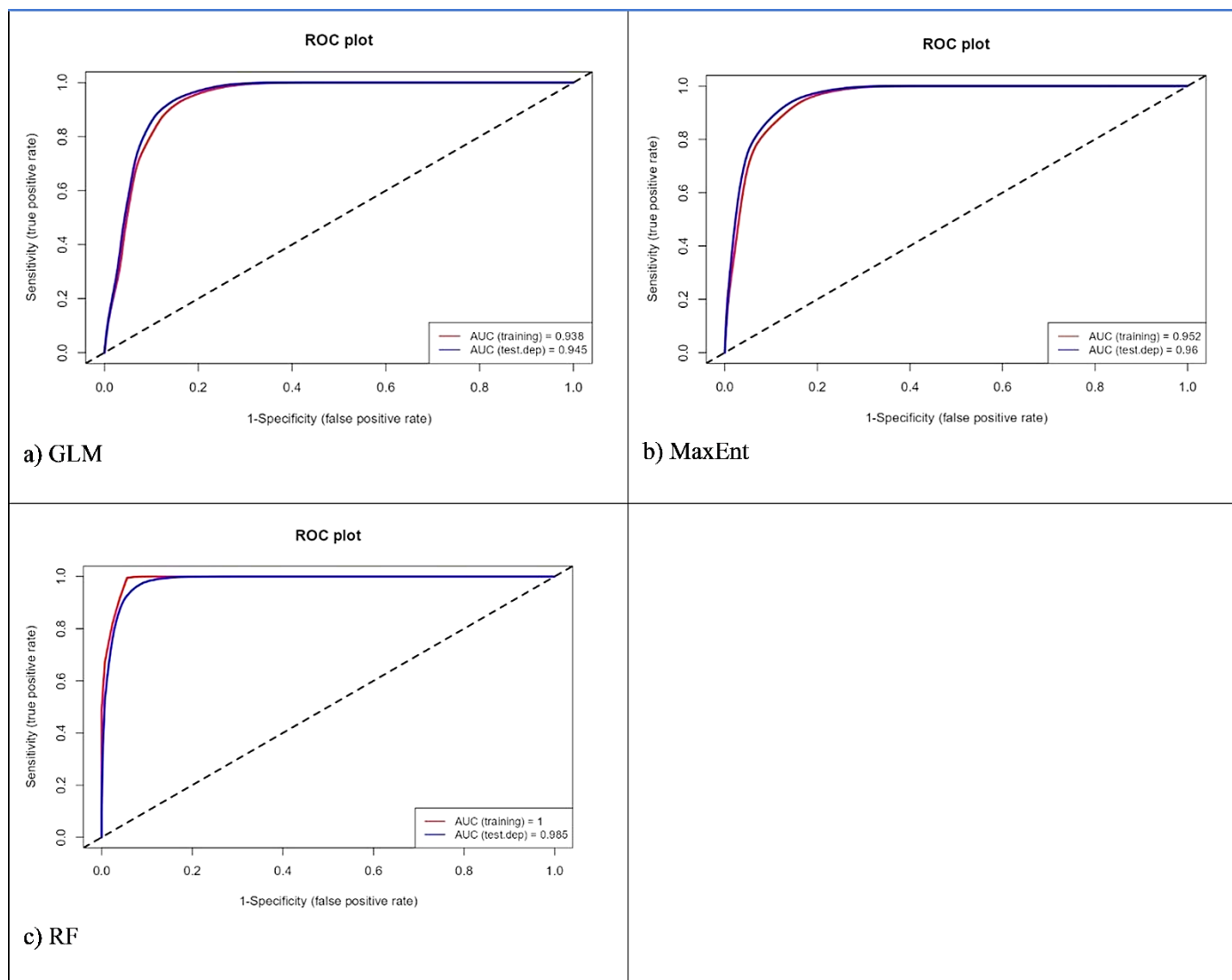


Figure 4-3: Area under the curve and Relative Operating Characteristics for *Bulinus globosus* using three different models, namely (A) GLM, (B) MaxEnt, and (C) RF.

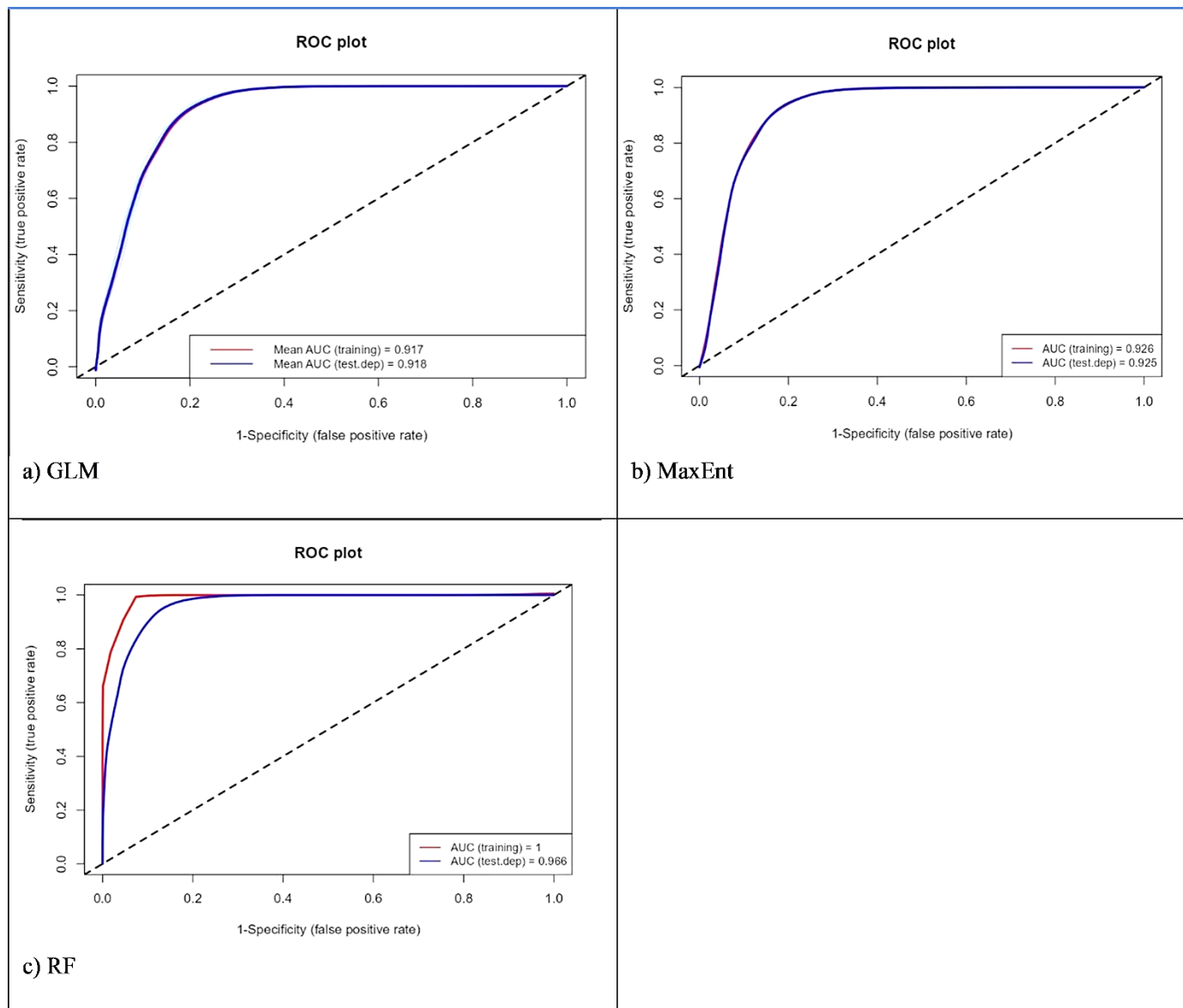


Figure 4-4: Area under the curve and Relative Operating Characteristics for *Biomphalaria pfeifferi* using three different models, namely (A) GLM, (B) MaxEnt, and (C) RF.

All three models performed well in the historical distribution areas of *B. africanus*, *B. globosus* and *B. pfeifferi*. Based on its accuracy in determining species distribution limits, the RF model performed better than MaxEnt and GLM.

4.2.1 Historical bioclimatic suitable habitats

Among the three models that modelled *B. africanus*, precipitation-related variables had the greatest influence on the suitability for schistosomiasis, indicating that most *B. africanus* species thrive in

rainfall environments (precipitation of the wettest month and quarter), as shown by the response curves (Figure 4-5) and relative variable importance (Figure 4-6 to 4-8). The suitable habitat for *B. africanus* in terms of Isothermality (bio3) ranged from 40 to 65%. The species showed optimal performance in environments where the Maximum Temperature of the Warmest Month (bio5) was between 21 to 25 °C. Additionally, *B. africanus* preferred the Mean Temperature of the Wettest Quarter (bio8) within the range of 6 to 26°C. *Bulinus africanus* does not favour high rainfall environments and thrives in regions with low to moderate precipitation levels for Precipitation of the Wettest Month (bio13) and Precipitation of the Wettest Quarter (bio16). Precipitation Seasonality (bio15) exhibited minimal variation, typically peaking at 0.4, indicating that conditions with consistent rainfall throughout the wet quarter are optimal for *B. africanus*. *Bulinus africanus* does not prefer low Soil Water for the Coldest Month. Its response declines, suggesting a low preference for excessively dry conditions. Conversely, *B. africanus* prefers soil water in the Wettest Quarter, demonstrating tolerance and the ability to thrive in moist soil conditions.

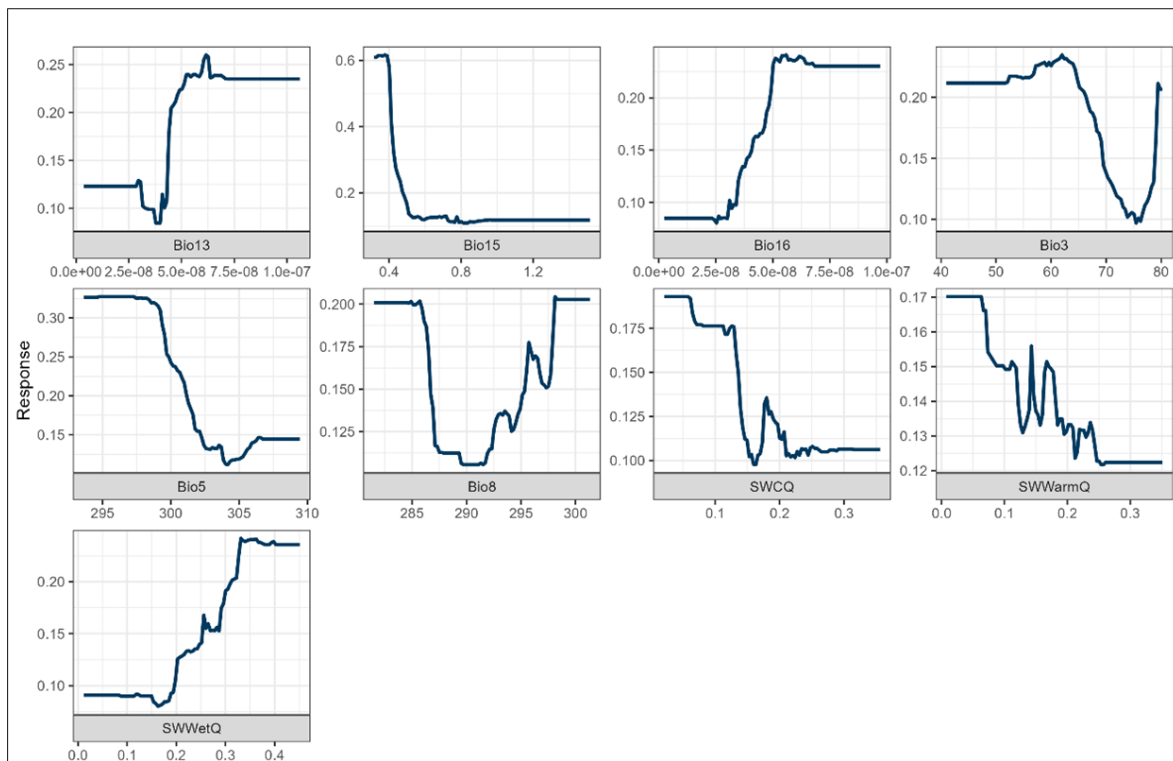


Figure 4-5: Response curves for *Bulinus africanus* against bioclimatic variables using the ensemble model (Bio13 ms⁻¹, Bio15 %, Bio16 ms⁻¹, Bio3 %, Bio5 K, Bio8 K) and soil variables (SWCQ m³ m⁻³—soil water for the coldest quarter, SWWarmQ m³ m⁻³—soil water for the warmest quarter, and SWWetQ m³ m⁻³—soil water for the wettest quarter).

For the GLM and MaxEnt, precipitation for the wettest quarter (bio16) (November to January) and precipitation for the wettest month (bio13) accounted for 65% in determining the suitability of schistosomiasis. Moderate precipitation allows for the transportation of snails and supports the creation of new habitats and temporary snail habitats. Soil water for the wettest quarter contributed 32% to the suitability for schistosomiasis. In the RF model, bio 16 accounted for 35.5%, followed by soil water 32%. For the GLM and MaxEnt, temperature variables contributed 59% to schistosomiasis suitability. *Bulinus africanus* was found to be more suitable during the maximum temperature of the warmest month (bio5, 21.8°C). The results showed that for the mean temperature of the wettest month, *B. africanus* favoured cold to warm temperatures of 6.8°C and 26°C. Compared to *B. globosus*, *B. africanus* is better adapted to colonising cooler environments. Isothermality (bio3) accounted for 6.1% and did not affect schistosomiasis suitability. This indicates that *B. africanus* thrives in both cold and warm climates. For RF, combined temperature variables contributed 31.9%, while the mean temperature of the wettest quarter (bio8) contributed 13.3% to the suitability of schistosomiasis in SA. Thus, *B. africanus* suitability depends primarily on precipitation, temperature, and seasonal variations rather than annual averages. This is because the environment in SA varies significantly from season to season, and the parasites that cause schistosomiasis require specific conditions to survive and thrive. Thus, precipitation, temperature, and seasonality are critical factors in determining the suitability of the environment for these parasites.

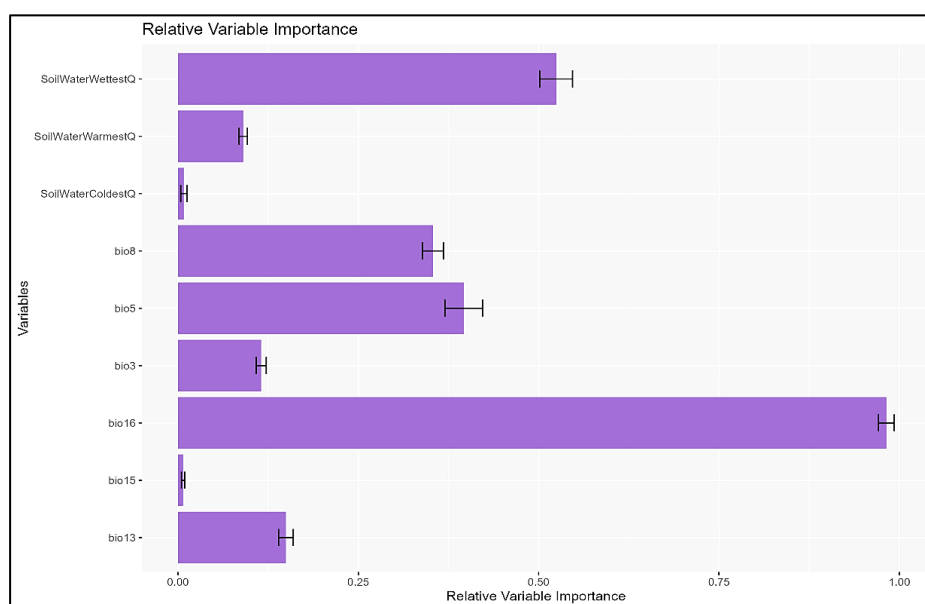


Figure 4-6: Relative variable importance for *Bulinus africanus* using the GLM model.

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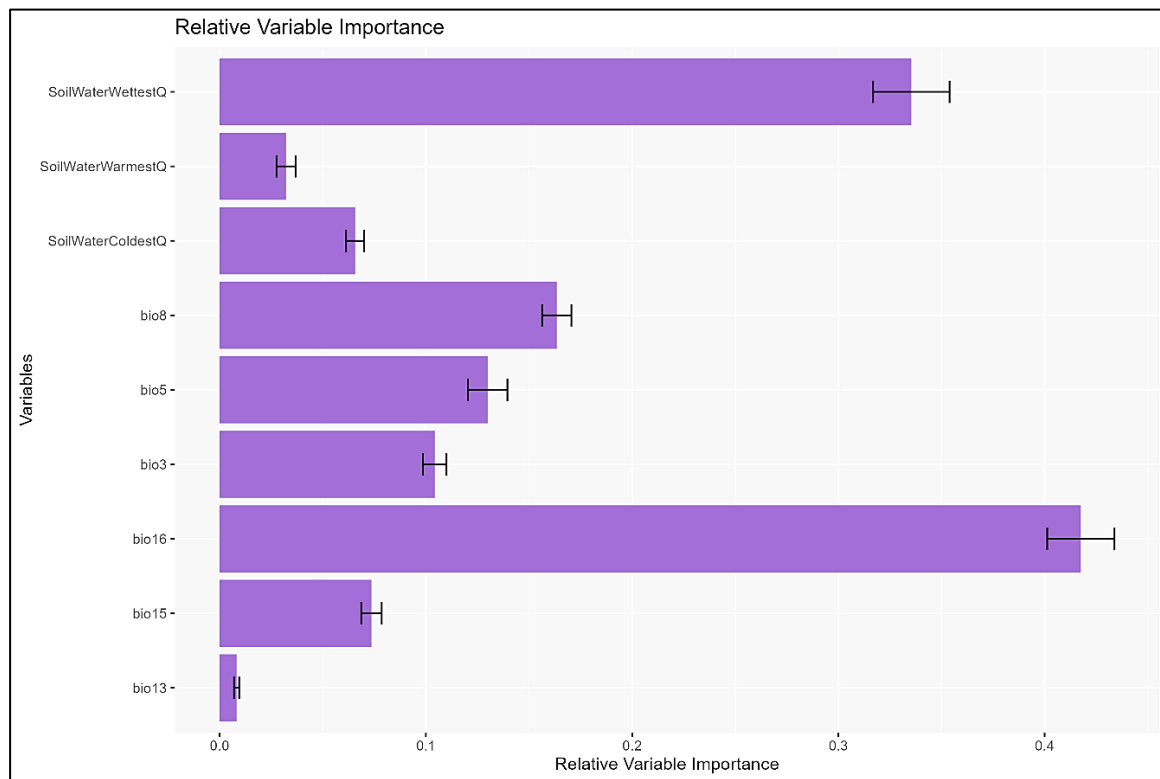


Figure 4-7: Relative variable importance for *Bulinus africanus* using the MaxEnt model.

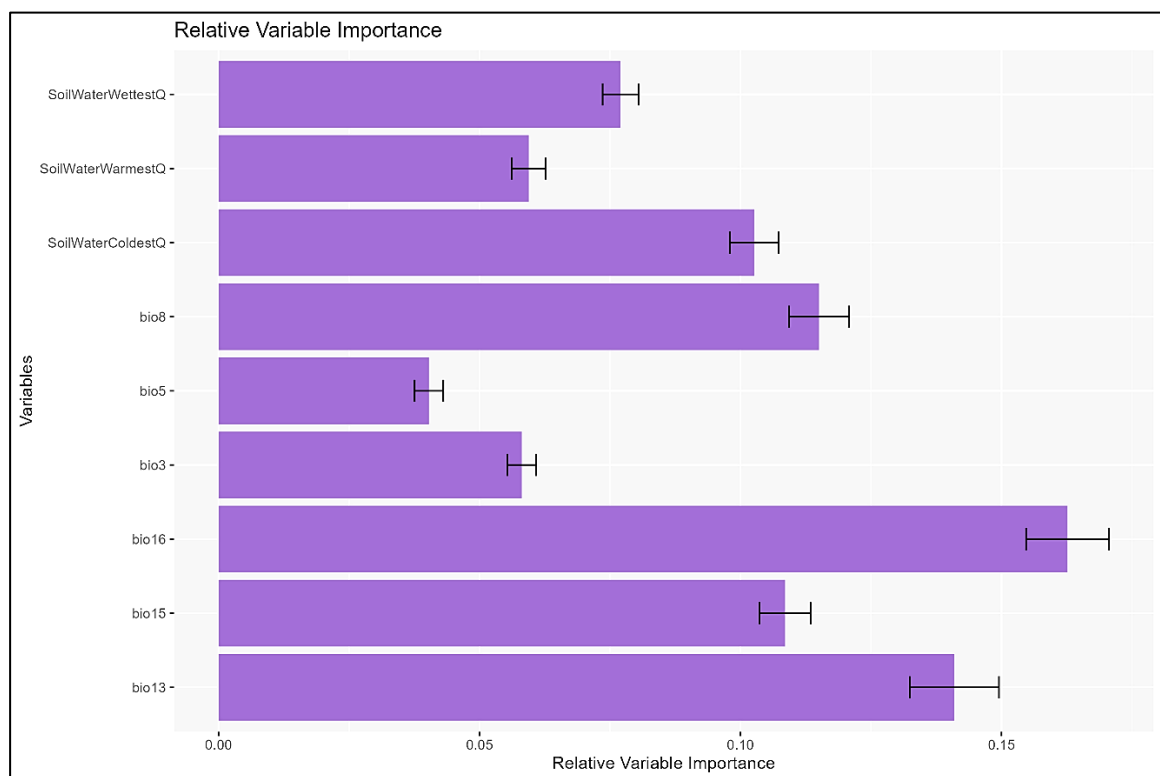


Figure 4-8: Relative variable importance for *Bulinus africanus* using the RF model.

Bulinus globosus distribution was influenced by temperature and precipitation variables in all four models, as shown by the response curves (Figure 4-9) and relative variable importance (Figure 4-10 to 4-12). According to the Temperature Annual Range (bio7), which represents the standard deviation of the monthly mean temperature, *B. globosus* thrives within temperatures ranging from 5K to 17K. The Mean Temperature of the Wettest Quarter (bio8) also suggests a preference for temperatures between 293K (19°C) and 298K (25°C). The response curves for *B. globosus* show an increasing trend in bio8. Therefore, *B. globosus* prefers warmer conditions with less rainfall than *B. africanus*. These findings indicate that *B. globosus* favours warm, humid regions within South Africa.

Furthermore, the results highlight that Precipitation Seasonality (bio15) plays a significant role in the distribution of *B. globosus*, peaking at 0.8. This suggests that the species is more prevalent in areas with consistent yearly precipitation. The response curves showed that *B. globosus* prefers lower Precipitation levels in the Wettest Quarter (bio16) and Precipitation in the Driest Quarter (bio17). This preference for lower rainfall suggests that *B. globosus* thrives in environments with reduced precipitation.

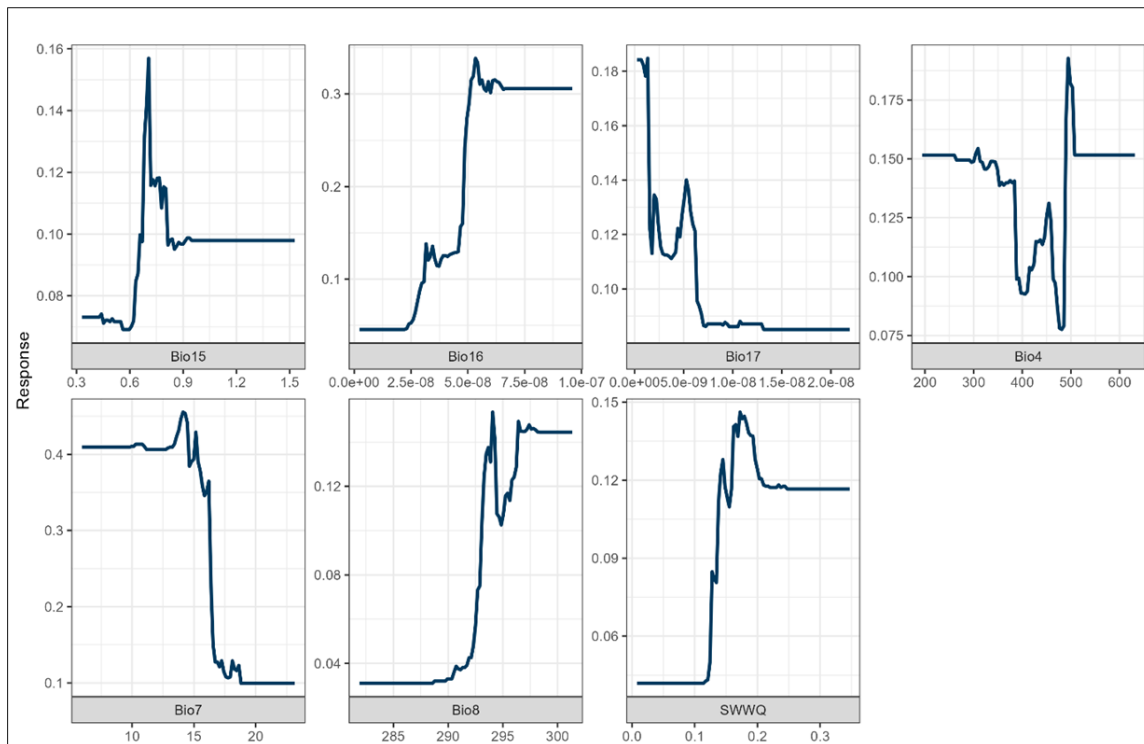


Figure 4-9: Response curves for *B. globosus* against bioclimatic variables using the ensemble model (Bio15 %, Bio16 ms⁻¹, Bio17 ms⁻¹, Bio4 K, Bio7 K, Bio8 K, and soil variables SWWQ m³ m⁻³- Soil water for the wettest quarter).

For the GLM model, bios16 and 17 contributed the most to the model, followed by bios8 and 7 (Figure 4-10). This suggests that the distribution of the species is strongly influenced by precipitation patterns, particularly the amount of rainfall during the wettest and driest quarters. Higher contributions from these variables indicate that they significantly impact the habitat suitability for the species. Soil Water for the Warmest Quarter contributed the least to the model. Its low contribution suggests that soil water content during the warmest quarter has a relatively minor influence on the habitat suitability for the species compared to other factors considered in the model.

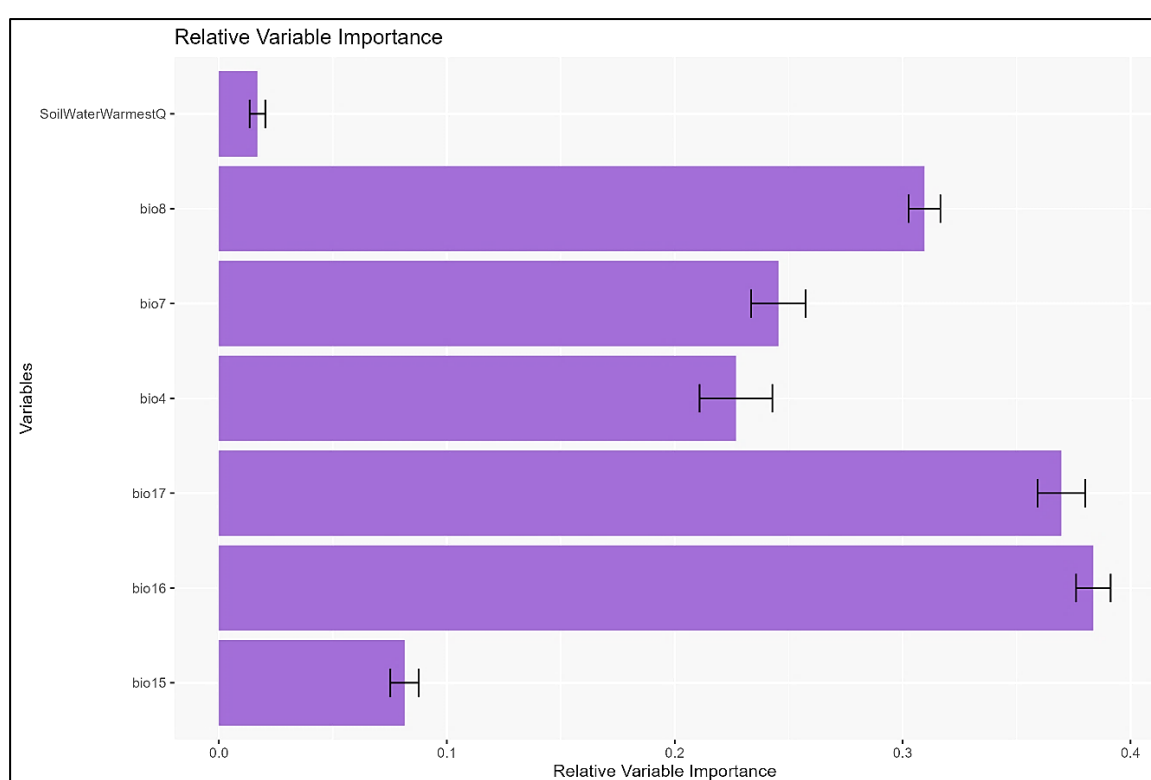


Figure 4-10: Relative variable importance for *B. globosus* using the GLM model.

The relative contribution analysis using the MaxEnt model revealed a slightly different pattern than the GLM model (Figure 4-11). The relative contribution using the MaxEnt showed that temperature variables (bio7 and bio8) contributed the most to the model, followed by precipitation variables (bio17 and bio16). Although the precipitation variables contributed substantially to the model, they ranked slightly lower in importance than the temperature variables. Interestingly, in contrast to the GLM model, Soil Water for the Warmest Quarter contributed more to the MaxEnt model. This suggests that soil water content during the warmest quarter has a more significant influence on habitat suitability.

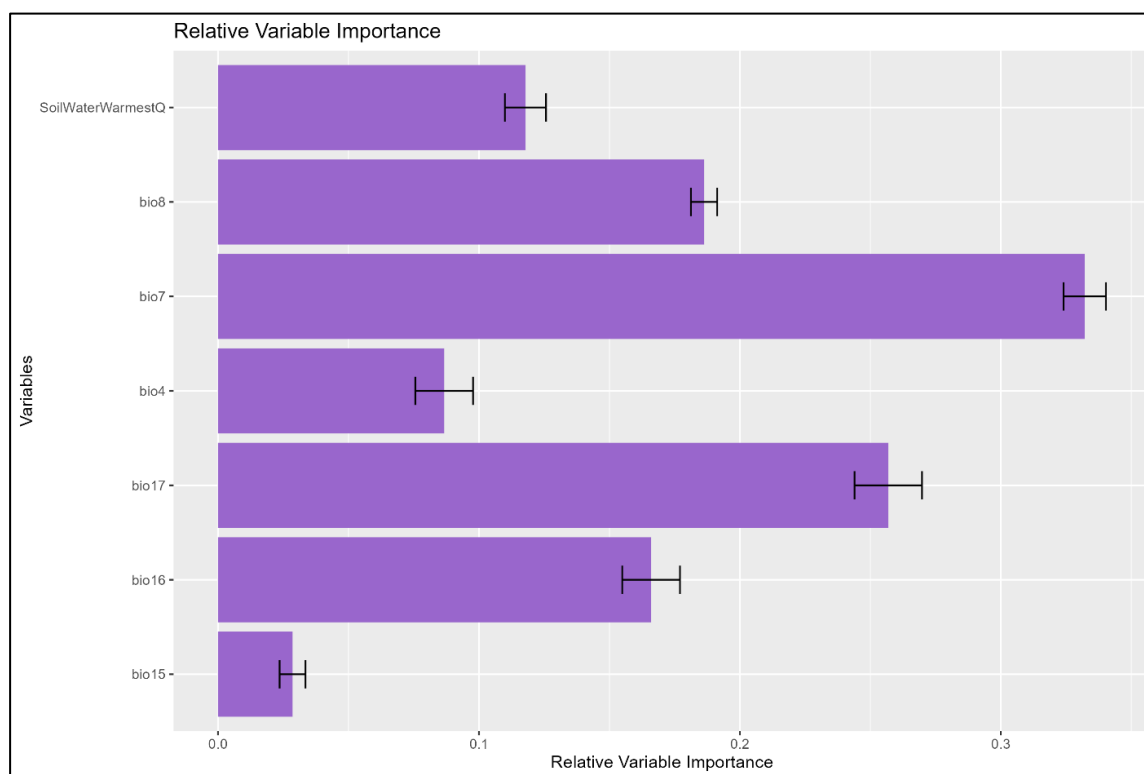


Figure 4-11: The relative variable importance for *Bulinus globosus* using the MaxEnt model.

The relative contribution analysis for the RF model, which outperformed both the GLM and MaxEnt models, revealed a similar trend to the MaxEnt model regarding the importance of temperature variables (Figure 4-12). Temperature variables made the most significant contribution to the RF model. This highlights the importance of temperature-related factors in influencing species distribution. The high contribution of temperature variables suggests that the range and average temperature during specific quarters strongly affect habitat suitability, mirroring the results from the MaxEnt model. Precipitation variables were identified as important predictors in the RF model, specifically bio16 and bio17.

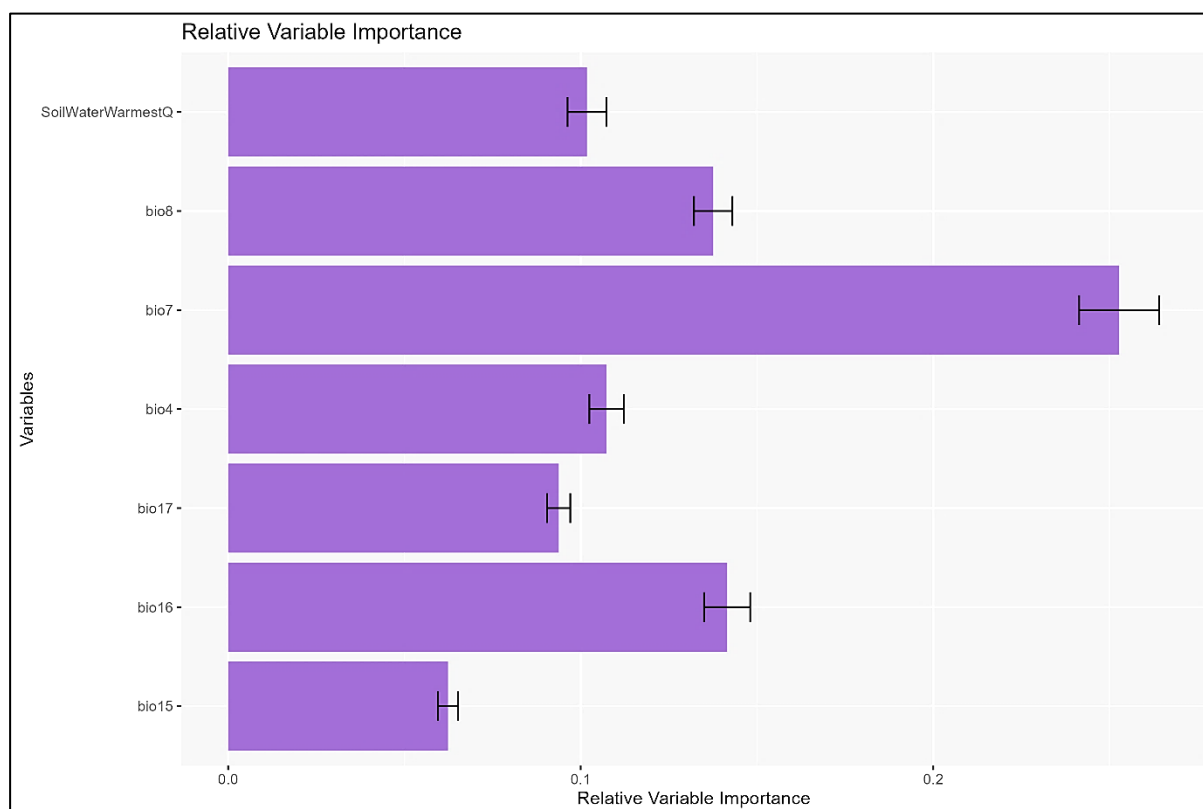


Figure 4-12: The relative variable importance for *Bulinus globosus* using the RF model.

The response curves for *B. pfeifferi* show that Temperature Seasonality (bio4) exhibited a notable response within the range of 300 to 350, indicating sensitivity to fluctuations in temperature throughout the year (Figure 4-13). Optimal conditions for *B. pfeifferi* were observed between 18°C and 25°C, suggesting a preference for moderate temperatures conducive to its habitat. Annual Precipitation (bio12) and Precipitation Seasonality (bio16) demonstrated peaks in moderate rainfall environments. This suggests that *B. pfeifferi* tends to thrive in regions with consistent but not excessive precipitation levels throughout the year. Furthermore, Precipitation of the Warmest Quarter (bio18) indicated a preference for environments with low to moderate rainfall during the warmest quarter. This preference aligns with the species' adaptation to habitats with stable moisture levels, ensuring suitable conditions for its survival and reproduction.

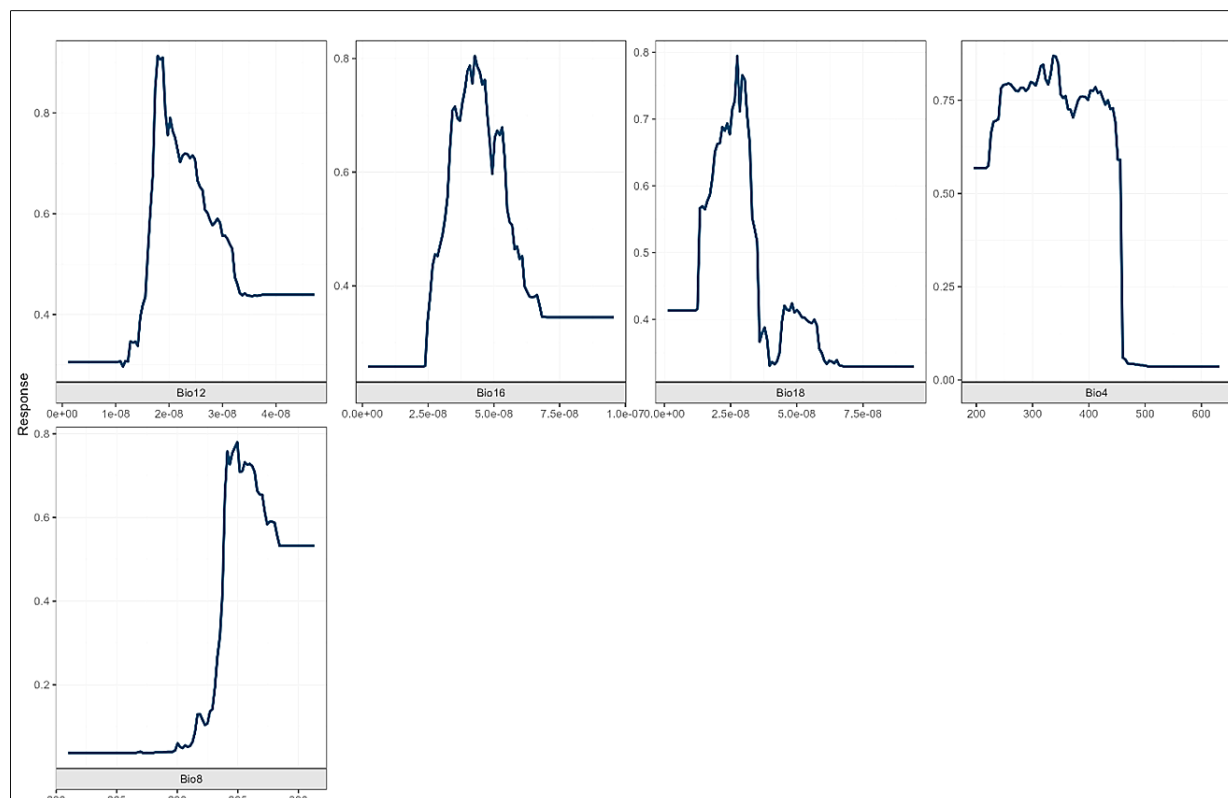


Figure 4-13: Response curves for *Biomphalaria pfeifferi* against bioclimatic variables using the ensemble model (Bio12 ms^{-1} , Bio16 ms^{-1} , Bio18 ms^{-1} , Bio4 K and Bio8 K).

In modelling *B. pfeifferi*, results showed that bio4 contributed the most, 47%, in all three models, as shown in (Figures 4-14 to 4-16). Bio4 is an influential factor affecting *B. pfeifferi*'s climate suitability. The GLM and MaxEnt models showed that *B. pfeifferi* prefers a climate with more variability in temperature throughout the year. Based on GLM and MaxEnt, bio4 accounts for 46.9% of *B. pfeifferi*'s suitability. The RF model also showed that bio4 22.9% and bio8 15.5% were the highest predictors of this snail's suitability. This is because bio4 and bio8 help determine the climate conditions the snail prefers. In SA, *B. pfeifferi* is marginally suited to the climate because of variations in night and day temperatures and high daytime temperatures of 28°C. There was a notable difference in temperature tolerance for *B. pfeifferi* compared to *B. globosus*. It is pertinent to note that despite being widely distributed throughout the country, *B. pfeifferi* snails are not tolerant of high temperatures.

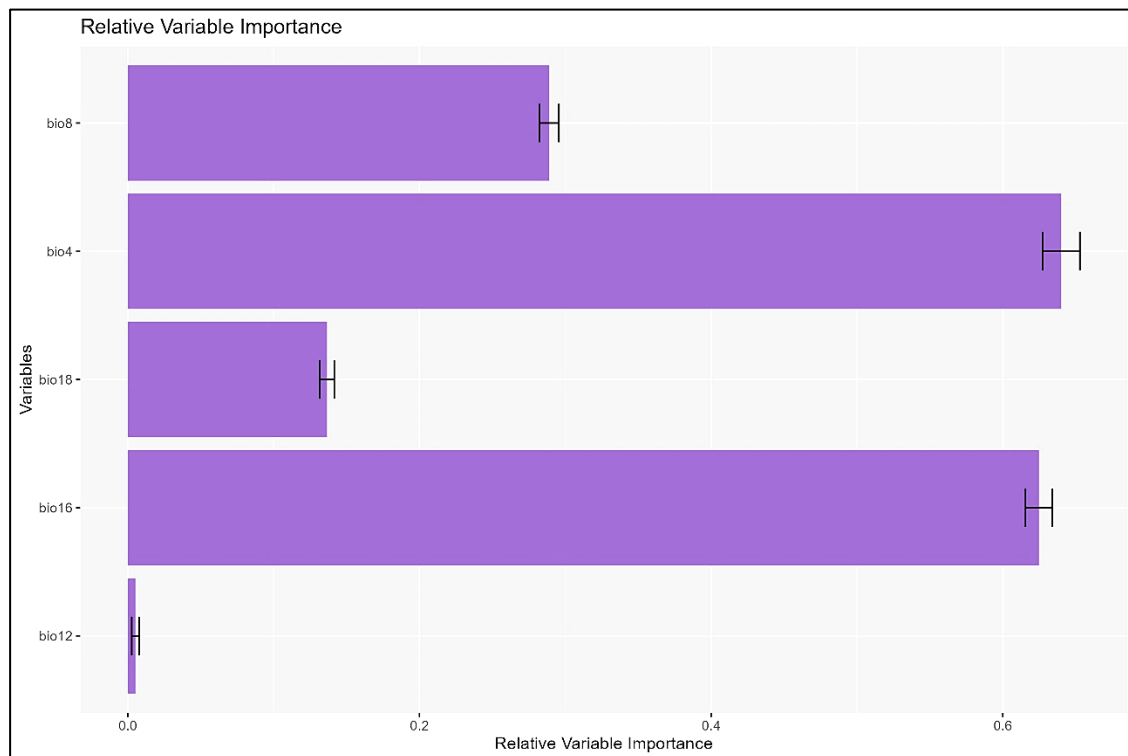


Figure 4-14: The relative variable importance for *Biomphalaria pfeifferi* using the GLM model.

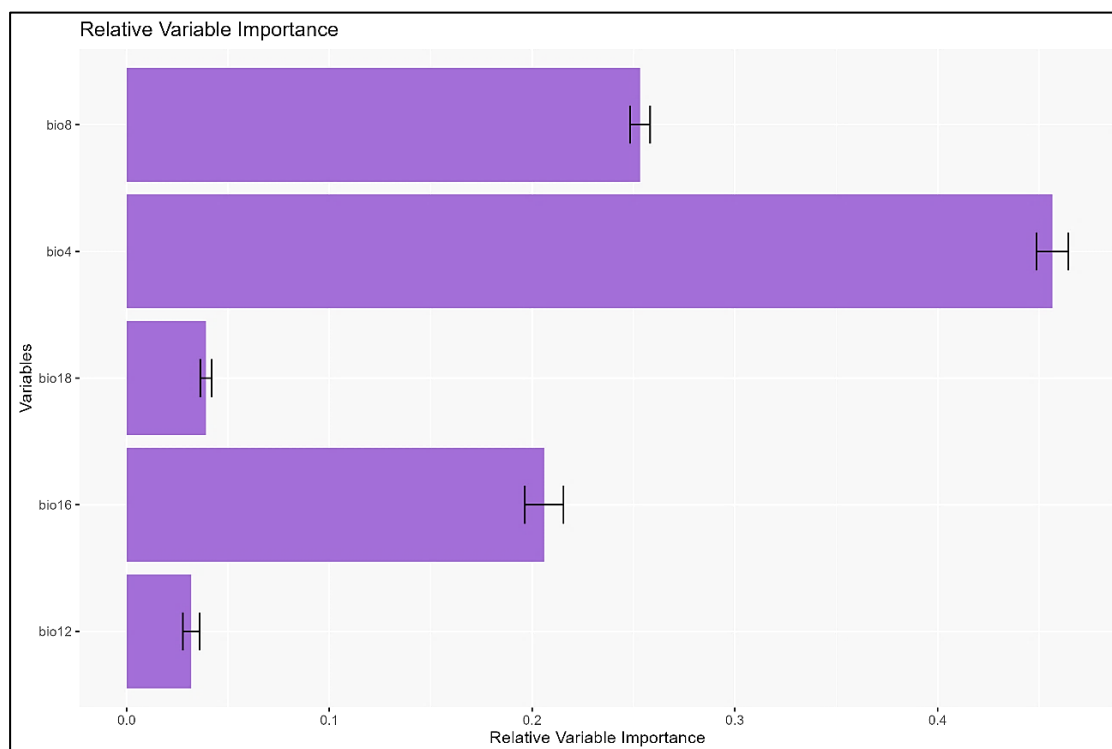


Figure 4-15: The relative variable importance for *Biomphalaria pfeifferi* using the MaxEnt model.

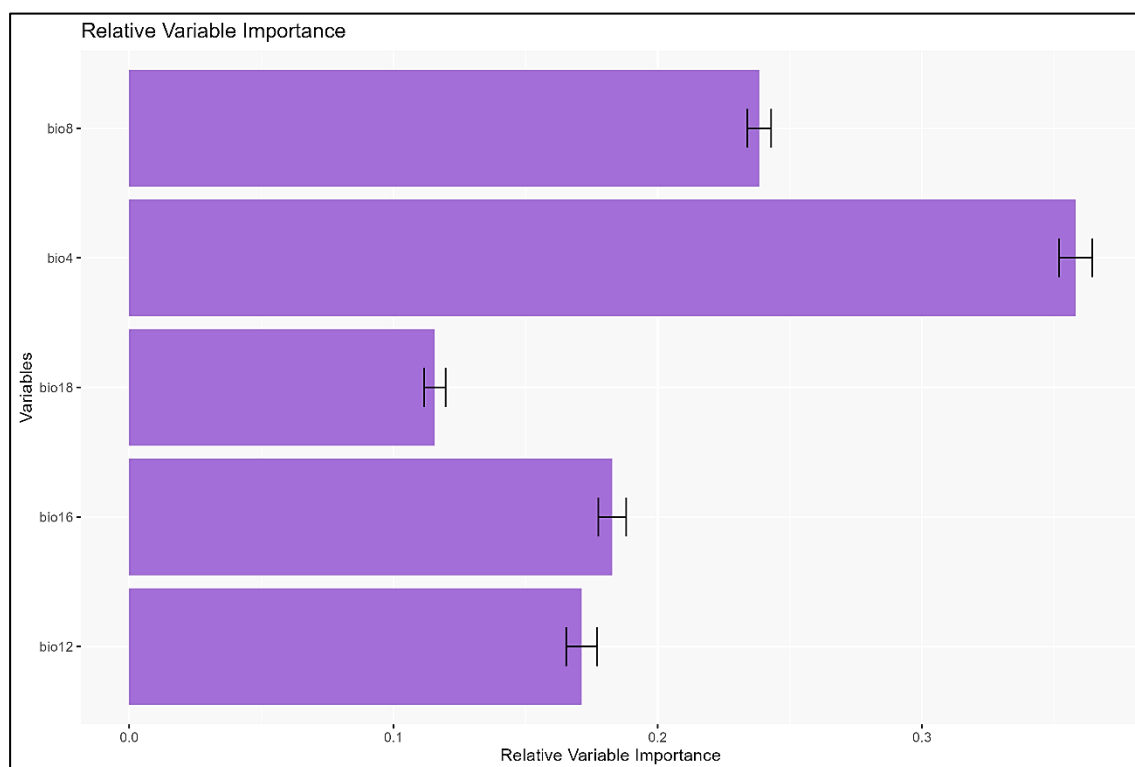


Figure 4-16: Using the RF model, the relative variable importance for *Biomphalaria pfeifferi*.

The results from the abovementioned study highlight the importance of rainfall and temperature variables in determining the suitability of habitats for different species of snails associated with schistosomiasis. Understanding these climatic preferences is essential for predicting and managing the distribution of these species and, consequently, the transmission of schistosomiasis within South Africa.

4.2.2 Historical spatial distribution of *Schistosoma*-transmitting snails

The ecological models are reasonably accurate at predicting the distribution of intermediate hosts based on bioclimatic variables. Precipitation and temperature are known factors in the development of intermediate snail hosts. The results showed that temperature and rainfall can influence the distribution of schistosomiasis in SA. Figures 4-17 to 4-19 illustrate the results for the three chosen ENMs. Red shows highly suitable areas, whereas yellow depicts moderately suited locations. Green shows areas that are not suitable for schistosomiasis transmission. Additionally, snail presence probability varied with location, indicating the varying suitability of sites for *B. pfeifferi*, *B. globosus*, and *B. africanus*.

Bulinus africanus was distributed in the eastern part of Gauteng province, parts of Mpumalanga and the North West Province (Figure 4-17). *Bulinus africanus* was found to be widespread west of the Eastern Cape province. *Bulinus africanus* can survive in areas with temperatures (of 15° to 30°C) and moderate rainfall, making it well-suited to its distribution range. The GLM, MaxEnt and the ensemble model showed that parts of the Western Cape were suitable for transmitting schistosomiasis. Even though ecological models predict suitable precipitation and temperatures for the Western Cape, schistosomiasis does not occur under those conditions. Figure 4-18 shows that *B. globosus* is distributed in the northern and eastern areas of SA, particularly in the Limpopo, Mpumalanga, Gauteng, and eastern regions of the North West Province. The distribution extends to the coastal areas in KwaZulu-Natal. *Bulinus globosus* was commonly found in the eastern regions of SA and to the south of Humansdorp. Parts of the Western Cape also have suitable environments for transmitting schistosomiasis. The GLM shows Cape Town to be ideal for schistosomiasis transmission, while MaxEnt, RF, and ensemble indicate the southern Western Cape as moderate suitability. It was found that *B. pfeifferi* was more abundant and distributed spatially across SA than *B. africanus* and *B. globosus*. Hence, most *B. pfeifferi* observations were found across SA. The spatial distribution of *B. pfeifferi* is like that of *B. globosus*. *B. pfeifferi* can be seen distributed in the northern and coastal areas of Kwa-Zulu Natal and around the coast of the Eastern Cape (Figure 4-19). *Biomphalaria pfeifferi* and *B. globosus* are characterised by similar temperatures and rainfall patterns in the same regions. The differences in *B. globosus* and *B. pfeifferi*'s distribution are due to the required rainfall and temperature thresholds these species can tolerate.

Figure 4-19 further illustrates that the Northern Cape, such as the Kgalagadi Transfrontier Park, has an increased potential for transmitting schistosomiasis. This could be due to the ideal temperature and rainfall conditions for intermediate hosts in this region. However, no snail vectors were found or sampled in the Northern Cape.

THE HISTORICAL DISTRIBUTION OF SCHISTOSOMA-TRANSMITTING SNAILS IN SOUTH AFRICA

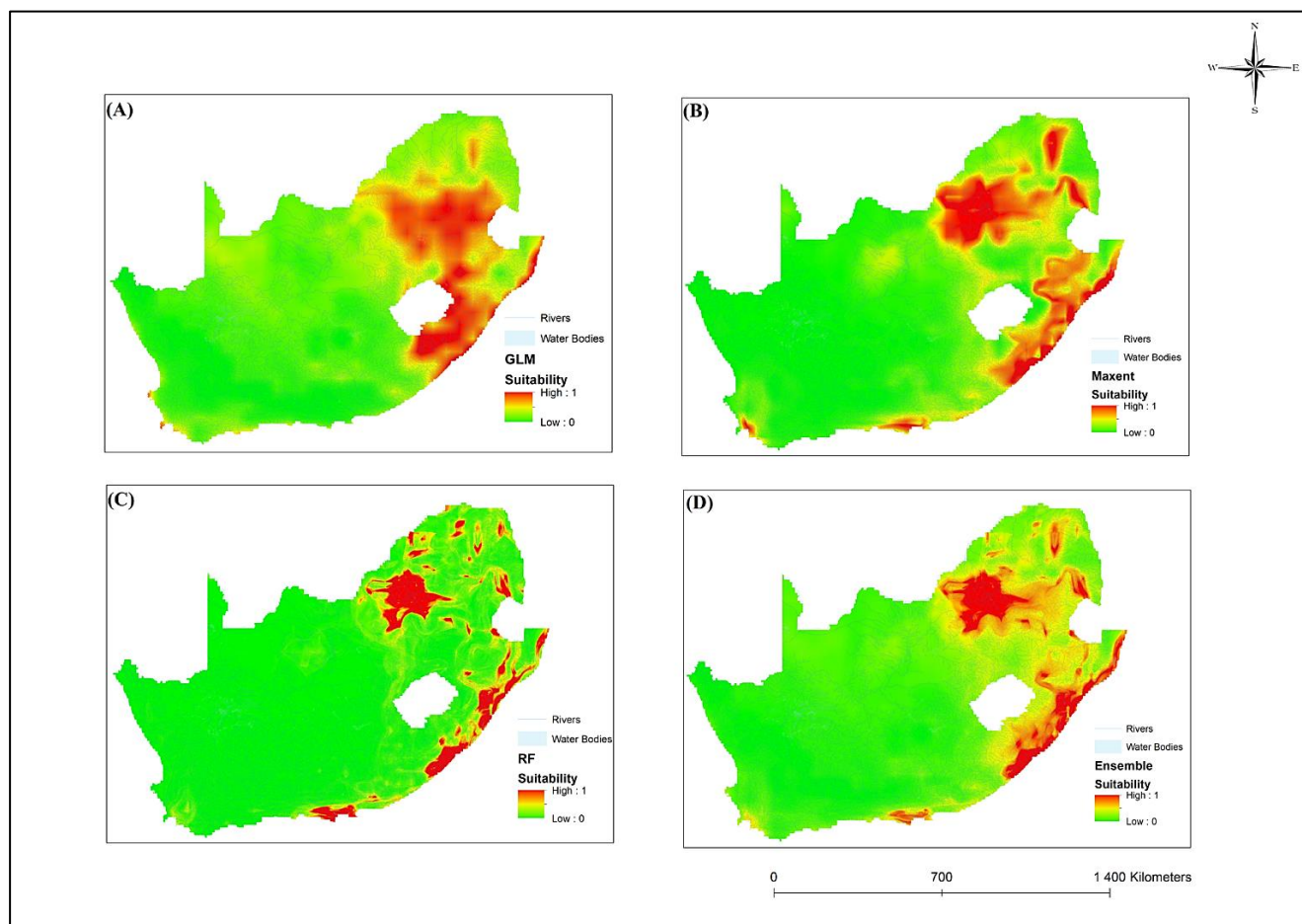


Figure 4-17: Areas where bioclimatic variables favour *Bulinus africanus* distribution in South Africa using four different models: (A) GLM, (B) MaxEnt, (C) RF, and (D) Ensemble.

THE HISTORICAL DISTRIBUTION OF SCHISTOSOMA-TRANSMITTING SNAILS IN SOUTH AFRICA

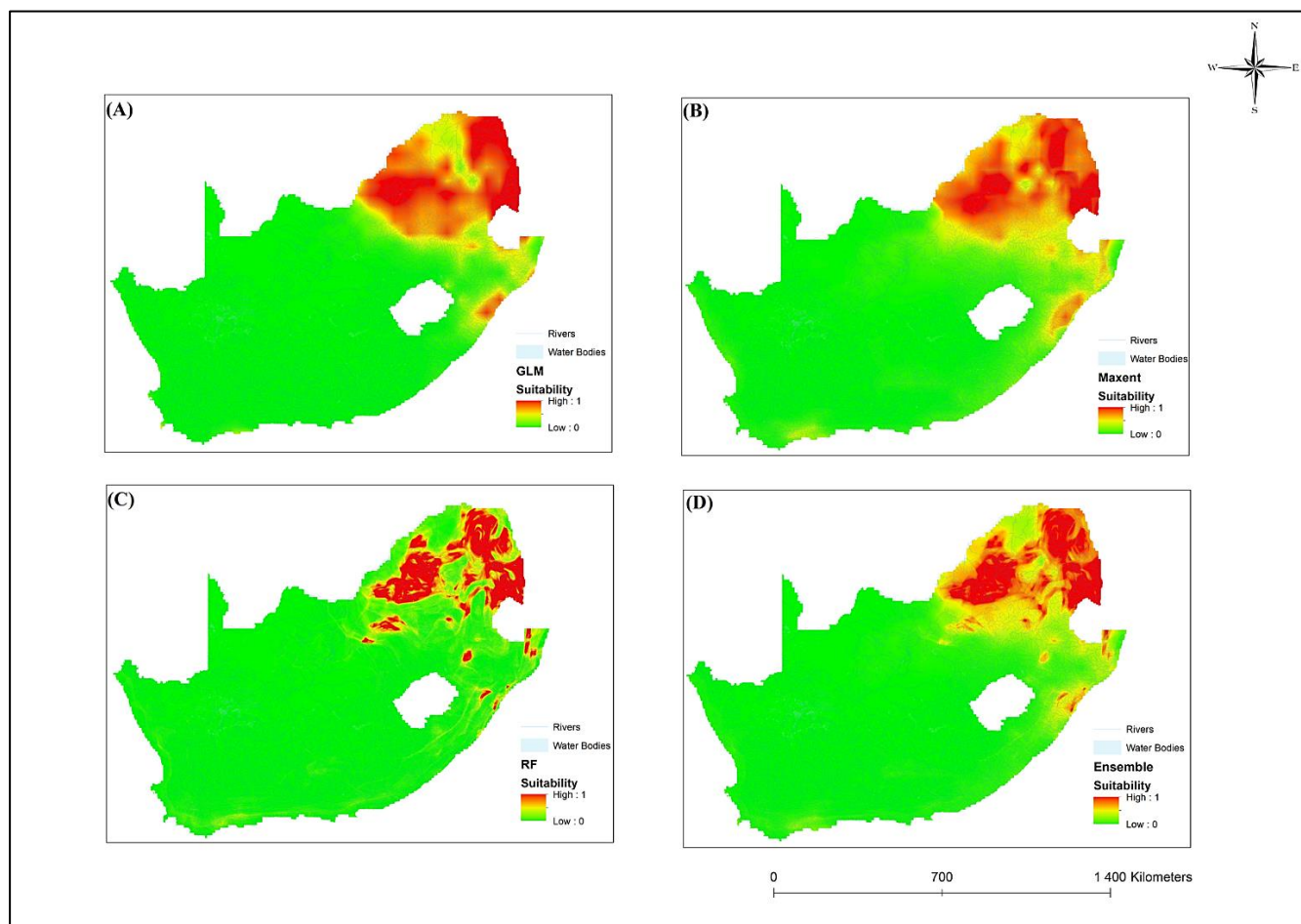


Figure 4-18: Areas where bioclimatic variables favour *Bulinus globosus* distribution in South Africa using four different models: (A) GLM, (B) MaxEnt, (C) RF, and (D) Ensemble.

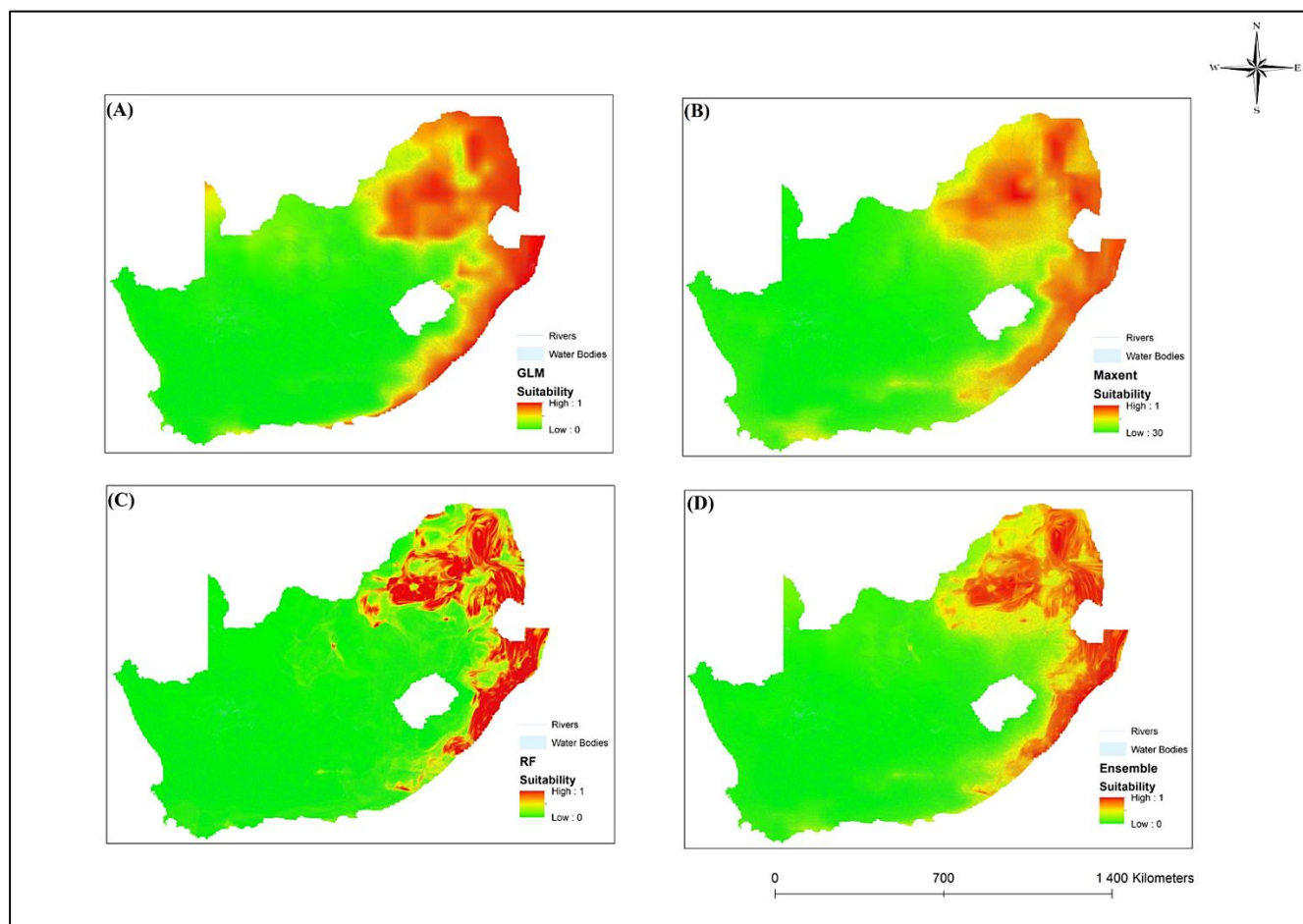


Figure 4-19: Areas where bioclimatic variables favour *Biomphalaria pfeifferi* distribution in South Africa using four different models: (A) GLM, (B) MaxEnt, (C) RF, and (D) Ensemble.

4.3 Discussion

The first objective of the thesis was to characterise the historical distribution of intermediate hosts of schistosomiasis in SA using ecological niche models. The results showed that temperature and rainfall can influence the distribution of schistosomiasis in SA. The study used GLM, MaxEnt, RF and an ensemble to model the distribution of *B. africanus*, *B. globosus*, and *B. pfeifferi*. The RF model outperformed the other models in modelling the distribution of schistosomiasis, following MaxEnt and GLM, respectively. The results of Wouyou et al. (2022) were similar, with RF outperforming four ecological models. In addition, Ponpetch et al. (2021) modelled the potential distribution of *S. mansoni* in Ethiopia and found that RF outperformed the other seven ENMs. They further found that the ensemble performed better than individual ENMs (Ponpetch et al., 2021).

The findings of this thesis indicated a complex interplay between climatic elements like rainfall and temperature in determining the suitability of environments for intermediate hosts. In addition, rainfall, especially during the wettest quarter and month, is vital for forming habitats conducive to the parasites that cause schistosomiasis. Temperature also plays a significant role, with *B. africanus* preferring cooler conditions for thriving. Furthermore, *B. africanus* demonstrated a capacity to adjust to varying temperatures, with its suitability largely hinging on seasonal fluctuations rather than annual temperature averages. Understanding how temperature and rainfall variations can influence intermediate hosts' habitats is important. The subsequent section discusses how historical bioclimate influences the intermediate hosts' suitability.

4.3.1 Intermediate host snail's historical bioclimate suitability

Rainfall variables were the most influential in modelling the habitat suitability for *B. africanus*. De Kock et al. (2004) found that *B. africanus* species are predominantly found in areas receiving 300 mm to 700 mm of annual rainfall. Precipitation of the wettest quarter (November to January) and precipitation of the wettest month were key bioclimatic variables in the GLM and MaxEnt models, accounting for 65% of schistosomiasis suitability, while soil moisture during the wettest quarter contributed 32%. Adekiya et al. (2019) indicated a link between rainfall patterns and schistosomiasis prevalence, as moderate rain facilitates snail dispersal and habitat formation. Moderate precipitation allows for the transportation of snails and supports the creation of new and temporary snail habitats (Freitas, 2006). Temperature factors were also significant, making up 59% of the suitability, with *B. africanus* favouring cooler conditions. Appleton (1978) and de Kock and Van Eeden (1986) found that *B. africanus* has an optimal reproduction temperature range of 23°C to 26°C. The RF model showed that the wettest quarter's precipitation was most significant at 36%, followed by soil moisture at 32% and combined temperature variables at 32%. These findings suggest that *B. africanus* can adapt to both cold and warm climates, with suitability largely dependent on precipitation, temperature, and seasonal changes rather than yearly averages due to the variable seasonal environment in SA and the specific conditions required by schistosomiasis-causing parasites to survive (Moodley, 2003; Manyangadze et al., 2021).

The distribution of *B. globosus* is strongly affected by temperature and precipitation, which are key variables in all three models studied. Bios 16 and 17 are responsible for 42% of the habitat suitability for infected snails, with heavy rains potentially causing snail migration due to flooding.

Therefore, potential habitats are created, allowing schistosomiasis-transmitting snails to migrate actively to nearby favourable habitats (Guo et al., 2021). A study by Pennance et al. (2016) found that *Schistosoma*-transmitting snails are more abundant during post-rainy seasons and more likely to transmit the disease. Madsen et al. (2011) conducted a study on schistosomiasis along the lake shore of Malawi and reported that *B. globosus* is prevalent in post-rainy seasons or early winter. In addition, temperature variables contribute to 38% of the snails' habitat suitability, with *B. globosus* showing a preference for warmer conditions indicated by bio8 and the annual temperature range. The MaxEnt model also highlights temperature as a significant factor, with bio7 and bio18 being the top contributors. Qin et al. (2017) studied *Thuja sutchuenensis* and found that bio18 was the most suitable, followed by bio14 and bio6. According to the results from this study, similar to GLM and MaxEnt, the annual temperature range in the RF was the most influential variable in determining the suitability for *B. globosus*. A study by Joubert et al. (1984) concluded that *B. globosus* is more resistant to high temperatures than *B. africanus*. There has been an increase in temperatures in SA, especially in tropical areas like Limpopo and Mpumalanga (Tshiala et al., 2011). Consequently, it could lead to an increase in the abundance of *B. globosus* species in the future. Joubert et al. (1984) showed that *B. globosus* could withstand temperatures of 34°C - 40°C. Shiff et al. (1975) found that *B. globosus* could survive in thermally harsh environments with increasing temperatures.

For *B. pfeifferi*, it was found that temperature variability throughout the year was the most significant factor, contributing 47% to the species' habitat suitability in all three models used. As a result, the snail is provided with the temperature fluctuations it needs to thrive (Moodley, 2003). The GLM and MaxEnt models indicated a preference in *B. pfeifferi* for climates with greater temperature fluctuations. According to these models, bio4 was responsible for nearly 47% of the snail's habitat suitability. The species showed a decline in suitability in moderate to high rainfall, as indicated by the response curves for bio12 and bio16. This is because *B. pfeifferi* does not do well during the summer seasons. Manyangadze et al. (2016) studied schistosomiasis in the Ndumo area of the uMkhanyakude district and found that *B. pfeifferi* were suitable in the cold and dry seasons (winter) following the rainy season. Moodley (2003) also found that *B. pfeifferi* was influenced by winter minimum temperatures. Christensen et al. (2018) found similar results, in which *B. pfeifferi* bred extensively following rainy seasons. It was found that bio18 accounted for 45% of snail suitability. A study in Ethiopia by Xue et al. (2011) showed that moderate rainfall is instrumental in

increasing schistosomiasis by accumulating sufficient surface water in ponds. During heavy rainfall events, water levels rise, causing water turbulence. As a result, flow rates may increase, disrupting snail habitats and reducing cercariae survival (Xue et al., 2011).

Additionally, *B. pfeifferi* was found to prefer temperatures above 16.8°C. The RF model also identified bio4 and bio8 as top predictors of the snail's habitat suitability, highlighting the importance of these factors in determining the preferred climate conditions for *B. pfeifferi*. In South Africa, *B. pfeifferi* is somewhat suited to the climate, which is characterised by variations in night and day temperatures and high daytime temperatures around 30°C. It is pertinent to note that despite being widely distributed throughout the country, *B. pfeifferi* snails are not tolerant of high temperatures (Brown, 2002). Furthermore, a study by Sturrock (2001) showed that *B. pfeifferi* mortality was high at 32°C. In addition, Deka (2022) found that bio3 and bio4 had a higher relative contribution to modelling the distribution of *Biomphalaria straminea*. This might be because *B. pfeifferi* and *B. straminea* belong to the same genus, suggesting these species are likely affected or influenced by similar environmental factors.

4.3.2 The historical spatial distribution of Schistosoma-transmitting snails

The ecological models have shown a fair level of precision in modelling where intermediate hosts are expected to be found using bioclimatic factors to delineate their fundamental niche. Both precipitation and temperature play a significant role in the growth of intermediate snail hosts. This shows that climate change can modify species distribution patterns (Pedersen et al., 2017). The study's findings indicated that both temperature and rainfall have an impact on how schistosomiasis is distributed in SA, with these findings being corroborated by (Moodley, 2003)

Bulinus africanus is prevalent in the eastern regions of Gauteng, as well as in Mpumalanga and North West Province. It is also widespread to the west of the Eastern Cape. *Bulinus africanus* is better adapted to colonising cooler environments and cannot tolerate high temperatures (Moodley, 2003). The mortality of intermediate hosts may be due to temperature increases (de Kock and Wolmarans, 2005). This is likely due to the species' tolerance of extreme environments and adaptability to environmental changes (Pretorius et al., 1980; Moodley, 2003). This species thrives in environments with moderate rainfall and temperatures ranging from 15°C - 30°C, which aligns with its observed distribution. According to the GLM, MaxEnt, and ensemble models, the Western

Cape has suitable conditions for schistosomiasis transmission. However, schistosomiasis does not occur there despite the ecological models indicating favourable temperature and precipitation for the Western Cape. Appleton and Stiles (1976) concluded that the natural acidity of waterbodies such as rivers and dams in this province could negatively affect intermediate hosts.

Bulinus globosus predominantly inhabits the eastern and northern territories of SA, including Limpopo, Mpumalanga, Gauteng, and the eastern parts of North West Province, with its presence also noted along the coastal belt of KwaZulu-Natal. This is likely because *B. globosus* requires hotter temperatures and moderate rainfall (Moodley, 2003). *Bulinus globosus* and *B. africanus* are sensitive to dry conditions and are closely related to temperature (de Kock and Wolmarans, 2005). The *Bulinus* group is influenced by temperature and water flow (Quayle et al., 2010). Most *B. africanus* individuals were found at lower temperatures than *B. globosus*. This may be because *B. africanus* thrives in cooler climates (Appleton and Stiles, 1976; Brown, 1980). With increasing temperatures, *B. globosus* is more likely to survive than *B. africanus* (Davis and Carney, 1973). In this way, *B. africanus* species can colonise habitats on the highveld of SA and Gauteng. The species is also prevalent south of Humansdorp and in certain areas of the Western Cape. The Generalized Linear Model identifies Cape Town as a prime location for transmitting schistosomiasis, whereas MaxEnt, RF and ensemble models suggest that the southern regions of the Western Cape are of moderate suitability for disease transmission. Despite the favourable climate conditions for schistosomiasis, it does not occur in parts of the Western Cape, likely due to high salinity and acidity levels in rivers and dams of the province (Pretorius et al., 1980). Conversely, anthropogenic atmospheric CO₂ reacts with water to form carbonic acid (H₂CO₃), increasing water acidity. Interestingly, snails from populations exposed to heavy metal mining pollution exhibited greater tolerance to acidic conditions than those from unpolluted areas. These snails appeared naturally adapted to low-pH environments, displaying better short-term survival rates in acidic conditions (Lefcort et al., 2015). Conversely, a study by Letlaila et al. (2024) reported *B. globosus* is found to prefer much lower salinity levels (100–300 ppm) compared to *B. pfeifferi* (601–1000 ppm). This implies that *B. pfeifferi* would likely be able to survive the higher salinity levels found in the Mbombela region, whereas *B. globosus* would not.

Biomphalaria pfeifferi is more prevalent and widely spread throughout SA than *B. africanus* and *B. globosus*, with a notable presence in the northern and coastal regions of Kwa-Zulu Natal and

along the Eastern Cape coast. The distribution covers most of Gauteng, Limpopo and Mpumalanga. *B. pfeifferi* preferred warmer temperatures with average rainfall (Christensen et al., 2018). The distribution patterns of *B. pfeifferi* and *B. globosus* are influenced by similar climatic conditions, specifically temperature and rainfall, which they can endure within certain thresholds. *Bulinus globosus* prefers warmer temperatures (19°C to 26°C), whereas *B. pfeifferi* prefers milder temperatures (18°C to 24°C) and is found in the post-rainy seasons (Moodley, 2003). Additionally, the Northern Cape, including areas like the Kgalagadi Transfrontier Park, shows potential for schistosomiasis transmission due to favourable conditions for intermediate hosts despite the absence of recorded snail vectors in that region. Moodley (2003) concluded that no disease occurred in the Northern Cape, but the temperature in the province was suitable for schistosomiasis.

In this thesis, ensemble models performed better than individual ENM models, as reported in other ecological studies. According to the ensemble models created in the present study, the most suitable habitats for *B. africanus*, *B. globosus* and *B. pfeifferi* were found in the eastern and coastal regions of SA. The most suitable areas included SA's tropical and rural areas, which are also near freshwater bodies. These findings agree with those reported in (Ponpetch et al. (2021) regarding high schistosomiasis infection rates in villages near lakes. Results from ENM showed that temperature and precipitation were essential factors in snail distribution. This finding corroborates with Xue et al. (2011), who reported that variations in rainfall and temperature could affect schistosomiasis transmission.

4.4 Chapter Conclusion

From objective 1, temperature and rainfall impact the schistosomiasis distribution in SA. This means climate variability and change can affect schistosomiasis transmission, leading to shifts in the distribution of infected snails. If temperatures and precipitation levels change significantly, schistosomiasis outbreaks' geographical distribution and severity could change. Achieving this objective contributed to the current understanding of schistosomiasis distribution in SA. It also contributed to the historical distribution of *Schistosoma haematobium* and *Schistosoma mansoni*. The following chapter will build on the results presented here. Chapter 5 will focus on the future distribution of *Schistosoma*-transmitting snails using ENMs, and bioclimatic data from Global Circulation Models.

CHAPTER 5

The following chapter presents the results for Objective 2: ‘*The distribution of Schistosoma-transmitting snails under climate change projections*’. Predicting the future range of *Schistosoma*-transmitting snails is essential in understanding how climate change may influence the spread of schistosomiasis. This is one of the first studies to predict the future distribution of *B. africanus*, *B. globosus* and *B. pfeifferi* in South Africa. Three ENMs and GCMs were used to predict the future distribution of the intermediate host snails under two RCPs (4.5 and 8.5) for 2040-2070 and 2070-2100.

THE DISTRIBUTION OF *SCHISTOSOMA*-TRANSMITTING SNAILS UNDER CLIMATE CHANGE PROJECTIONS

5.1 Predicting the future distribution of *Schistosoma*-transmitting snails

The species distribution predictions were analysed for 2040-2070 and 2070-2100. Across these periods, the models performed well in predicting the species distribution by having similar AUC and TSS scores, although slight variations are observed. This could be due to ecological model differences and species distribution pattern shifts. In addition, it is also important to note that as the prediction timeframe extends to the far future (2070 to 2100), uncertainty in climate projections increases. This can affect the accuracy of the predictions, leading to variations in performance in different climate models.

This chapter evaluated the performance of three climate and ecological models in predicting the distribution of *B. africanus* under two climate change scenarios, RCP 4.5 and RCP 8.5. The baseline model for RCP 4.5 had an AUC of 0.99 and a TSS of 0.95. The Access1-0 and bcc-csm1-1-m models varied with AUC values from 0.88 to 1.00 and TSS from 0.66 to 0.94, while hadgem2-cc had an AUC of 0.86 to 0.99 and TSS of 0.64 to 0.95. For the RCP 8.5 scenario, Access1-0 had AUCs of 0.87 to 1.00 and TSS of 0.66 to 0.92, bcc-csm1-1-m showed a performance of 0.86 to 1.00 and TSS of 0.65 to 0.92, and hadgem2-cc 0.88 to 1.00 and TSS from 0.63 to 0.93 (Appendices A and B).

For *B. globosus*, the baseline model showed high AUC scores of 0.94 to 0.99 and TSS scores of 0.78 to 0.94 for GLM, MaxEnt, RF, and ensemble models. The Access1-0 model's performance varied, with AUC scores from 0.90 to 0.99 and TSS scores from 0.74 to 0.93 over different periods. The bcc-csm1-1-m and hadgem2-cc models also displayed fluctuating AUC scores of 0.88 to 0.99 and TSS scores of 0.64 to 0.90. Under the RCP 8.5 scenario, Access1-0 had AUC scores between 0.93 and 0.99 and TSS scores from 0.76 to 0.94. The bcc-csm1-1-m model showed AUC scores from 0.89 to 0.99 and TSS scores between 0.66 and 0.95, while hadgem2-cc had AUC scores of 0.92 to 0.99 and TSS scores ranging from 0.73 to 0.94 (Appendices C and D).

For *B. pfeifferi* under RCP 4.5, GLM, MaxEnt, RF, and the ensemble model demonstrated high AUC scores (0.92 to 0.99) and TSS scores (0.73 to 0.94). The Access1-0 model showed a range

of AUC (0.87 to 0.98) and TSS (0.66 to 0.90) scores over different periods. The bcc-csm1-1-m and hadgem2-cc models also showed variable AUC (0.86 to 0.97) and TSS (0.64 to 0.91) scores. Under the RCP 8.5 scenario, Access1-0 had AUC scores from 0.87 to 0.99 and TSS scores between 0.76 and 0.92. The bcc-csm1-1-m model's AUC scores ranged from 0.89 to 0.99 with TSS scores of 0.74 to 0.92, while hadgem2-cc showed AUC scores from 0.88 to 0.99 and TSS scores of 0.70 to 0.94 (Appendices E and F). The variations in AUC values across periods and climate scenarios can reflect changes in the species' range due to projected climate changes.

Overall, the AUC values consistently remained high across different climate scenarios, indicating that the ensemble model predicts the distribution of *B. africanus*, *B. globosus* and *B. pfeifferi* well. The variations in AUC values across periods and climate scenarios can reflect changes in the species' range due to projected climate changes. These statistics highlight the ensemble model's reliability in predicting the potential impacts of climate change on the distribution.

5.1.1 Predicted suitable habitats for the intermediate host snails under the emission scenario RCP 4.5

Two out of three climate models agreed that the suitable habitat for *B. africanus* in isothermality (bio3) is between 51 and 55°C, while all three models concurred that the optimum temperature in Maximum Temperature of Warmest Month (bio5) is between 20 and 27°C. Optimal temperatures for the Mean Temperature of Wettest Quarter (bio8) are similar among the climate models, ranging from 28 to 30°C. This indicated that *B. africanus* will be able to survive in temperatures as high as 30°C, higher than in its baseline range (26°C). Precipitation of Wettest Month (bio13) preferences were consistent among the models, ranging between 80-100 mm (Table 5-1). The findings showed that *B. africanus* is likely suited to environments with low rainfall levels monthly. Precipitation Seasonality (bio15) showed little variation among the models, with peaks between 0.50 and 1.35. The models agreed that *B. africanus* will favour precipitation of the wettest quarter (bio16) in areas with rainfall between 500 and 700 mm. Across all climate models, the optimal conditions for *B. africanus* included adequate rainfall throughout the wet quarter, maintaining soil moisture without reaching levels that cause flooding. These conditions will allow the species to derive the most benefits, such as migrating to newly established habitats.

According to the Temperature Annual Range (bio7), *B. globosus* will thrive at temperatures between 13°C and 17°C, and the Mean Temperature of the Wettest Quarter (bio8) suggests a preference for 24°C to 30°C (Table 5-1). This indicates that *B. globosus* prefers warm, humid regions in SA. The results showed that bio15 (Precipitation seasonality) indicated that *B. globosus* distribution peaked between 0.80 and 1.2 across all models. The models also indicated that *B. globosus* prefers lower levels of bio16 (260-450 mm) with little variation among the models. For 2070-2100, *B. globosus* responds well to bio16 at 600-1000mm and a high optimum in low rainfall environments (0 to 35 mm; bio17). This is because the species has adapted to the changing climate and can be expected to survive in more extreme weather conditions, such as heavy rainfall, during which it may migrate to alternative habitats.

For *B. pfeifferi* in 2040-2070, optimal values in Temperature Seasonality (bio4) differed among the models (-75 to 50). However, due to its spatial variability in SA, for bio8, optimal temperatures ranged between 22 and 27°C across all models. Annual Precipitation (bio12) for 2040-2070 showed slight variation between the models, with access1-0 (750mm), bcc-csm-1-m (450-500mm), and hadgem2-cc (600-750mm). All models indicated that Precipitation of the Wettest Quarter (bio16) is optimal for *B. pfeifferi* at 350 mm, and Precipitation of the Warmest Quarter (bio18) confirms that *B. pfeifferi* will thrive in environments with low annual rainfall (350 mm). In 2070-2100, bio16 and 18 showed an increase of 100-150mm in rainfall during the wet and warm quarters (Table 5-1).

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Table 5-1: *Bulinus africanus*, *Bulinus globosus* and *Biomphalaria pfeifferi* preferable environments using different climate models for RCP 4.5 2040-2070 and 2070-2100.

Species	access1-0		bcc-csm1m-1		hadgem2cc		
<i>B. africanus</i>	2040–2070	2070–2100	2040–2070	2070–2100	2040–2070	2070–2100	
	Bioclimatic variables						
	Bio3 (°C)	55	84	51	50	75	65
	Bio5 (°C)	20–25	25 and 32	20–27	20–25	20–25	26–27
	Bio8 (°C)	25	28	25	26	26–30	27–30
	Bio13 (mm)	100	5–100	0–80	180	50	70
	Bio15 (Coefficient of Variation)	0.50	0–0.50	1.35	1.20	0.50	0.50
	Bio16 (mm)	500	515–750	500–700	500–750	540–1000	500
	Soil water volume for the wettest quarter	0.30	0.50	0.20	0.20	0.00	0.30
	Soil water volume for the coldest quarter	0.40	0.40	0.35	0–0.1	0.30	0.30
	Soil water for the warmest quarter	0.40	0.30	0.30	0.30	0.35	0.25
<i>B. globosus</i>	Bio4 (standard deviation ×100)	100	100	80	75	55	–50
	Bio7 (°C)	13–17	14–16	16–17	17	14–15	14
	Bio8 (°C)	26	27	26	25	24–25	26–27
	Bio15 (Coefficient of Variation)	1.00	0.80	1.35	1.2	0.80	1.25

THE DISTRIBUTION OF SCHISTOSOMA-TRANSMITTING SNAILS UNDER CLIMATE CHANGE PROJECTIONS

Table 5-1 continued

Species		access1-0		bcc-csm1m-1		hadgem2cc	
		2040–2070	2070–2100	2040–2070	2070–2100	2040–2070	2070–2100
<i>B. globosus</i>	Bioclimatic variables						
	Bio16 (mm)	260	600–1000	350–450	650	350	700–800
	Bio17 (mm)	10	0	30	35	10	0
	Soil water for the warmest quarter	0.20	0,3	0.30	0.20	0.25	0.25
<i>B. pfeifferi</i>	Bio4 (standard deviation ×100)	120	–50	50	50	50	–75
	Bio8 (°C)	24	22	24	25–27	23	25–26
	Bio12 (mm)	750	520	450–500	550–700	600–750	600
	Bio16 (mm)	350	470	350	350	350	500
	Bio18 (mm)	250	350	250	180	250	350

5.1.2 Predicted suitable habitats for the intermediate host snails under the emission scenario RCP 8.5

While there was a slight variation in isothermality, all three climate models agree that *B. africanus* would thrive at 80°C. For bio5, the optimal temperature range for *B. africanus* was consistent among all models at 22°C-26°C. This slight decrease from RCP 4.5 indicates 20°C-27°C for bio5. This illustrated that climate suitability can favour *B. africanus* by 1°C cooler in the more severe scenario. In Bio8, where access1-0 suggested 27°C, bcc-csm-1-m indicated 10°C-16°C, and hadgem2-cc shows 15°C-17°C. Meanwhile, RCP 4.5 models range from 28°C to 30°C. This indicates that *B. africanus* will be suited to cooler to warm temperatures in the near future. Despite differences in bio8, climate models indicated that *B. africanus* prefers rainfall amounts of 180-300 mm for bio13. RCP 4.5 climate models showed that *B. africanus* favours 80-100 mm for the wettest month. However, in RCP 8.5, there is an increased response to rainfall. This shows that *B. africanus* will withstand moderate rainfall during the wettest month. Both scenarios indicate that *B. africanus* requires adequate rainfall throughout the wet quarter to maintain soil moisture without causing flooding.

The precipitation variation coefficient changes from 0.80 to 0–0.50, then from 1.20 to 0.80, stabilising at 0.40. Bio16 preferences also varied, with access1-0 indicating 700 mm, bcc-csm-1m indicating 450 mm, and hadgem2-cc ranging from 550-750 mm. For the wettest quarter, all models agreed that suitable soil water environments are between 0.15 and 0.16. *Bulinus africanus* thrives in 0.25-0.45 for the coldest and warmest quarters across all models, maintaining consistency in soil water preferences (Table 5-2). Between 2070 and 2100, the bio3 value is constant at 80°C. This shows no variation in *B. africanus* suitability compared to 2040-2070. In 2070-2100, suitability was slightly changed by an increase in 1°C-2°C. bio8 fluctuated between 25°C and 30°C, and bio13 increased to 250mm compared to 2040-2070. Meanwhile, bio15 and 16 are unchanged at 0.80 and 700mm, respectively.

Bio4 show different optimum climates for *B. globosus* in all three climate models. Access1-0 suggests -50°C, bcc-csm-1-m at 200°C, and hadgem2-cc at -5°C. Based on bio7, *B. globosus* prefers temperatures between 10°C and 19°C. In bio8, all models agree that *B. globosus* thrives at 25-30°C. This is an increase in temperature from RCP 4.5 in both periods. This showed that *B. glo-*

bosus would become more resilient to warmer and hotter temperatures. Similarly, all models indicate suitability for bio15 at 1.00-1.50. The models' optimum thresholds in bio16 differ, with access1-0 suggesting 600 mm, bcc-csm-1-m showing 250-400 mm, and hadgem2-cc suggesting 0-250 mm. Bio17 also displayed varying optimum values across the models, with access1-0 at 25 mm, bcc-csm-1-m at 50 mm, and hadgem2-cc at 0-100 mm. Soil water for the warmest quarter was consistent with all three climate models, indicating *B. globosus* thrives at 0.10-0.40. Between 2070 and 2100, there was a slight variation in the climate models for bio7 (12°C-18°C). The results for 2070-2100 found that bio8 remained constant with the same climate suitability as 2040-2100 (Table 5-2). It was found that bio16 and 17 decreased in rainfall across all climate models (500mm and 0-50mm), respectively. This showed that *B. globosus* climate suitability can be changed as the intermediate host will favour habitats with decreased rainfall.

For 2040-2070, bio4, *B. pfeifferi* thrives at -10°C for access1-0 and bcc-csm1-1-m, and 50°C for hadgem2-cc. Meanwhile, in RCP 4.5, bio4 was at -75 to 50°C. However, all three models indicated that the temperature preferences for *B. pfeifferi* varied between 23°C to 28°C, indicating a common preference for these environmental conditions (Table 5-2). Both scenarios (RCP 4.5 and 8.5) indicate that these were the optimal temperatures for bio8. This shows that *B. pfeifferi* favours habitats at 23°C to 28°C. Regarding bio12, all models agreed that *B. pfeifferi* flourishes when annual rainfall is between 500 and 800 mm. RCP 4.5 showed more variation (450-750mm). It indicates that *B. pfeifferi* prefers moderate to high yearly rainfall in RCP 8.5. Bio16, as predicted by climate models, indicates that *B. pfeifferi* thrives when rainfall is between 350 and 400mm. For RCP 4.5, 350mm was also found optimal. Similarly, bio18 shows agreement across models, suggesting *B. pfeifferi*'s preference for environments with rainfall between 200 and 450 mm. Between 2070 and 2100, there is a slight variation in climate models, suggesting the optimal bio8 is 22°C to 27°C. This shows that *B. pfeifferi*'s climate suitability will be 1°C cooler than in 2040-2070. Two climate models show a decrease in bio12 for 2070-2100. It indicates that *B. pfeifferi* can colonise areas with low- moderate yearly rainfall (300-475mm). All climate climates for 2070-2100 indicated that bio16 ranges from 350 to 400mm, and bio18 varies from 250 to 400mm. Both scenarios (RCP 4.5 and 8.5) indicate that *B. pfeifferi* can thrive in environments with low rainfall for the warmest quarter.

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Table 5-2: *Bulinus africanus*, *Bulinus globosus* and *Biomphalaria pfeifferi* preferable environments using different climate models for RCP 8.5 2040-2070 and 2070-2100.

Species		access1-0		bcc-csm1-1		hadgem2cc	
		2040-2070	2070-2100	2040-2070	2070-2100	2040-2070	2070-2100
<i>B. africanus</i>	Bioclimatic variables						
	Bio3 (°C)	80	80	60	75	75	73
	Bio5 (°C)	22–26	22–26	20–26	25–28	20–27	24–27
	Bio8 (°C)	27	28	10–16	25	15–17	28–30
	Bio13 (mm)	180	250	180–200	200	180	250–300
	Bio15 (Coefficient of Variation)	0.80	0–0.50	1.20	0.80	0.40	0.40
	Bio16 (mm)	400	700	500–750	450	220	550–750
	Soil water volume for the wettest quarter	0.10	0.16	0.30	0.15	0.10	0.15
	Soil water volume for the coldest quarter	0.30	0.25	0.35	0–0.10	0.4	0.45
	Soil water for the warmest quarter	0.25	0.30	0.30	0.35	0.30	0.25
<i>B. globosus</i>	Bio4 (standard deviation ×100)	-50	50–100	200	150	-5	0
	Bio7 (°C)	17–19	15	17–18	17–18	10–13	12
	Bio8 (°C)	25–30	25–30	25	25	25 and 30	23 and 30
	Bio15 (Coefficient of Variation)	1.00–120	1.00	0.90–1.00	0.7	1.50	1.20
	Bio16 (mm)	600	0–100	250–400	250–350	0–250	500
	Bio17 (mm)	25	0–20	50	50–10	0–100	25

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		Soil water for the warmest quarter					
		0.10–0.20	0,3	0.25	0.35	0.4	0.25
<i>B. pfeifferi</i>	Bio4 (standard deviation ×100)	-10	-10	100	-10	50	-50
	Bio8 (°C)	28	22	26	25-27	23	25–26
	Bio12 (mm)	500–750	700–850	700–800	350–475	500	400
	Bio16 (mm)	400	600–850	400	350	350	400–500
	Bio18 (mm)	200–350	200–350	300–450	350–450	250	400

5.2 Predicted geographical distribution of *Schistosoma* transmitting snails

The climate models were reasonably accurate at predicting the future distribution of intermediate hosts based on the bioclimatic variables. According to the results, temperature and rainfall will influence the future distribution of schistosomiasis in SA. *Bulinus africanus*, *B. globosus* and *B. pfeifferi* have different habitat preferences but can coexist at certain locations (Pedersen et al., 2017). The results show a shift in spatial patterns over time, indicating a rise in unsuitable habitats. Nonetheless, pockets of suitable habitats were identified in regions previously considered unsuitable, like the Western Cape. Figures 5-1 to 5-3 illustrate the results for the climate models and different intermediate snail species. Grey areas show non-suitable habitat (0-0.33), green depicts regions that have low suitability habitat (0.33-0.66), orange illustrates areas that have a moderate suitability habitat (0.66-0.90) and red shows high suitability habitat (0.90-1.00).

5.2.1 Predicted future spatial distribution of *Schistosoma* transmitting snails using climate models

For the baseline period, the ecological models showed moderate suitability habitat for *B. africanus* around the eastern part of Gauteng province, parts of Mpumalanga and the North West Province (Figure 5-1A). *Bulinus africanus* was found to be widespread west of the Eastern Cape Province. For the access1-0 climate model, RCP 4.5 and 8.5 (2040-2070), GLM, MaxEnt and RF showed that areas in the Eastern Cape would likely become highly suitable (Figure 5-1A). The GLM further showed that in RCP 8.5, newly suitable locations could be established around the Drakensberg and eastern Free State Province. Moderately suitable areas will decline, and more will be considered non-suitable habitats for *B. africanus*. In RCP 8.5 (2070-2100), newly highly suitable areas will be established around the northeast coast of KwaZulu-Natal and Eastern Cape (Figure 5-1B). Notably, while new geographical locations are found, the contraction of the suitable regions is evident overall. The consistent distribution patterns for both RCP scenarios indicated that shifts in suitable habitats and non-suited areas would occur. This highlighted the evolving suitability levels in specific provinces such as Gauteng and the Eastern Cape.

For the baseline period, *B. globosus* was widely distributed in the eastern and northeastern areas of SA, particularly in the Limpopo, Mpumalanga, Gauteng, and eastern regions of the North West

Province. The distribution extends to the coastal areas in KwaZulu-Natal (Figure 5-1C). For the access1-0 climate model, RCP 4.5 and 8.5 (2040-2070), GLM and RF show an increase in highly suitable habitats for *B. globosus* around the northeastern areas of Limpopo, Mpumalanga, and the northeastern regions of the North West Province (Figure 5-1C). In RCP8.5 (2040-2070), highly suitable areas are more defined in the eastern geographical regions of Limpopo. Random forest showed highly concentrated suitable locations around the North West province. Overall, for RCP 4.5 and 8.5, there is a decrease in low-suitable areas that will become non-suitable for *B. globosus* (Figure 5-1D), showing a reduction in highly suitable areas and an increase in moderately suited geographic locations. Highly suitable areas are found over the eastern areas in the Limpopo province and on the north coast of KwaZulu-Natal. The ensemble models show a decline in highly and moderately suited habitats. Previous low-suitable areas will become non-suitable for *B. globosus*. This highlights the intricate interplay between climate and habitat suitability over time.

The baseline showed that *B. pfeifferi* was more abundant and distributed spatially across SA than *B. africanus* and *B. globosus*. The spatial distribution of *B. pfeifferi* is similar to *B. globosus*. *Biomphalaria pfeifferi* can be seen distributed in the northern and coastal areas of Kwa-Zulu Natal and around the coast of the Eastern Cape. The distribution covers most of Gauteng, Limpopo, and Mpumalanga (Figure 5-1E). For the access1-0 climate model, RCP4.5 and 8.5 (2040-2070) GLM showed highly suitable habitats for *B. pfeifferi* will decline, especially in the extreme eastern parts of Limpopo and Mpumalanga.

The RF model showed slight variations between the different periods. In the baseline period, *B. pfeifferi* was found in parts of the Gauteng Province; by RCP 4.5 (2040 -2070), highly suitable habitats will contract (Figure 5-1E). The new geographical areas extend from the KwaZulu-Natal north coast to the Eastern Cape coast. *Biomphalaria pfeifferi* will likely expand its geographical distribution in SA with climate change. This is because the species can tolerate a wide range of temperatures. Overall, for RCP 4.5 (2040-2070), the ensemble model depicts a more moderately suitable habitat and less highly suited areas. Compared to RCP 4.5, RCP 8.5 showed more moderate suitable areas and a decline in low suitability (Figure 5-1F). In RCP 4.5 and 8.5 (2070-2100), GLM showed increased *B. pfeifferi* suitable areas compared to RCP4.5 (2040-2070). MaxEnt showed that most areas will be less suitable. The ensemble model showed a decline in moderate and highly suitable areas for *B. pfeifferi* in SA.

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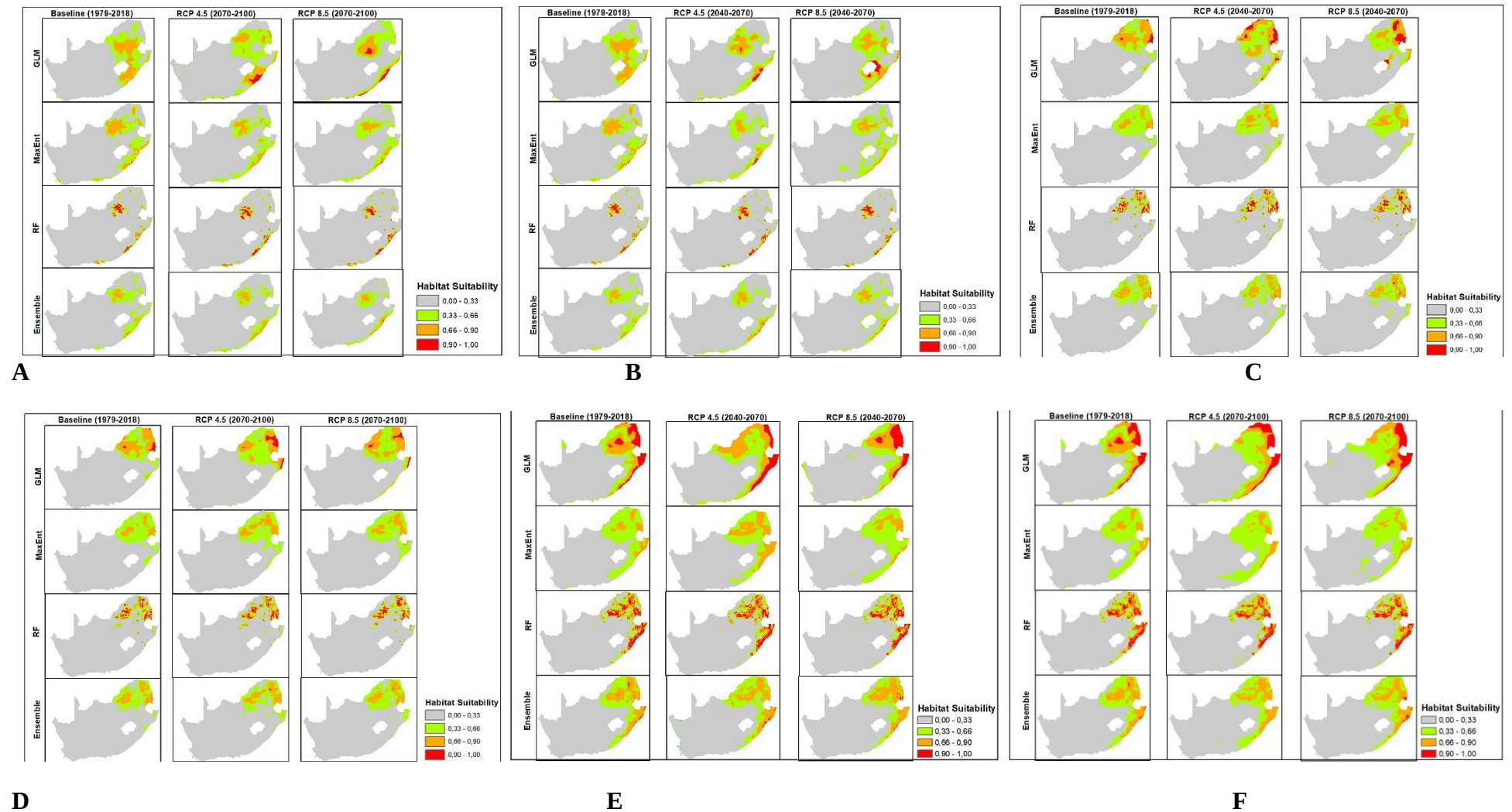


Figure 5-1: Ecological models using access1-0 for three time periods. A-B (*B. africanus*), C-D (*B. globosus*) and E-F (*B. pfeifferi*).

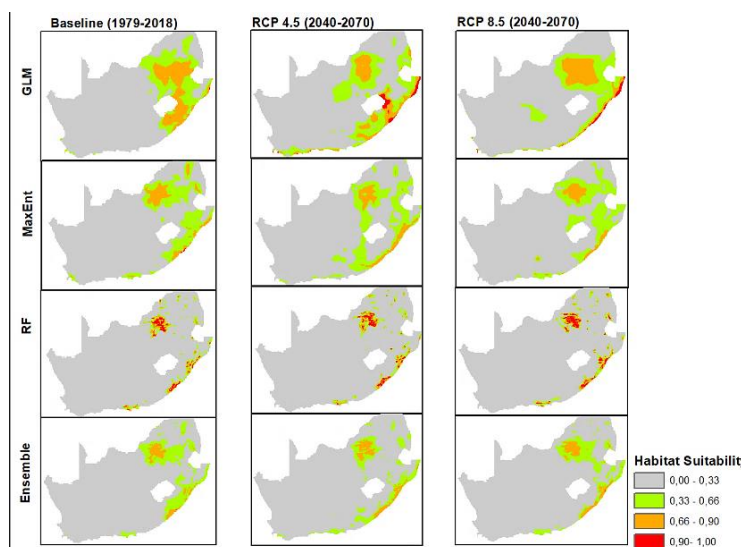
According to the bcc-csm1-1m model, there is a slight variation in suitable habitats. However, the distribution showed a similar pattern to access-1.0. For *B. africanus*, RCP4.5 showed a decline in moderate suitability over the North West, Gauteng, and Eastern Cape Provinces. This indicates that *B. africanus* will likely be contracting in the abovementioned Provinces. The GLM model showed potential for new suitable areas over the north coast of KwaZulu-Natal and Drakensberg. Overall, the ensemble model showed a decline and contraction of *B. africanus* in low and moderate suitable regions of SA (Figure 5-2A). Similarly, in RCP8.5, the ensemble model showed similar patterns as in RCP4.5; Gauteng and parts of the North West Province depicted a decrease in low to moderate suitable habitats and an increase in non-suitable areas (Figure 5-2B).

RCP 4.5 (2040-2070) showed an increase or expansion of *B. globosus* suitable areas towards the east part of the country (Figure 5-2C). The GLM model showed that *B. globosus* would increase in moderately suitable areas towards the Free State province and in highly suitable locations on the east coast. In the MaxEnt model, moderately suitable areas are concentrated over SA's north-east and eastern parts. Overall, there will be a decline in low suitability for *B. globosus* in SA. In contrast to RCP 4.5 and 8.5 (2040-2070), RCP 4.5 and 8.5 (2070-2100) showed a decline in highly suitable areas in SA. This illustrates that a few areas in SA are highly suitable for *B. globosus*. According to the GLM and MaxEnt models, moderately suitable habitats for *B. globosus* are shown to be over the eastern regions of SA, such as Limpopo and Mpumalanga. Ensemble models showed moderate habitat suitability over the North West and Gauteng province (Figure 5-2D).

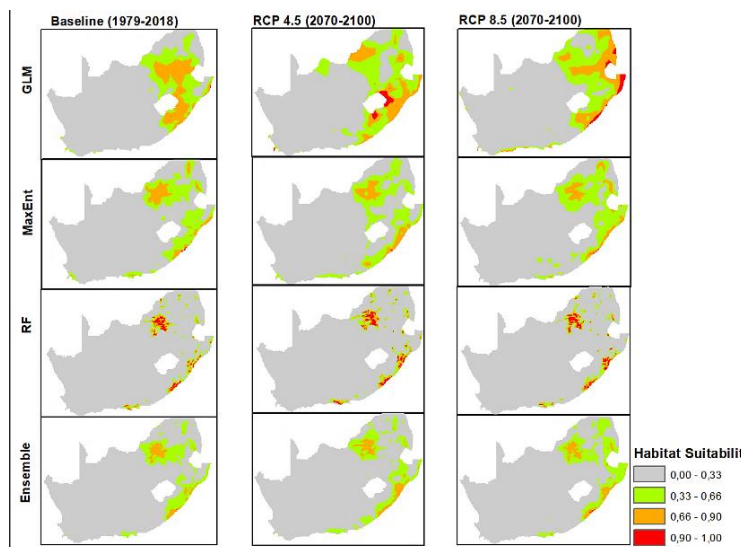
In RCP 4.5, GLM and MaxEnt showed a decline in moderately suitable habitats of *B. pfeifferi* over the Gauteng and North West Provinces. This shows that *B. pfeifferi* will contract in the abovementioned and expand in the eastern provinces. GLM showed an increase in suitable areas around the eastern parts of SA extending towards the north coast of Kwa-Zulu Natal. The ensemble model showed that currently suitable regions would decline in SA, particularly in the Eastern Cape (Figure 5-2E). Similar to RCP 4.5, GLM in RCP8.5 also showed an increase in suitable areas around the north coast of KwaZulu-Natal and the eastern regions of Mpumalanga (Figure 5-2F). In RCP 4.5 (2070-2100), GLM also showed an increase in moderately suitable habitats of *B. pfeifferi* across northeastern areas of the North West province. MaxEnt showed a rise in moderately suitable areas in parts of the Mpumalanga and Limpopo provinces. In RCP 8.5 (2070- 2100), GLM showed newly suitable areas in the eastern part of SA along the borders of Limpopo and Mpumalanga.

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MaxEnt showed a decrease in suitable habitats and an increase in low-suitable areas. The ensemble model suggested a transition to moderately suitable habitats and a decrease in well-suited regions. In the subsequent timeframes (2070-2100) under RCP 4.5 and 8.5, the models indicated expanded suitable areas for *B. pfeifferi* compared to the earlier 2040-2070 under RCP4.5. However, the ensemble model showed a decreasing moderate and increasing low habitat suitability trend. This indicates that climate will affect the distribution ranges, and the snails will move into these new ranges.

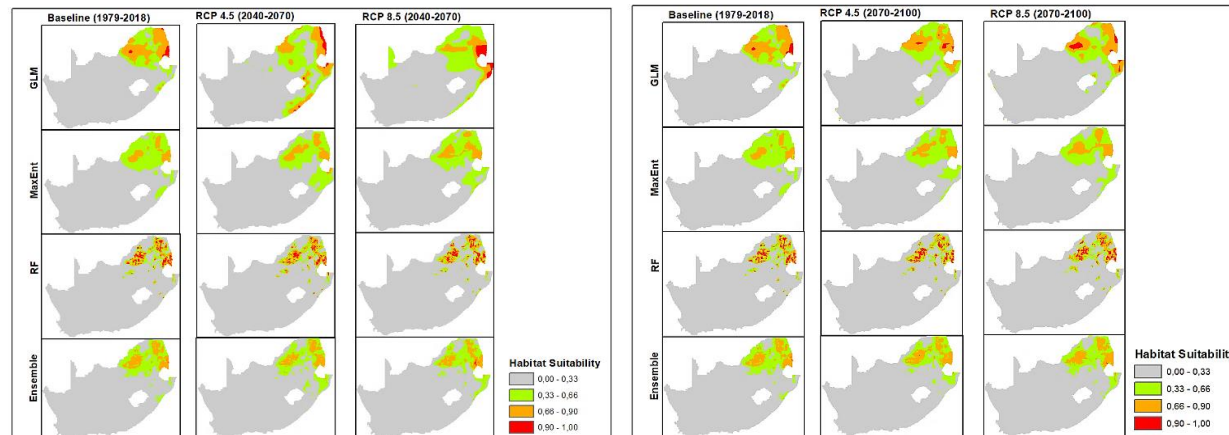


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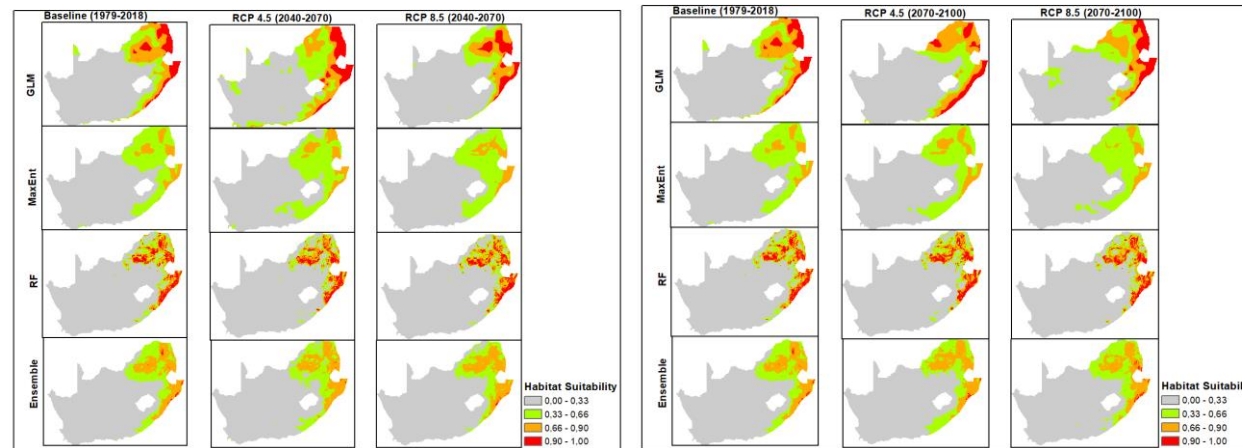
B

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C

D



E

F

Figure 5-2: Ecological models using bcc-csm1-1m for three time periods. A-B (*B. africanus*), C-D (*B. globosus*) and E-F (*B. pfeifferi*).

Based on the hadgem2-cc model, there is a slight variation in suitable habitats. However, the distribution showed a similar pattern to access-1.0 and bcc-csm1-1m. For *B. africanus*, moderately suitable RCP4.5 (2040-2070) areas will contract, with most suitability distributed in the Gauteng province and alongside the coastal regions of the Eastern Cape. Low suitable habitats will increase in the Kwa-Zulu Natal Province (Figure 5-3A). In RCP8.5 (2040-2070), similar distribution patterns of *B. africanus* were observed. Moderately suitable habitats will decline over the Gauteng province and increase over the coastal areas of Kwa-Zulu Natal. There will be an increase in no suitability for *B. africanus* and a decrease in low suitable habitat areas. This shows that *B. africanus* habitat will contract. Similar distribution patterns were observed in RCP4.5 and 8.5 (2070-2100); there will be a decline in habitat suitability in SA, with more concentrated moderate suitability in the Gauteng province and high suitability along the Eastern Cape coast. Overall, there will be a decline in low suitable areas and an increase in non-suitable habitats of *B. africanus* in SA (Figure 5-3B).

For *B. globosus*, RCP4.5 (2040-2070) shows suitable habitats along the border of Mpumalanga and Swaziland (Figure 5-3C). There will be an increase in the distribution of moderate suitability habitats along the northeastern areas of Mpumalanga, Limpopo, and parts of the North West province. In RCP 4.5 and 8.5 (2070-2100), there is a predicted increase in moderately suitable habitats in the northeastern part of SA. A decline in low-suitability habitats and increased non-suitable areas for *B. globosus* were observed. (Figure 5-3D).

For *B. pfeifferi*, highly suitable habitats will contract along the eastern areas of SA, especially in Kwa-Zulu Natal. There is a wide spread of moderate habitats for *B. pfeifferi* along the Kwa-Zulu Natal northern areas, northeastern areas of Limpopo and Mpumalanga, and eastern parts of the North West and Gauteng (Figure 5-3E). There will be an increase in habitats unsuitable for *B. pfeifferi* on the west of the Eastern Cape Province and a decrease in low suitable areas around the Gauteng Province. In RCP 4.5 and 8.5 (2070-2100), *B. pfeifferi* highly suitable areas, will decline (Figure 5-3F). Like RCP 4.5 and 8.5 (2040-2070), most moderate habitats for *B. pfeifferi* are expected to become widely distributed towards the northeastern and eastern regions of the country.

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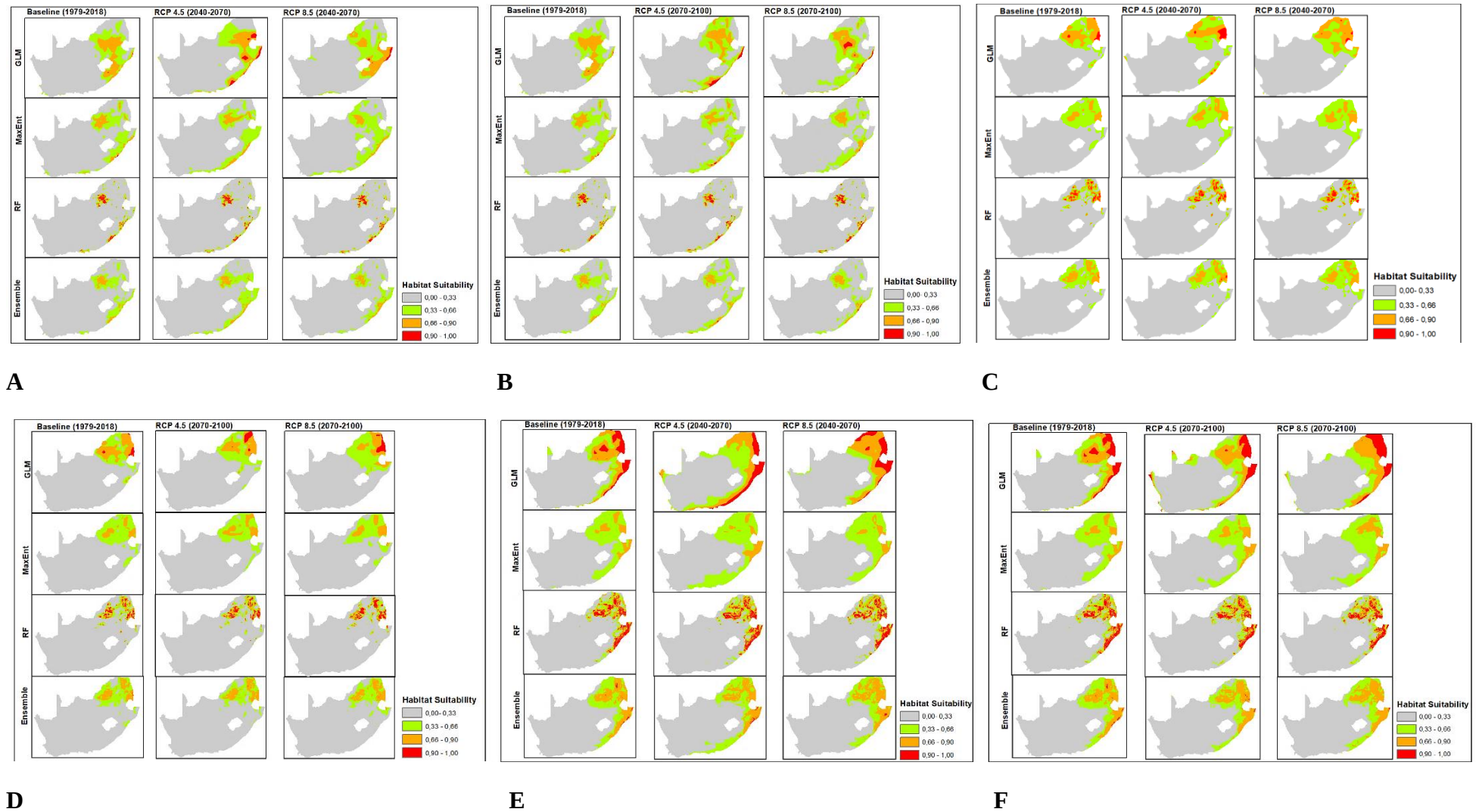


Figure 5-3: Ecological models using hadgem2-cc for three time periods. A-B (*B. africanus*), C-D (*B. globosus*) and E-F (*B. pfeifferi*).

5.3 Discussion

The second objective of the thesis was to characterise the distribution of intermediate hosts of schistosomiasis in SA using ecological and climate models. This is one of the first studies to predict the future distribution of *B. africanus*, *B. globosus* and *B. pfeifferi* in SA. Three ENMs and GCMs were used to predict the future distribution of the intermediate host snails under two RCPs (4.5 and 8.5) for 2040-2070 and 2070-2100. Across these periods, the models performed well in predicting the species distribution by having similar AUC and TSS scores, although slight variations are observed. This could be due to ecological model differences and species distribution pattern shifts. Overall, the AUC values consistently remained high across different climate scenarios, indicating that the ensemble model predicts the distribution of *B. africanus*, *B. globosus* and *B. pfeifferi* well. The variations in AUC values across periods and climate scenarios can reflect changes in the species' range due to projected climate changes. These statistics highlight the ensemble model's reliability in predicting the potential impacts of climate change on the distribution.

5.3.1 Predicted suitable habitats based on bioclimatic factors.

Bulinus africanus can tolerate warmer temperatures, with climate models suggesting it can survive in temperatures up to 30°C, which is higher than its baseline range (26°C). The species prefers an optimum temperature in the warmest month between 20 and 27°C. A study by Appleton (1978) determined that cooler temperatures played a greater role in *B. africanus* development than hotter temperatures. The results showed that *B. africanus* would adapt to warmer and humid habitats. *Bulinus africanus* can thrive in environments with moderate rainfall, specifically between 80-100 mm during the wettest month and 500-700 mm during the wettest quarter, which helps maintain soil moisture without causing flooding. A previous study found that moderate rainfall facilitates the movement of snails and the creation of temporary snail habitats (Adekiya et al., 2019). Temperature is a significant factor in the distribution of *B. africanus* in SA (de Kock and Wolmarans (2004). Their study on *Bulinus* species highlighted that more than 70% of samples from this group were found in habitats with slow-moving or stagnant water (de Kock and Wolmarans (2004). Fast-flowing water during heavy rainfall can disrupt snail habitats and reduce parasitic cercariae survival (Xue et al., 2011). Hence, the results showed that *B. africanus* will continue to thrive in the wettest quarter when soils have higher moisture levels without flooding.

The climate models showed that *B. globosus* is inclined towards warm, humid climates, with an optimal temperature range for the mean temperature of the wettest quarter being 24°C-30°C, which is higher than its baseline range (22°C). Joubert et al. (1984) showed that *B. globosus* could withstand temperatures (34°C-40°C). Shiff et al. (1975) concluded that *B. globosus* could survive in thermally harsh environments as they are abundant in increasing temperatures. Kalinda et al. (2017) found that *B. globosus* thrives in habitats at 20°C-30 °C, exhibiting optimal growth and reproduction. Below this range, their metabolism and reproductive activity decline, and they become less active. Conversely, temperatures exceeding 30°C induce stress, heighten disease vulnerability, and increase mortality rates, reducing snails' presence in such areas (McCreesh et al., 2014). Additionally, temperature impacts the suitability of snail habitats by affecting vegetation, oxygen levels, and water availability (Oso and Odaibo, 2021). Therefore, this thesis found that *B. globosus* benefits from warm, humid summer conditions. *Bulinus globosus* has demonstrated adaptability to climate changes, enduring heavy rainfall and seeking new habitats when necessary.

The climate models showed that *B. globosus* typically prefers regions with lower rainfall during the wettest quarter, ranging from 260 - 450 mm. However, projections suggest it could adapt to higher rainfall levels of 600-1000 mm (2070-2100). The presence of water in an environment is a key factor in determining snail populations (Manyangadze et al., 2021). Rainfall can create temporary habitats for snails and cause them to be relocated to new areas due to the movement of water, which can lead to a reduction in local snail density when heavy rains occur (Manyangadze et al., 2021). Snails are likely to be displaced if water flow exceeds 0.3 m/s. For RCP 8.5, it was found that rainfall for the wettest and driest quarters will decrease across all climate models (500mm and ≤ 50 mm respectively). This indicated that the climate suitability for *B. globosus* can vary, as the intermediate host prefers habitats with reduced rainfall. Therefore, the current climate suitability for this species is likely to change, with *B. globosus* favouring habitats with less rainfall. A study by Pennance et al. (2016) found that schistosomiasis-transmitting snails are more abundant during post-rainy seasons and more likely to transmit the disease. Predicting the exact impact of rainfall on snail populations and the spread of infections is challenging due to the different effects of rainfall on various species and locations (Brooker, 2007).

Biomphalaria pfeifferi can tolerate warmer temperatures, with climate models suggesting it can survive in mean temperatures of the wettest quarter up to 28°C, which is higher than its baseline range (21°C). Adekiya (2018) found similar findings, namely that *B. pfeifferi* ranges from 20°C to

28 °C. This shows that *B. pfeifferi* varies in geographical distribution; the snail can colonise cooler to warmer areas in SA. Warm and humid summer conditions are conducive to the thriving of *B. pfeifferi*, as these climates promote their life cycle stages, from egg deposition through hatching to larval development, by increasing snail activity (Nandy and Aditya, 2022). For RCP 8.5, climate models showed a slight decrease in optimal temperatures to 22°C-27°C in the future, showing adaptability to cooler conditions. There was a notable difference in temperature tolerance for *B. pfeifferi* compared to *B. globosus*. It is pertinent to note that despite being widely distributed throughout the country, *B. pfeifferi* snails are not tolerant of high temperatures (Brown, 2002). Furthermore, a study by Sturrock (2001) showed that *B. pfeifferi* mortality was high at 32°C.

The climate models showed that *B. pfeifferi* is suited to environments with low rainfall during the warmest quarter (200-450 mm) and can colonise areas with low to moderate yearly rainfall (300-475 mm). Manyangadze et al. (2016) studied schistosomiasis in the Ndumo area of the uMkhanyakude district and found that *B. pfeifferi* were suitable in the cold and dry seasons (winter) following the rainy season. Christensen et al. (2018) found similar results, in which *B. pfeifferi* bred extensively following rainy seasons. A study in Ethiopia by Xue et al. (2011) showed that moderate rainfall is instrumental in increasing schistosomiasis by accumulating sufficient surface water in ponds. During heavy rainfall events, water levels rise, causing water turbulence. As a result, flow rates may increase, disrupting snail habitats and reducing cercariae survival (Xue et al., 2011). Therefore, *B. pfeifferi* was found to favour habitats that do not have high rainfall. In addition, Nwoko et al. (2003b) studied the spatial and seasonal distribution of human schistosomiasis intermediate host snails in Kwa-Zulu Natal and found a decrease in the abundance of *B. pfeifferi* during rainy and hot/dry days.

5.3.2 Predicted spatial distribution of *Schistosoma*-transmitting snails

According to the results, temperature and rainfall influence the future distribution of schistosomiasis in SA. *Bulinus africanus*, *B. globosus* and *B. pfeifferi* have different habitats but coexist at certain locations. Similarly, Pedersen et al. (2017) found that species have different foci but overlap at most locations in Zimbabwe. The thesis discovered a shift in spatial distribution over time, indicating a rise in unsuitable habitats. However, there were still pockets of suitable habitats in previously unsuitable areas.

Over the past four decades, SA has undergone a notable warming trend, with local temperature increases approximately twice that of the global average, particularly since the late 20th century (Kruger and Sekele 2012). This trend is characterised by a rise in warm extremes and a decline in cold extremes, with more pronounced changes in the western, northeastern, and eastern regions, aligning with prior studies that also identified a warming pattern, although less significantly in the central areas of the country (Kruger and Shongwe 2004, New et al., 2006). In addition, the climate models showed that *B. africanus* is expected to experience a reduction in moderately suitable areas between 2040 and 2070 under the RCP 4.5 climate scenario. The areas where the species is likely to thrive are predicted to become more concentrated in Gauteng Province and along the Eastern Cape's coastal regions. A moderate rise in temperature could render these unsuitable regions suitable. This was found in future habitats for *B. africanus* that are becoming more climatically suitable for habitats with temperatures up to 30°C.

Conversely, there will be more areas with lower suitability for the species in Kwa-Zulu Natal Province. This could be due to increased rainfall days, resulting in flash floods (Le Roux et al., 2017). *Bulinus africanus* prefers slow-flowing waters because fast-flowing waters will lead to snail mortality (Manyangadze et al., 2016). In addition, the climate categorisation of the Kwa-Zulu Natal Province is temperate with hot summers and no dry season, which means that rising temperatures during the summer can cause the local snail population to dry out, resulting in a decline in suitable areas and an increase in areas with lower suitability (Nwoko et al., 2023a). In contrast, the RCP 8.5 climate scenario showed a moderate suitability decline in parts of Gauteng and an increase along the Kwa-Zulu Natal coast. However, with an increase in temperature in the coastal areas of Kwa-Zulu Natal Province, the temperatures could suit *B. africanus* as the unsuitable areas may reduce, as shown in the results. Overall, the ensemble model forecasts a decrease in both low and moderate suitability regions for *B. africanus* in SA, leading to a general reduction in the species' range due to an increase in non-suitable habitats.

For *B. globosus*, climate predictions for RCP 4.5 between 2040 and 2070 suggest an expansion of habitats where the species can be along the border of Mpumalanga and Swaziland. There will also be more moderately suitable areas for the snail in northeastern Mpumalanga, Limpopo, and parts of the North West Province. The models used for these predictions also suggest an increase in moderately suitable habitats extending towards the Free State Province and highly suitable areas on the east coast. These provinces are situated in the interior and eastern parts of the country. In

an annual report, the Department of Environmental Affairs (2013) stated that by 2035, there would be a 2°C increase in the interior of SA. This suggests that *B. globosus* would find hotter temperatures more suitable. Climate models also predicted that habitats with temperatures of 30°C would become more ideal for *B. globosus*.

Temperature influences snail growth, reproduction, and population dynamics, affecting the development rates of both parasites and their snail hosts (Kalinda et al., 2017). Predictions about climate change are crucial for identifying areas at high risk, as warmer temperatures may speed up the development of hosts and parasites yet potentially reduce their survival. Studies on the impact of rising temperatures on snail populations have shown contrasting views. McCreesh et al. (2015) argue that warmer temperatures could expand suitable habitats and thus increase disease prevalence. In contrast, Pedersen et al. (2014b) contend that higher temperatures might shrink suitable habitats, decreasing disease transmission. Stensgaard et al. (2019) raised the possibility that snails may adapt to warmer temperatures, enhancing habitat suitability and disease prevalence. These differing perspectives might all apply to specific regions. In areas where low temperatures previously created unsuitable habitats, climate change-induced warming could make these habitats suitable. However, regions with suitable habitats might become unsuitable due to further temperature increases. This is similar to the finding in this thesis that the Free State Province is naturally cooler than other provinces in SA. As a result, the climate models in this thesis suggest a shift towards moderately suitable habitats that were previously unsuitable in the Free State. Kalinda et al. (2017) support this by noting that snails can endure temperatures around 15.5°C in colder seasons. Still, warmer temperatures could lead to a surge in snail numbers and a consequent rise in disease prevalence.

However, from 2070 to 2100, both climate scenarios (RCP 4.5 and 8.5) predict a reduction in areas highly suitable for the snail, indicating a potential future decrease in optimal climate suitability for *B. globosus* in SA. Yang and Bergquist (2018) used climate models to predict the future distribution of intermediate host snails and found that *S. haematobium* from 2021 to 2050 may decline in Africa, the Middle East, and southern Europe. Based on laboratory and field data, a separate model was created to estimate the impact of rising temperatures on *S. haematobium* and its intermediate host, *B. globosus*. This model suggests that with each 1°C increase in temperature, snail numbers and cercariae production could drop by up to 14% and 8%, respectively (Kalinda et al., 2018).

These findings are consistent with other research indicating that suitable habitats for *S. haematobium* near the equator in Africa will shrink due to future climate changes (Stensgaard et al., 2019). Nwoko et al. (2023) found that a decrease in suitability could be due to increased temperature and a decrease in rainfall. Summer months can become hot and dry, and snails will desiccate, reducing disease prevalence. However, there is increasing concern that urogenital schistosomiasis might spread to cooler regions, such as SA and the Ethiopian highlands (Stensgaard et al., 2019).

Under the climate scenario RCP 4.5, between 2040 and 2070, *B. pfeifferi* is expected to contract a significant portion of its highly suitable habitats, especially in the eastern regions of SA, like Kwa-Zulu Natal. *Biomphalaria pfeifferi* is anticipated to decrease and change locations. This could be due to little or no resilience to increased temperatures above 30°C (Joubert et al., 1986; Manyangadze et al., 2021). However, in this thesis, areas with moderate habitat suitability are predicted to expand in the northern parts of Kwa-Zulu Natal, the Eastern Cape coast, northeastern Limpopo, Mpumalanga, and eastern areas of the North West and Gauteng provinces. *Biomphalaria pfeifferi* will likely expand its geographical distribution in SA with climate change. This is because the species can tolerate a wide range of temperatures below 30°C. Stensgaard et al. (2013) discovered that *B. pfeifferi* is expected to extend its range in eastern and southern Africa. Stensgaard et al. (2013) also emphasised the significance of particular snail-parasite interactions in prediction models, noting that intermediate host snail species are more resilient to rising temperatures. In SA, the spread of *B. pfeifferi* could expand with the effects of climate change, assuming that their absence is because of unsuitable climate rather than an absence of adequate freshwater environments. A study in the 1980s found that many areas in southern Africa without *Biomphalaria* snails still possess habitats that seem fitting for these snails, indicating that unfavourable climate, especially temperature, might be the key factor keeping them away (Brown, 1980).

The ecological ensemble model forecasts a general decline in highly suitable habitats and an increase in moderately suitable ones. From 2070 to 2100, RCP 4.5 and 8.5 scenarios suggest an overall increase in areas suitable for the snail, but with a trend towards more moderate habitats and fewer highly suitable ones, indicating a shift in the snail's distribution due to climate change. Highly suitable habitats for *B. pfeifferi* will decline, especially in the extreme eastern parts of Limpopo, Mpumalanga, Gauteng and North West provinces. Despite its widespread presence in SA and its preferences for summer conditions, *B. pfeifferi* cannot withstand temperatures exceeding

30°C, with mortality reportedly occurring at higher temperatures (Adekiya, 2018). Hence, the future distribution of *B. pfeifferi* will contract in the eastern regions of SA.

5.4 Chapter Conclusion

Under RCP 4.5 and 8.5 climate scenarios, the ensemble models predict a varying future for *B. africanus*, *B. globosus*, and *B. pfeifferi*. For *B. pfeifferi*, there is an expected decline in highly suitable habitats, particularly in the eastern regions of SA, with a shift toward more moderate habitats that may expand in the northern parts of Kwa-Zulu Natal and other provinces, indicating a potential geographical distribution expansion despite the contraction in the east. *Bulinus globosus* is anticipated to experience a reduction in highly suitable areas but may find more moderate habitats in the interior and eastern parts of SA, possibly increasing suitable habitats due to the species' tolerance to higher temperatures. Conversely, *B. africanus* is projected to face a general decrease in low and moderate suitability regions, reducing its range, although some coastal areas may become more suitable with rising temperatures. Overall, while there may be an increase in moderately suitable habitats for these snails, the highly suitable areas are expected to decline, suggesting a complex interplay of habitat suitability changes due to climate change. The following chapter will focus on the impacts of climate change on the future distribution of *Schistosoma*-transmitting snails.

CHAPTER 6

The following chapter presents the results for Objective 3: *‘The impacts of climate change on the distribution of Schistosoma-transmitting snails.* The impact of climate change on *Schistosoma*-transmitting snail distribution has profound implications for the spread and control of schistosomiasis. The chapter examines how climate change affects the projected distribution of intermediate host snails.

THE IMPACTS OF CLIMATE CHANGE ON THE DISTRIBUTION OF *SCHISTOSOMA*-TRANSMITTING SNAILS

6.1 The potential changes of suitable areas for *Schistosoma*-transmitting snails under different climate scenarios

Table 6-1 illustrates the change in climate suitability for the intermediate host snails across three climate scenarios under two emission scenarios. Values highlighted in red show the high increases in climate suitability, while blue indicates high declines in suitability. *Bulinus africanus* under RCP 4.5 (2070-2100) had the largest increase in suitability, covering 356,000 km², while RCP 8.5 (2040-2070) experienced a significant decline of 138,000 km². *Bulinus globosus* in RCP 4.5 (2070-2100) showed the biggest increase, spanning 153,000 km², whereas RCP 8.5 (2070-2100) had the most substantial decline, with a decrease of 132,000 km². *Biomphalaria pfeifferi* in RCP 8.5 (2040-2070) had the highest increase, covering 255,000 km², while RCP 4.5 (2040-2070) witnessed the most significant decline, with a decrease of 159,000 km².

Table 6-1: Intermediate host snails change in climate suitability for climate models (access1-0, bcc-csm1-1-m and hadgem2-cc).

Climate Model	Species	Emission Scenario	Decline in suitability (km ²)	No Change (km ²)	Increase in Suitability (km ²)
access1-0	<i>Bulinus africanus</i>	RCP 4.5 (2040-2070)	144,000 (11%)	953,000 (75%)	175,000 (14%)
		RCP 4.5 (2070-2100)	145,000 (11%)	771,000 (61%)	356,000 (28%)
		RCP 8.5 (2040-2070)	138,300 (12%)	936,000 (71%)	198,000 (17%)
		RCP 8.5 (2070-2100)	151,000 (12%)	832,000 (66%)	289,000 (23%)
	<i>Bulinus globosus</i>	RCP 4.5 (2040-2070)	97,000 (8%)	976,000 (77%)	186,000 (15%)
		RCP 4.5 (2070-2100)	66,000 (5%)	1,041,000 (83%)	153,000 (12%)
		RCP 8.5 (2040-2070)	89,000 (8%)	1,024,000 (80%)	147,000 (12%)
		RCP 8.5 (2070-2100)	132,000 (10%)	1,027,000 (82%)	101,000 (8%)

THE IMPACTS OF CLIMATE CHANGE ON THE DISTRIBUTION OF SCHISTOSOMA-TRANSMITTING SNAILS

	<i>Biomphalaria pfeifferi</i>	RCP 4.5 (2040-2070)	159,000 (13%)	944,000 (75%)	156,000 (12%)
		RCP 4.5 (2070-2100)	111,000 (9%)	960,000 (76%)	188,000 (15%)
		RCP 8.5 (2040-2070)	193,000 (15%)	812,000 (64%)	255,000 (20%)
		RCP 8.5 (2070-2100)	164,000 (13%)	918,000 (73%)	177,000 (14%)
bcc-csm1-1-m	<i>Bulinus africanus</i>				
		RCP 4.5 (2040-2070)	139,000 (11%)	836,000 (66%)	297,000 (23%)
		RCP 4.5 (2070-2100)	154,000 (12%)	969,000 (76%)	149,000 (12%)
		RCP 8.5 (2040-2070)	130,000 (10%)	971,000 (76%)	171,000 (14%)
		RCP 8.5 (2070-2100)	132,000 (10%)	839,000 (66%)	301,000 (24%)
	<i>Bulinus globosus</i>				
		RCP 4.5 (2040-2070)	99,000 (9%)	966,000 (77%)	166,000 (14%)
		RCP 4.5 (2070-2100)	113,000 (9%)	1,022,000 (81%)	124,000 (10%)
		RCP 8.5 (2040-2070)	127,000 (10%)	956,000 (76%)	176,000 (14%)
		RCP 8.5 (2070-2100)	107,000 (9%)	1,047,000 (83%)	105,000 (8%)
	<i>Biomphalaria pfeifferi</i>				
		RCP 4.5 (2040-2070)	180,000 (14%)	804,000 (64%)	274,000 (22%)
		RCP 4.5 (2070-2100)	110,000 (9%)	907,000 (72%)	243,000 (19%)
		RCP 8.5 (2040-2070)	98,000 (8%)	908,000 (72%)	253,000 (20%)
		RCP 8.5 (2070-2100)	290,000 (23%)	811,000 (64%)	159,000 (13%)
hadgem2-cc	<i>Bulinus africanus</i>				
		RCP 4.5 (2040-2070)	162,000 (13%)	955,000 (75%)	155,000 (12%)
		RCP 4.5 (2070-2100)	116,000 (9%)	953,000 (75%)	203,000 (16%)
		RCP 8.5 (2040-2070)	125,000 (10%)	1,000,000 (79%)	147,000 (12%)
		RCP 8.5 (2070-2100)	138,000 (13%)	924,000 (72%)	210,000 (15%)

THE IMPACTS OF CLIMATE CHANGE ON THE DISTRIBUTION OF SCHISTOSOMA-TRANSMITTING SNAILS

<i>Bulinus globosus</i>	RCP 4.5 (2040-2070)	100,000 (8%)	1,017,000 (81%)	142,000 (11%)
	RCP 4.5 (2070-2100)	106,000 (8%)	1,041,000 (83%)	112,000 (9%)
	RCP 8.5 (2040-2070)	85,000 (7%)	1,029,000 (82%)	145,000 (12%)
	RCP 8.5 (2070-2100)	105,000 (8%)	992,000 (79%)	162,000 (13%)
<i>Biomphalaria pfeifferi</i>	RCP 4.5 (2040-2070)	161,000 (12%)	903,000 (71%)	196,000 (16%)
	RCP 4.5 (2070-2100)	95,000 (8%)	954,000 (76%)	211,000 (17%)
	RCP 8.5 (2040-2070)	216,000 (16%)	902,000 (72%)	142,000 (12%)
	RCP 8.5 (2070-2100)	163,000 (13%)	925,000 (73%)	172,000 (14%)

• Suitability in change for the access1-0 climate model

This study used the ensemble based on ecological niche models to assess changes in habitat suitability for *B. africanus*, *B. globosus*, and *B. pfeifferi* across various climate models, time frames, and emission scenarios. The colour red shows an increase in bioclimatic suitability (0.5), yellow shows no change in bioclimatic suitability (0), and blue show a decrease in bioclimatic suitability (-0.5).

Under the RCP 4.5 scenario between 2040-2070, *B. africanus* is projected to face an 11% decrease in habitat suitability, with a 75% no change and a 14% potential for increased suitability, particularly westward in SA and central Free State. However, Kwa-Zulu Natal and northern Eastern Cape may see reduced distribution (Figure 6-1). From 2070-2100, the species may encounter an 11% decrease, a 61% probability of no change, and a 28% rise in suitability, with gains to the west of SA and east of Mpumalanga, while declines may focus on northeastern Limpopo and Kwa-Zulu Natal. Under the more severe RCP 8.5 scenario for 2040-2070, a 12% decrease in suitability is expected, with a 71% chance of no change and a 17% increase, particularly inland in the Eastern Cape. From 2070-2100, a 12% decrease is projected, alongside a 66% likelihood of no change and a 23% increase, with suitability rising in coastal Eastern Cape, Gauteng, and Free State but declining in parts of Mpumalanga and KwaZulu-Natal.

For *B. globosus* under RCP 4.5 from 2040-2070, an 8% decrease in suitability is projected, with a 77% chance of no change and a 15% increase, especially inland in the Eastern Cape and parts of Free State, while eastern SA may see declines. From 2070-2100, the projections show a 5% decrease, an 83% probability of no change, and a 12% increase in suitability. Under RCP 8.5 between 2040-2070, there is a predicted 8% decrease in suitability with declines in extreme northeastern Limpopo, coastal KwaZulu-Natal, and parts of Gauteng, North West, and eastern Free State with an 80% chance of no change and a 12% increase. For 2070-2100, a 10% decrease is expected, with an 82% likelihood of no change and an 8% increase in suitability (Figure 6-1).

For *B. pfeifferi*, RCP 4.5 (2040-2070) showed a 13% decline in suitability, a 75% chance of no change, and a 12% increase in suitability. There is a significant decrease in suitability in eastern SA and parts of the Eastern Cape. An increase in suitability was shown when moving west and south of the North West province and towards the coastal areas of the Western Cape of SA. RCP 4.5 (2070-2100) showed a 9% decline in suitability, a 76% chance of no change, and a 15% increase in suitability. The gains can be seen in the North West, Free State, and parts of the Northern Cape and Eastern Cape. RCP 8.5 (2040-2070) show a 15% decline in suitability, a 64% chance of no change, and a 20% increase in suitability. RCP 8.5 (2070-2100), a 13% decline in suitability, a 73% chance of no change, and a 14% increase in suitability. Increases in suitability are seen towards the inner areas of the Eastern Cape, parts of the North West and Free State (Figure 6-1). The decline in suitability areas includes the coast of the Eastern Cape, Gauteng, and parts of Limpopo.

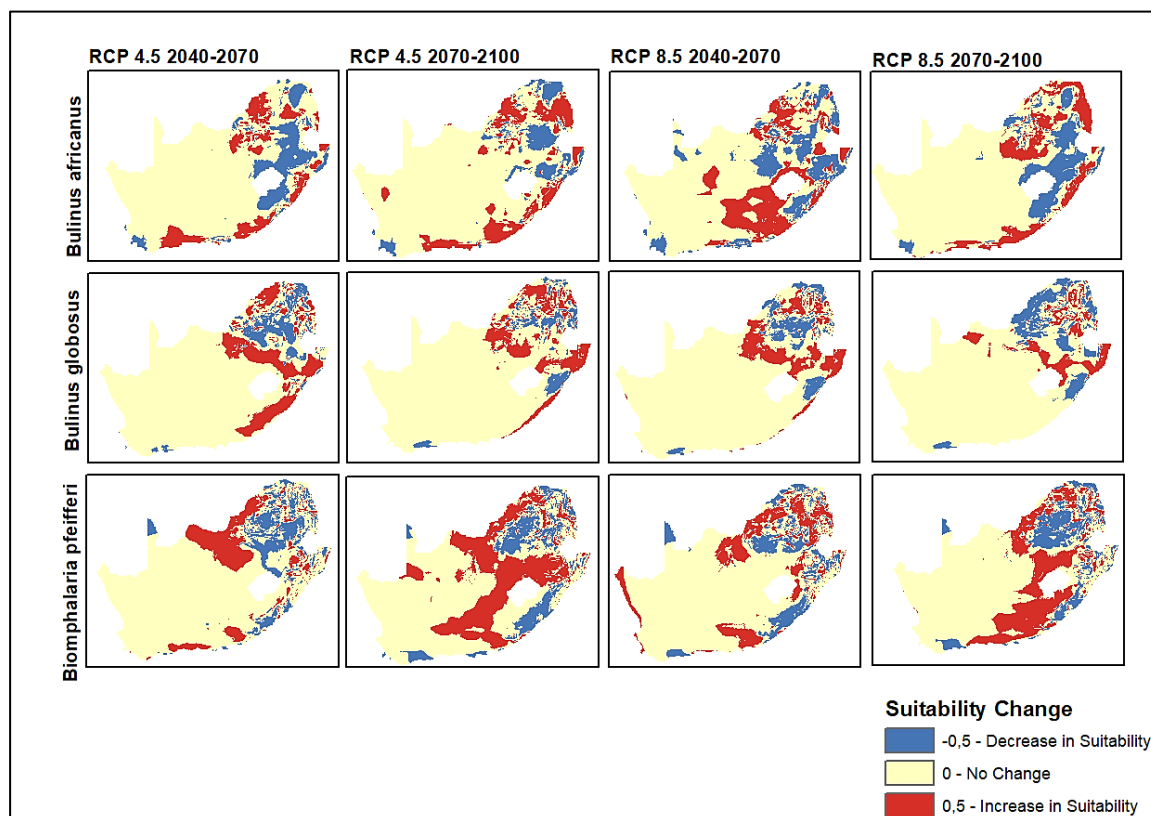


Figure 6-1: Change in suitability for *B. africanus*, *B. globosus* and *B. pfeifferi* using the access1-0 climate model for RCP4.5 and 8.5.

- **Suitability in change for the bcc-csm1-1m climate model**

For the bcc-csm1-1m model, *B. africanus*, RCP 4.5 (2040-2070), there is an 11% decline in suitability, a 66% chance of no change, and a substantial 23% increase in suitability (Figure 6-2). The increases are seen moving west in the western part of SA, including parts of the Free State, Eastern Cape province, and the southwest coast. The decline in suitability can be seen in Limpopo, Gauteng, Mpumalanga, and parts of the Kwa-Zulu Natal province. RCP 4.5 (2070-2100) shows a 12% decline in suitability, a 76% chance of no change, and a 12% increase in suitability. In RCP 8.5 (2040-2070), there is a 10% decline in suitability, a 76% chance of no change, and a substantial 14% increase in suitability. There is a decline in the inland of the Eastern Cape and parts of eastern Limpopo. In RCP 8.5 (2070-2100), there is a significant 10% decline in suitability; areas that experience a decrease in suitability are Free State and part of the North West and Gauteng provinces, respectively. There is a 66% chance of no change and a significant 24% increase in suitability.

For the bcc-csm1-1m model, *B. globosus*, RCP 4.5 (2040-2070), there was a 9% decline in suitability, a 77% chance of no change, and a 14% increase in suitability. Under RCP 4.5 (2070-2100), there is a 9% decline in suitability, an 81% chance of no change, and a 10% increase in suitability. Increases can be seen in the KwaZulu-Natal province and part of the southern Eastern Cape (Figure 7). In RCP 8.5 (2040-2070), there is a 10% decline in suitability, a 76% chance of no change, and a 14% increase in suitability. The rise in suitability extends from the southern Free State to the Northern areas of KwaZulu-Natal and the southwestern coast areas of the Eastern Cape (Figure 6-2). In RCP 8.5 (2070-2100), there is a 9% decline in suitability, an 83% chance of no change, and an 8% increase in suitability.

For *B. pfeifferi*, in RCP 4.5 (2040-2070), there is a 14% decline in suitability, a 64% chance of no change, and a significant 22% increase in suitability. Increased suitability is shown moving westwards in SA. The decline in habitat areas is focused on Gauteng, northern parts of Limpopo, eastern regions of the North West province and the east coast. Under RCP 4.5 (2070-2100), there is a 9% decline in suitability, a 72% chance of no change, and a modest 19% increase in suitability. In RCP 8.5 (2040-2070), there is an 8% decline in suitability, a 72% chance of no change, and a 20% increase in suitability. Under RCP 8.5 (2070-2100), there is a 23% decline in suitability, a 64% chance of no change, and a 13% increase in suitability. The Northern and Eastern Cape provinces in SA show an increase in suitable areas. Parts of the northern North West and Kwa-Zulu Natal are also ideal for *B. pfeifferi* (Figure 6-2).

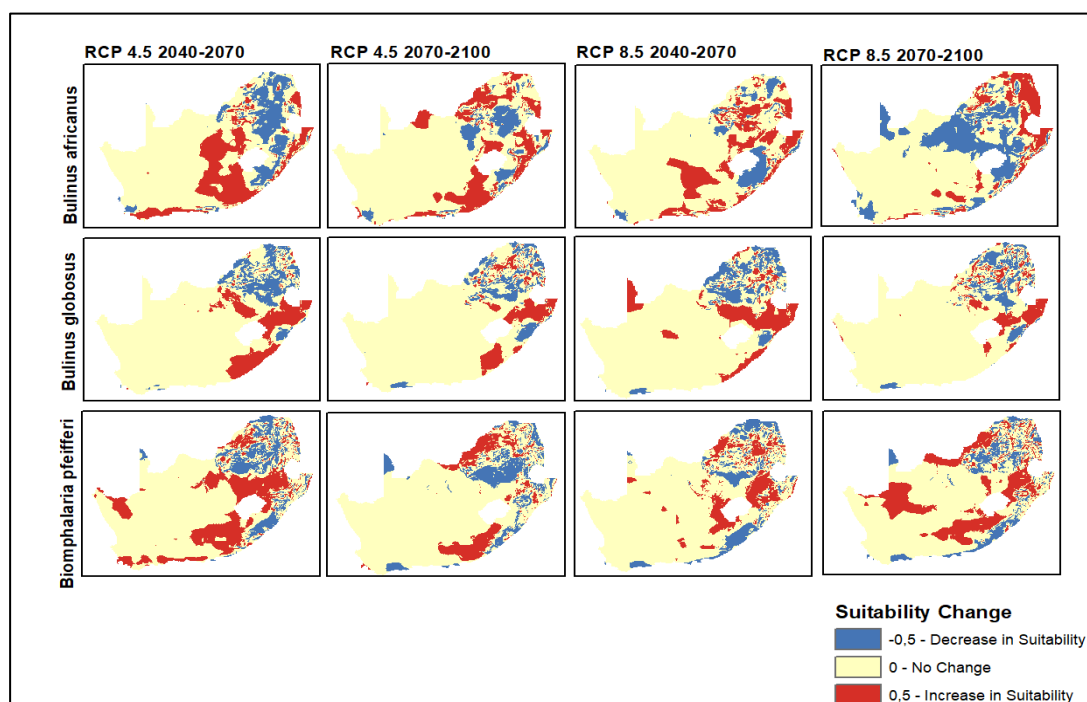


Figure 6-2: Change in suitability for *B. africanus*, *B. globosus* and *B. pfeifferi* using the bcc-csm1-1m climate model for RCP4.5 and 8.5.

- **Suitability in change for the hadgem2-cc climate model**

For *B. africanus*, there is a 13% decline in suitability, a 75% chance of no change, and a 12% increase in climate suitability (Figure 6-3). Under RCP 4.5 (2070-2100), there is a 9% decline in suitability, a 75% chance of no change, and a 16% increase in suitability. Areas that exhibit a decrease in climate suitability are in the Eastern Cape, part of the North West province. Under RCP 8.5 (2040-2070), there is a 10% decline in suitability, a 79% chance of no change, and a 12% increase in suitability. The decrease in suitability is situated across eastern parts of SA, such as east Mpumalanga, Gauteng, and areas in the North West Province. Increases in suitability are seen in northwest areas of Limpopo and the north coast in Kwa-Zulu Natal. Under RCP 8.5 (2070-2100), there is a 13% decline in suitability, a 72% chance of no change, and a 15% increase in suitability. There is a significant rise in suitability towards the west of the Eastern Cape province, the eastern areas of the Northwest, and part of Gauteng.

For *B. globosus*, Under RCP 4.5 (2040-2070), there is an 8% decline in suitability, an 81% chance of no change, and an 11% increase in suitability. An increase in suitable areas is found in the Eastern Cape, parts of the Drakensberg, and northern areas of Kwa-Zulu Natal. The decline can

be seen in parts of the North West province and the eastern regions of Limpopo and Mpumalanga. In RCP 4.5 (2070-2100), there is an 8% decline in suitability, an 83% chance of no change, and a 9% increase in suitability. Most of the rise in suitability is found in northeastern areas of SA (Figure 8). Under RCP 8.5 (2040-2070), there is a 7% decline in suitability, an 82% chance of no change, and a 12% increase in suitability. Under RCP 8.5 (2070-2100), there is an 8% decline in suitability, a 79% chance of no change, and a 13% increase in suitability. Suitable areas expand from the eastern Free State into the northern and northeastern regions of Kwa-Zulu Natal.

For *B. pfeifferi*, RCP 4.5 (2040-2070) showed a 12% decline in suitability, a 71% chance of no change, and a 16% increase in suitability. Areas that exhibited a decrease are concentrated in the Gauteng and North West provinces. Other declining regions include parts of Limpopo, Mpumalanga, and the Eastern Cape (Figure 6-3). Under RCP 4.5 (2070-2100), there is an 8% decline in suitability, a 76% chance of no change, and a 17% increase in suitability. RCP 8.5 (2040-2070) showed a 16% decline in suitability, a 72% chance of no change, and a 12% increase in suitability. Under RCP 8.5 (2070-2100), there is a 13% decline in suitability, a 73% chance of no change, and a 14% increase in suitability.

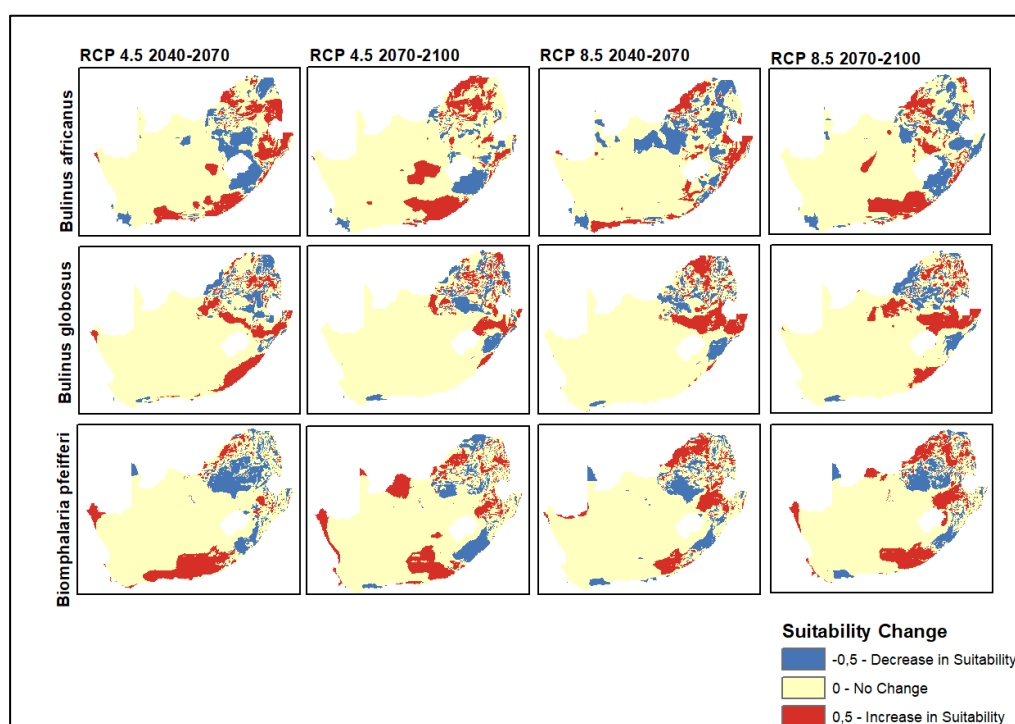


Figure 6-3: Change in suitability for *B. africanus*, *B. globosus* and *B. pfeifferi* using the hadgem2cc climate model for RCP4.5 and 8.5.

6.2 Discussion

The third objective of the thesis was to examine the impacts of climate change on the predicted distribution of *Schistosoma*-transmitting snails. *Bulinus africanus* will experience a notable increase of 356,000 km² in suitability under RCP 4.5 from 2070-2100 and under RCP 8.5 from 2040-2070 with a suitable area of 198,000 km². *Bulinus globosus* will have its largest suitability increase (186,000 km²) under RCP 4.5 from 2040 to 2070 and 147,000 km² under RCP 8.5 from 2040 to 2070. *Biomphalaria pfeifferi* will see a significant rise in suitability (274,000 km²) under RCP 4.5 from 2040-2070 and under RCP 8.5 from 2070-2100, an increase of (290,000 km²; Figure 6-4). Therefore, it is evident that 2040-2070 will see notable increases in suitability for all species and emission scenarios. However, the most notable rise for *B. pfeifferi* under RCP 8.5 will occur from 2070 to 2100.

The results showed that habitat suitability predictions for *B. africanus* and *B. pfeifferi* indicate that South Africa exhibits a clear gradient in climate suitability. These intermediate hosts have extensively concentrated suitability regions and new endemic areas previously climatically unsuitable. Furthermore, the results showed that RCP 8.5 generally presents a lower percentage of both increases and decreases in suitability for all three species than RCP 4.5. Hence, there will be a noticeable shift in spatial distribution, with an increase in areas where habitats are unsuitable, although suitable habitats will remain.

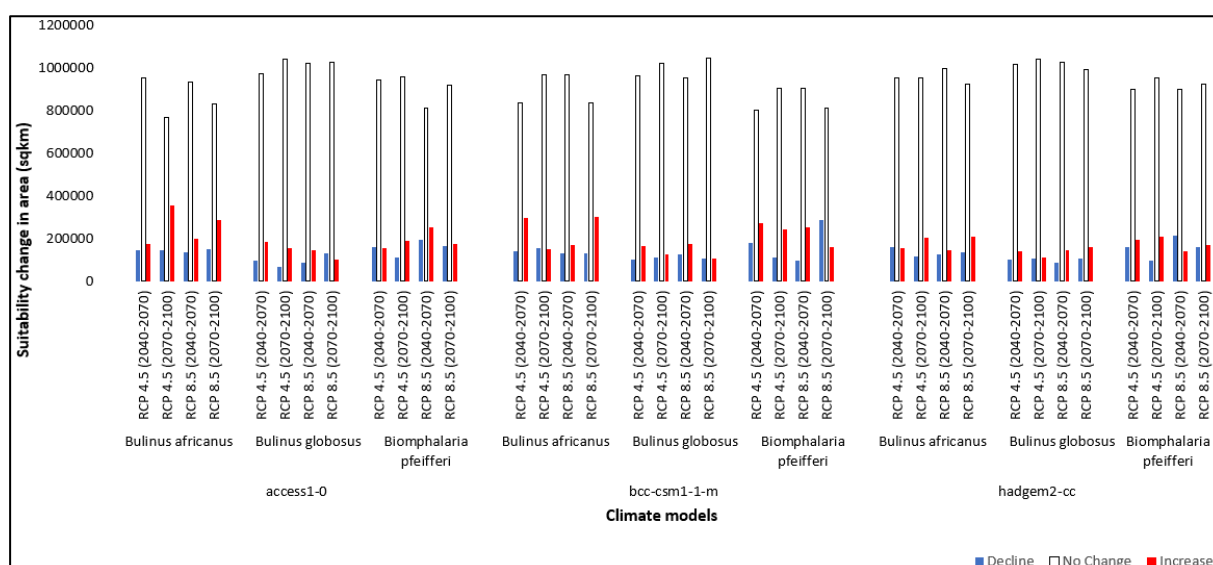


Figure 6-4: Climate suitability in change for *B. africanus*, *B. globosus* and *B. pfeifferi* across different climate models and scenarios. The red bars indicate an increase, and the blue illustrates a decrease in suitability.

6.2.1 Potential new endemic areas for *Schistosoma*-transmitting snails under different climate scenarios

For *B. africanus* under RCP 4.5, all models predict a decrease in habitat suitability in Kwa-Zulu Natal, Limpopo, Gauteng, Mpumalanga, parts of the North West and the northern Eastern Cape with expansions to new areas such as the southwest coast and in central Free State. Mbokodo et al. (2020) found temperature gradients from east to west and south to north, including the cooler temperatures at the elevated Drakensberg Mountains in the east. The Free State is situated at an elevated height and can be cooler than the other provinces (Mavis et al., 2018). This explains the expansion to these new areas as climates heat up; areas at higher elevations that were not endemic could become suitable for the temperature-sensitive schistosomes. The rise in temperatures could spread existing intermediate hosts to these higher altitudes, and species not affected by schistosomes may become vulnerable or come into contact with these parasites (Tumwebaze et al., 2019). Stensgaard et al. (2019) raise the possibility that snails may adapt to warmer temperatures, enhancing habitat suitability and disease prevalence. Future projections suggest a rise in daily maximum temperatures by as much as 6°C in SA's interior during 2070-2099, which could lead to more frequent and severe heatwaves. (Mbokodo et al., 2020). Due to this, the climate models showed a decline in climate suitability in parts of the North West, Gauteng, Limpopo and Mpumalanga. The decline in climate suitability is due to increasing temperatures that *B. africanus* cannot tolerate, leading to desiccation.

An increase in climate suitability can also be found in the northwest Limpopo and the north coast of Kwa-Zulu Natal. Yang and Bergquist (2018) found that between 2021 and 2050, *S. haematobium* will be expanding in central and eastern areas in SA (Figure 6-5). This showed that *B. africanus* will adapt to warmer and more humid habitats. In the extreme emission scenario, RCP 8.5, the models predicted widespread eastern declines in northeastern Limpopo, Kwa-Zulu Natal, Free State, North West, and Gauteng. Mangal et al. (2008) indicated that schistosomiasis, particularly intestinal schistosomiasis caused by *S. mansoni*, was higher in areas where temperatures ranged from 20°C to 30°C. However, they also found that the infection rates dropped when temperatures exceeded 30°C, possibly because the snails that serve as intermediate hosts for the disease had higher mortality rates at these temperatures. Mbokodo et al. (2020) modelled future temperatures in SA and found that the climate models accurately reflect the observed temperature patterns,

showing the highest values, averaging above 36°C, in the northwestern dry regions of SA. As shown in Chapter 5, *B. africanus* respond well to temperatures up to 30°C. Temperatures above the suited temperature will lead to a decline or contraction of the host. This means a temperature rise could reduce the species' range if they find the increasing temperatures intolerable. Conversely, if the temperature rise is slight and precipitation levels stay acceptable for the species, their range might not change much.

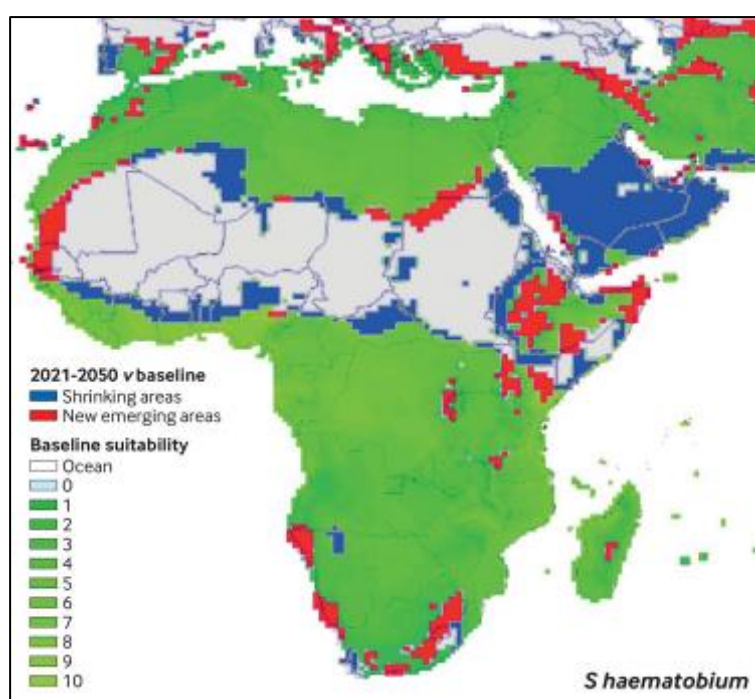


Figure 6-5: Predicted changes in the geographical risk zones for urogenital schistosomiasis between 2021 and 2050 in Africa and the Middle East. It uses a suitability scale from 0, representing unsuitable conditions, to 10, indicating the most suitable conditions for *S. haematobium*. Source: Yang and Bergquist (2018).

Under RCP 4.5, climate models showed that *B. globosus* is expected to decline, with some inland areas of the Eastern Cape and parts of the Free State potentially seeing an increase. Similarly to *B. africanus*, this illustrates that *B. globosus* will expand to previously unsuitable areas such as the Free State Province. The Koppen Geiger climate classification indicates that regions in SA deemed perpetually unsuitable for *B. globosus* are categorised under a temperate climate with cooler summers and no dry season (Cui et al., 2021). As temperatures rise, it is anticipated that these cooler summers will become warmer, leading to a rise in snail populations and a higher incidence of

related diseases (Cui et al., 2021). In addition, a study found that there is a decreasing yearly trend in the number of cold nights, the temperature of the coldest nights, and the length of cold periods for Bloemfontein, a City in the Free State province (Mengistu et al., 2023). Hence, *B. globosus* will colonise areas that will become warmer.

Climate suitability increases for *B. globosus* are also anticipated in the KwaZulu-Natal province, southern Eastern Cape, parts of the Drakensberg, and northern areas of Kwa-Zulu Natal. Ernould et al. (1999) found an increase in *B. globosus* infections during dry seasons. Mengistu et al. (2023) assessed the impact of future extreme temperature events in SA and found that there is a growing frequency of extremely hot days, as shown by the yearly rise in the count of hot days, the temperature of the hottest days, and the duration of warm periods. This increase will allow *B. globosus* to expand into warmer areas. Myers and Rother (2012) have also noted an anticipated rise in the prevalence of climate-sensitive diseases due to SA's increasingly hot and dry climate.

Under RCP 8.5, declines are predicted in extreme northeastern Limpopo, coastal KwaZulu-Natal, parts of Gauteng, North West and eastern Free State. Kalinda et al. (2018) created a simulation model assessing the impact of temperature increases on *S. haematobium* and its host snail, *B. globosus*. The simulation suggested that a 1°C temperature increase could reduce snail numbers and cercariae production by up to 14% and 8%, respectively. The habitat suitability for *B. globosus* is expected to decline due to climate change, with a general trend towards less suitable habitat (Pedersen et al., 2014b). However, suitability is likely to rise from the southern Free State to the Northern areas of KwaZulu-Natal, the southwestern coast areas of the Eastern Cape, and expand from the eastern Free State into the northern and northeastern regions of Kwa-Zulu Natal. Mengistu et al. (2023) found that temperatures rise more in coastal areas than inland. Consequently, coastal regions experience more moderate and consistent air temperatures (smaller daily temperature variations). The suitable regions have either temperate or subtropical climates, with summers that are warm to hot and mild to warm winters. Therefore, the warm and moist climate could be the elements that affect the future distribution of *B. globosus*.

Under RCP 4.5, the suitability for *B. pfeifferi* will decrease in eastern SA, parts of the Eastern Cape, Gauteng, northern parts of Limpopo, eastern regions of the North West province, and the east coast. Stensgaard et al. (2019) predicted a decrease in the habitat suitable for intermediate host

snails, which are vital in transmitting *S. mansoni* in Africa, for four out of five *Biomphalaria* species studied. However, the impact of climate change will vary across Africa, with some regions facing habitat contraction and others, particularly in the south, potentially seeing an expansion. A study predicted that the total area in sub-Saharan Africa conducive to the transmission of *S. mansoni* would shrink by 14% between 2061 and 2080 due to temperatures rising above the highest heat tolerance of the primary host snail, *B. pfeifferi* (Stensgaard et al., 2019, Figure 6-6). The research also indicated that other snail species known as intermediate hosts are more resilient to temperature increases, highlighting the need to consider unique snail-parasite relationships in predictive models. The results showed that the climate models predicted increases in the west and south of the North West province, coastal areas of the Western Cape, the North West, Free State, parts of the Northern Cape, and moving westwards in SA. McCreesh et al. (2015) found that infection risk may increase by up to 20% over most of eastern Africa over the next 20 and 50 years. Increases may occur in Rwanda, Burundi, southwest Kenya and eastern Zambia, and *S. mansoni* may become newly endemic in some areas. The Free State, Northern Cape and west of SA were previously unsuitable for transmission. However, the climate models predict these provinces to be climatically suitable. This shows that *B. pfeifferi* is a vector that can survive in warm temperatures such as the Free State and hotter conditions like Kwa-Zulu Natal.

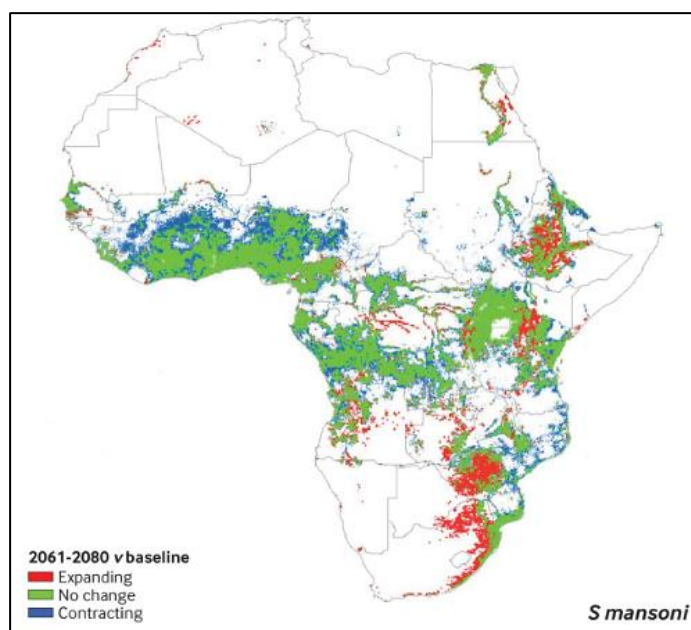


Figure 6-6: The risk area for intestinal schistosomiasis transmission in Africa is forecasted to decrease between 2061 and 2080. Areas represented in blue are expected to contract, and areas in red show an expansion of the *B. pfeifferi*. Source: Stensgaard et al., 2019.

Under RCP 8.5, declines are seen in the coast of the Eastern Cape, Gauteng, parts of Limpopo, Gauteng, and North West provinces, while increases are observed towards the inner areas of the Eastern Cape, parts of the North West and Free State, the Northern and Eastern Cape provinces, parts of the northern North West, and Kwa-Zulu Natal. This could be due to the climate in those areas being warmer than usual with moderate increases in temperature. Pedersen et al. (2014a) predicted a general trend towards less suitable habitats in the future, except for an increase in habitat suitability for *B. pfeifferi* by 2050, possibly due to higher temperature tolerance. However, by the end of the century, even *B. pfeifferi* habitats will become less suitable (Pedersen et al., 2014a).

How will climate change affect schistosomiasis?

The impact of climate change on the availability of habitat for schistosome parasite-snail interactions is undeniable and will differ based on the ecological characteristics of various intermediate host snail species. While this thesis showed that most areas in SA will exhibit no change of suitable areas for *Schistosoma*-transmitting snails, northeastern areas in SA indicate a mixed picture, with a potentially decreasing suitability, especially for *S. haematobium*. For *B. africanus*, under both emission scenarios, models generally project a decrease in habitat suitability, particularly in Provinces (Limpopo, Mpumalanga, North West and Gauteng), although there are some areas like the Kwa-Zulu Natal Province and southwestern Cape where suitability may increase. *Bulinus globosus* under both emission scenarios project a mixed trend, with Provinces (Limpopo and Mpumalanga) experiencing decreases in suitability and Kwa-Zulu Natal showing potential increases. For *B. pfeifferi*, the models generally project a decrease in habitat suitability, although there are also areas (North West, Gauteng and Eastern Cape) where suitability may increase. In addition, *B. pfeifferi* could have an increased distribution window as the climate gets warmer. This is expected to provide more optimal conditions for the parasite to establish and spread.

In this thesis, it is shown that climate change may decrease habitat suitability for intermediate hosts. This could occur due to increasing temperatures beyond the tolerance range of the snail's changes in precipitation patterns. Conversely, in other areas, climate change may increase habitat suitability. This could happen due to factors such as expanding suitable habitats as temperature and moisture conditions become more favourable or colonising new areas previously unsuitable due to climate constraints. Converse to the increase in the distribution of *S. mansoni*, climate

change could have a “beneficial” role since suitable areas for snail survival and parasite development could be lost from large areas in West and Central Africa (Stensgaard et al., 2013). However, this could easily be offset by the increased creation of freshwater sites such as dam construction and irrigation schemes. Predicted increases in dry spells in many parts of Africa with climate change have created environments in which schistosomes and snails flourish (Stensgaard et al., 2013). In addition, Pedersen et al. (2017) reported a downward trend in schistosomiasis infections in Zimbabwe over three decades due to a warmer and drier climate, although Mass Drug Administration and behavioural changes may have also played a role in this downward trend.

6.2.2 Climate change adaptation and mitigation

The IPCC's Special Report (IPCC, 2023) on global warming of 1.5°C discusses how climate change will impact human health by altering the distribution and abundance of vector-borne diseases like schistosomiasis, dengue fever and malaria. The report highlights that these diseases are expected to increase with a 1.5°C warming and even further at 2°C in most regions (Hoegh-Guldberg et al., 2019). From those mentioned above, it is evident that schistosomiasis will become endemic in previously non-endemic areas in SA. In this thesis, models showed that climate change would likely cause a shift in future distribution patterns to provinces such as parts of the Northern Cape, southern Western Cape, central Free State and parts of the northern KwaZulu-Natal. Most of the increase in climatic suitability was found in the RCP 4.5 emission scenario.

Schistosomiasis disproportionately affects impoverished communities due to limited access to services, infrastructure, and safe drinking water (Phillips et al., 2022). Access to clean water and sanitation is crucial in eliminating schistosomiasis transmission. Areas with limited water access often rely on open water sources, increasing exposure to the disease. Studies by Tanser et al. (2018) and Sacolo-Gwebu et al. (2019) show a clear link between water access and schistosomiasis infections. Lack of piped water and toilets in a household is associated with higher infection rates, emphasising the importance of improved water and sanitation infrastructure in combating schistosomiasis. This thesis showed that the predicted distribution was seen in provinces like Gauteng. The Roodeplaat Dam, a significant water source for irrigation and drinking in the northeast of the Gauteng province, is highlighted as a high-risk area for infections (Lomberg, 2010). Lack of access

to safe water, sanitation, and hygiene further exacerbates the prevalence of schistosomiasis in endemic regions, as community members engage in various water-related activities that expose them to contaminated water (Kabuyaya et al., 2018).

Males are more vulnerable to schistosomiasis than females due to their water-related activities, such as fishing and agricultural practices (Joof et al., 2020; Opara et al., 2021). This contradicts the findings by Ansha et al. (2020), where boys had a lower risk than girls. Aula et al. (2021) observed higher risk in girls. This is because girls accompany their mothers or sisters to open-source contaminated water to continue their daily activities (washing, bathing, collecting water for cooking). Despite varying observations, social and occupational roles influence these differences, with females in African countries engaging more in water-related tasks. Ngumbela, (2020) mentioned that older women bear the primary responsibility for childcare due to migration and disease. Consequently, there is a significant prevalence of female-headed households and single mothers.

The impacts of climate change can disproportionately impact the global South, mainly because of heightened social vulnerability in low-income areas. Poverty and inadequate healthcare services amplify disease risks, while limited financial resources hinder the pursuit of adaptation measures, which are also unevenly distributed (Heffernan, 2018). Residents in informal settlements and rural areas often struggle to afford proper healthcare, leading to an increased risk of schistosomiasis. Wealth levels have been inversely linked to schistosomiasis infections, highlighting the impact of socioeconomic factors on disease transmission. The thesis illustrated that the inner areas of the Eastern Cape province could potentially increase climate suitability for *Schistosoma*-transmitting snails. Eastern Cape is one of SA's poorest provinces after Limpopo, with 42.2% of the provincial population in the Eastern Cape still residing in poverty, with the most significant rates found in districts like Alfred Nzo (57.7%), OR Tambo (53.9%), and Joe Gqabi (49.8%) (Ngumbela, 2020). Northern KwaZulu-Natal also saw an increase in climate suitability for schistosomiasis. This province encounters challenges such as poverty, disparities in household income, income inequality, human development, education, health and access to essential services (Socio-Economic Review and Outlook, 2019). Therefore, the increasing impact of climate change is expected to worsen the existing socioeconomic vulnerabilities in these provinces, which could facilitate the spread of diseases such as schistosomiasis.

As shown in (Section 6.1), most of the increase in bioclimatic suitability for *Schistosoma*-transmitting snails occurs in RCP 4.5. This supports the IPCC's recognition of how climate change will impact human health by altering the distribution and abundance of vector-borne diseases. The potential rise in suitable habitats for *Schistosoma*-transmitting snails in regions like Eastern Cape, Northern KwaZulu-Natal, Limpopo and Mpumalanga could disproportionately affect disadvantaged communities due to existing socio-economic challenges. Factors like poverty, limited healthcare access, and poor infrastructure in these areas contribute to the vulnerability of populations to diseases like schistosomiasis. The combination of socio-economic issues and climate change increases the risk of disease transmission for these vulnerable groups. For instance, the lack of clean water and sanitation facilities in impoverished areas leads to higher exposure to schistosomiasis through reliance on open water sources.

Assessing the impact of climate change on infectious diseases is complex due to various factors. Metcalf et al. (2017) highlight that some disease processes are not easily observable, and many infections provide some level of immunity, reducing the number of susceptible individuals. Consequently, these factors alter transmission patterns, making it difficult to determine the specific influence of climate change on the issue (Metcalf et al., 2017).

Resilient water and sanitation infrastructure development is crucial for adapting to climate change and addressing schistosomiasis. With changing climate conditions affecting water sources, communities may turn to open water bodies infested with parasites that carry the disease schistosomiasis. Access to safe water and proper sanitation facilities is vital to minimise exposure to contaminated water and break disease transmission routes. Investing in climate-resilient infrastructure like piped water systems can help communities reduce the risk of schistosomiasis transmission in the face of climate change. Due to men participating in water-related activities involving agriculture, climate-smart agricultural techniques can aid in adaptation and mitigation, impacting schistosomiasis transmission. Sustainable farming practices that preserve soil moisture and decrease erosion can improve agricultural resilience to climate change and decrease snail habitats for schistosomiasis. Combining climate-resilient farming with disease control methods like habitat adjustments and snail control can boost food security, combat climate change effects, and lower schistosomiasis prevalence.

6.3 Chapter Conclusion

Under climate change scenarios RCP 4.5 and 8.5, habitat suitability for snail species that are intermediate hosts for schistosomiasis in SA is changing. *B. africanus* is predicted to experience habitat declines in several provinces but may expand into new areas like the southwest coast and central Free State. *Biomphalaria pfeifferi* is expected to see decreased climate suitability in eastern SA but could become a new endemic in the Free State, Northern Cape, and western regions. *Bulinus globosus* may decline in some areas but find new climate-suitable habitats in the Free State and parts of KwaZulu-Natal. These changes suggest that as climates warm, higher elevations and regions previously unsuitable due to cooler temperatures may become new frontiers for these intermediate hosts. However, it must be noted that this study only used bioclimatic and soil indicators, so even though it showed areas that will see an expansion, *Schistosoma*-transmitting snails might not exist. This could be due to habitat fragmentation or degradation caused by changes in land use or other human activities. Additionally, invaded species or competition could be a factor, as native snails face competition from invasive species with different ecological needs or competitive advantages.

CHAPTER 7

This study investigated the impact of climate change on the spatial distribution of schistosomiasis intermediate host snails in SA. It identified specific areas in the country where there could be an increase or decrease in these hosts. The conclusions are directly linked to the research objectives detailed in Chapter 1, Section 1.3, and are outlined in this chapter.

CONCLUSIONS, ASSUMPTIONS AND LIMITATIONS

South Africa, situated in the sub-Saharan region, is anticipated to see a significant rise in the population at risk for schistosomiasis due to the impact of climate change. Variations greatly influence the evolution and spread of vector-borne diseases in temperature, precipitation, and geographic distribution. Temperatures over Southern Africa are expected to increase most notably over the central interior of the region, with smaller increases over coastal areas. Under the A2 emission scenario, temperature increases of 1-2°C are projected for the near future, and for the far future, increases of more than 4°C are plausible for over the central interior. These climatic changes place SA among the most vulnerable countries in the world, especially given the current high incidence of several life-threatening diseases, combined with poverty and inequality of access to health. The prevalence of *Schistosoma* parasites is likely to be favoured by warmer conditions, leading to new transmission areas, and climate change is projected to change the patterns of distribution and transmission. This thesis aimed to determine the impact of climate change on the spatial distribution of intermediate host snails in schistosomiasis in SA.

This study provided novel insights into snail habitat spatial distribution prediction using climate models with machine learning as the preferred approach. Considering both *S. mansoni* and *S. haematobium*, this research enhanced the understanding of climate change impacts on schistosomiasis. This study used the available data to estimate the historical and predicted future distribution of *Schistosoma*-transmitting snails. Incorporating bioclimate input data from various climate scenarios and GCMs improved future distribution assessments, highlighting temperature and rainfall as key drivers. For the first time, this thesis has shown that *Schistosoma*-transmitting snails will expand to new areas when climatic conditions become more favourable. The projected habitat changes have significant implications for disease management, guiding targeted interventions to reduce disease burden and improve public health outcomes.

The key findings for each objective are as follows:

7.1 Model the historical distribution of *Schistosoma*-transmitting snails using ecological niche models.

- Temperature and rainfall significantly influence the distribution of schistosomiasis in SA.

- The Random Forest model was the most effective in modelling the historical distribution of intermediate hosts of schistosomiasis, followed by MaxEnt and GLM.
- The ensemble model outperformed individual ENMs in identifying suitable habitats for intermediate hosts.
- Rainfall, particularly during the wettest quarter and month, was vital for creating habitats for schistosomiasis parasites.
- *Bulinus africanus* historically preferred cooler conditions and demonstrates adaptability to temperature variations, with seasonal changes being more influential than annual averages.
- *Biomphalaria pfeifferi*'s historical habitat suitability was greatly influenced by temperature variability throughout the year.
- *Biomphalaria pfeifferi* was more prevalent and widely spread throughout SA than *B. africanus* and *B. globosus*, favouring warmer temperatures with average rainfall.
- *Bulinus globosus* distribution was greatly affected by temperature and precipitation, with a preference for warmer conditions and moderate rainfall.
- The most historically suitable areas for *B. africanus*, *B. globosus*, and *B. pfeifferi* were found in the eastern and coastal regions of SA.

Despite favourable conditions for schistosomiasis in the Western Cape, the disease does not occur there, possibly due to the natural acidity of water bodies.

7.2 Predict future distribution of *Schistosoma*-transmitting snails using climate models.

- The ensemble model predicts varying futures for *B. africanus*, *B. globosus*, and *B. pfeifferi* under RCP 4.5 and 8.5 climate scenarios.
- *Biomphalaria pfeifferi* may see a decrease in highly suitable habitats in SA's eastern areas, with potential habitat expansion in northern Kwa-Zulu Natal and other provinces.
- *Bulinus globosus* could experience fewer highly suitable areas but might find more moderate habitats in SA's interior and east, benefiting from its tolerance to higher temperatures.
- *Bulinus africanus* is expected to decline generally in low- and moderate-suitability regions, shrinking its range, though some coastal areas might improve with warmer temperatures.

- There is an expected overall decline in highly suitable habitats for these snails, with an increase in moderately suitable habitats, indicating complex habitat suitability changes due to climate change.

7.3 Examine the impacts of climate change on the predicted distribution of *Schistosoma*-transmitting snails in South Africa.

- Climate change scenarios RCP 4.5 and 8.5 indicate shifting habitat suitability for the intermediate hosts in SA.
- *Bulinus africanus* habitats are predicted to decrease in several provinces but potentially expand to the southwest coast and central Free State.
- *Biomphalaria pfeifferi* may face reduced climate suitability in eastern SA yet could emerge in the Free State, Northern Cape, and western areas.
- *Bulinus globosus* could experience habitat declines but might find suitable climates in the Free State and KwaZulu-Natal regions.
- The shifts suggest that warming climates could create new habitats for these snail species at higher elevations and cooler regions.

7.4 Limitations and assumptions of the study

The following are limitations and assumptions for each objective.

Objective I: It was assumed that long-term climate data provided sufficient information to model the snail habitats despite the lack of time observations in the historical occurrence data. This implied that the historical occurrence dataset did not record short and periodic events impacting the snail habitat. This suggests that because the occurrence data did not have a time variable, it can be inferred that short and periodic events, which might influence the snail habitat, were not directly observed. The limitation of this assumption, the exclusion of temporal data, particularly the irregular recording of initial observation dates of snails, limited the comprehensiveness of the dataset used for modelling the distribution of *Schistosoma*-transmitting snails. However, the absence of the time variable in the occurrence dataset did not pose a significant limitation for this study, as this thesis did not focus on the temporal dynamics of *Schistosoma*-transmitting snails. This study focused on climate change's impact on schistosomiasis intermediate host snails' historical and future distribution.

This thesis used only presence and pseudo-absence data, possibly leading to biased model predictions. Only climatic and soil variables were used to model the distribution of *Schistosoma*-transmitting snails. By focusing solely on climatic and soil variables, the model may not capture the full complexity of the ecological niche of the snails. This study focused on a national level, and the prediction of schistosomiasis would more accurate if focussed on a local level (municipal and district). More malacological surveys and modelling would provide more precision on vector location and identification in SA.

Objectives II and III: The prediction timeframe extends to the far future (2070 to 2100), and uncertainty in climate projections increases. This can affect the accuracy of the predictions, leading to variations in performance in different climate models. It is difficult to say whether the climate models used in this thesis are conservative or these additional effects might amplify the extent of changes predicted by the bioclimatic variables alone. The predicted geographical distribution may be wider than the range of *B. africanus*, *B. globosus* and *B. pfeifferi*. This is because we did not consider the impact of human activities (Stensgaard et al., 2013). The climate models used in this thesis are based on climate change scenarios, such as temperature and rainfall changes, and assume no change in natural and artificial habitats by 2080. The accuracy of disease spread predictions is highly dependent on future human activities that affect snail habitats, which are not currently included in our models. Human needs for freshwater resources will likely alter tropical freshwater habitats, impacting the intermediate host snails. The climate models showed that the intermediate host may expand its range, but more research is needed to understand its biotic requirements. The complexity of the schistosomiasis system, with multiple hosts and parasite strains, makes accurate predictions challenging.

7.5 The contribution to the body of knowledge

The thesis contributes to the body of knowledge by comprehensively analysing how climate change affects the spatial distribution of schistosomiasis intermediate host snails in SA. It offers novel insights into predicting snail habitat distribution using climate models combined with machine learning techniques. The research identifies key environmental factors, such as temperature and rainfall, that significantly influence the distribution of schistosomiasis. By modelling future distributions under different climate scenarios, the study predicted potential changes in habitat suitability for the snails, which could impact the transmission dynamics of schistosomiasis. This work is crucial for public health planning and developing strategies to control and prevent the

spread of schistosomiasis in the face of climate change. The following sections highlight the detailed contributions to the body of knowledge.

- I. This study introduced a new method by combining three ecological niche models and creating an ensemble model to predict *Schistosoma*-transmitting snails' distribution patterns in SA. This method expands tools for studying vector-borne diseases under climate change. According to Stensgaard et al. (2019), most studies usually considered the distribution of *S.mansoni*; however, this study provided a comprehensive analysis by considering both *S. mansoni* and *S. haematobium*, enhancing understanding of climate change impacts on schistosomiasis in SA. Ensemble modelling improved future distribution assessments by incorporating various climate scenarios and global circulation models. It was found that temperature and rainfall are key bioclimatic drivers affecting schistosomiasis distribution, offering insights into disease transmission mechanisms. The projected habitat changes for snails have significant implications for disease management, guiding targeted interventions to reduce disease burden and improve public health outcomes for the future.
- II. Before this thesis was conducted, historical snail occurrence data was not georeferenced. This posed a barrier to understanding the spatial distribution of *Schistosoma*-transmitting snails in SA. To overcome this, a geospatial database was created by digitising more than 15000 historical snail occurrences. This thesis establishes a digital archive of historical snail data to support continuous research and long-term studies monitoring snail distribution changes. Long-term studies are crucial for comprehending how disease transmission dynamics evolve with environmental shifts, aiding in creating effective public health strategies.
- III. This thesis bridged the gap between fine-scale historical snail occurrences and coarse-scale bioclimatic data by ERA 5 gridded data with a resolution of 0.5 x 0.5. Integrating ERA5 climate data at a fine scale improves the accuracy and reliability of ENMs for predicting snail habitat suitability. This approach aimed to enhance the precision of modelling species-climate relationships by using climate data that better represents the local environmental conditions snails encounter, ultimately boosting the effectiveness of distribution models. The thesis introduced a new methodological approach in eco-epidemiological re-

search by trying to adjust climate data to align with the resolution of snail occurrence records. Integrating fine snail distribution data with high-resolution climate data has practical implications for controlling and managing diseases. This research enhances the ability to predict snail habitat suitability in different climate conditions, guiding specific interventions and surveillance tactics to lessen the impact of schistosomiasis in at-risk populations.

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APPENDICES

The appendices are supplementary materials and referenced in the text where applicable.

APPENDIX A. AREA UNDER THE CURVE AND TSS SCORES FOR *B. africanus* USING RCP4.5

Table A. 1: AUC and TSS for *B. africanus* for the different climate and ecological models using RCP 4.5 in this study.

Climate model	Ecological model	AUC	TSS
Baseline	GLM	0.87	0.70
	MaxEnt	0.95	0.77
	RF	0.95	0.93
	Ensemble	0.99	0.95
Access1-0 (2040-2070)	GLM	0.92	0.71
	MaxEnt	0.95	0.77
	RF	0.99	0.91
	Ensemble	0.98	0.90
	GLM	0.88	0.66
	MaxEnt	0.95	0.80
	RF	0.99	0.91
	Ensemble	0.98	0.93
bcc-csm1-1-m (2040-2070)	GLM	0.88	0.69
	MaxEnt	0.94	0.77
	RF	0.99	0.92
	Ensemble	0.98	0.92
	GLM	0.85	0.65
	MaxEnt	0.94	0.77
	RF	0.99	0.91
	Ensemble	1	0.94
hadgem2-cc (2040-2070)	GLM	0.86	0.69
	MaxEnt	0.94	0.77
	RF	0.99	0.91
	Ensemble	0.99	0.91
	GLM	0.86	0.64
	MaxEnt	0.94	0.77
	RF	0.98	0.91
	Ensemble	0.99	0.95

APPENDIX B. AREA UNDER THE CURVE AND TSS SCORES FOR *B. AFRICANUS* USING RCP8.5

Table B. 2: This study uses AUC and TSS for *B. africanus* for the different climate and ecological models using RCP 8.5.

Climate model	Ecological model	AUC	TSS
Access1-0 (2040-2070)	GLM	0.87	0.66
	MaxEnt	0.94	0.76
	RF	0.99	0.91
	Ensemble	1	0.93
	GLM	0.91	0.71
	MaxEnt	0.95	0.79
	RF	0.99	0.91
	Ensemble	1	0.92
bcc-csm1-1-m (2040-2070)	GLM	0.90	0.69
	MaxEnt	0.96	0.81
	RF	0.99	0.92
	Ensemble	1	0.92
	GLM	0.86	0.65
	MaxEnt	0.94	0.75
	RF	0.99	0.91
	Ensemble	1	0.92
hadgem2-cc (2040-2070)	GLM	0.88	0.66
	MaxEnt	0.95	0.77
	RF	0.99	0.91
	Ensemble	1	0.93
	GLM	0.88	0.63
	MaxEnt	0.95	0.79
	RF	0.99	0.92
	Ensemble	1	0.91

APPENDIX C. AREA UNDER THE CURVE AND TSS SCORES FOR *B. GLOBOSUS* USING RCP4.5

Table C. 3: This study uses AUC and TSS for *B. globosus* for the different climate and ecological models using RCP 4.5.

Climate model	Ecological model	AUC	TSS
Baseline	GLM	0.94	0.78
	MaxEnt	0.95	0.79
	RF	0.98	0.89
	Ensemble	0.99	0.94
Access1-0 (2040-2070)	GLM	0.90	0.74
	MaxEnt	0.95	0.79
	RF	0.98	0.89
	Ensemble	0.99	0.93
(2070-2100)	GLM	0.92	0.74
	MaxEnt	0.94	0.78
	RF	0.98	0.89
	Ensemble	0.99	0.93
bcc-csm1-1-m (2040-2070)	GLM	0.88	0.64
	MaxEnt	0.94	0.77
	RF	0.98	0.88
	Ensemble	0.99	0.93
(2070-2100)	GLM	0.93	0.73
	MaxEnt	0.94	0.76
	RF	0.98	0.88
	Ensemble	0.99	0.93
hadgem2-cc (2040-2070)	GLM	0.91	0.72
	MaxEnt	0.95	0.78
	RF	0.98	0.89
	Ensemble	0.99	0.90
(2070-2100)	GLM	0.93	0.75
	MaxEnt	0.95	0.78
	RF	0.98	0.89
	Ensemble	0.99	0.90

APPENDIX D. AREA UNDER THE CURVE AND TSS SCORES FOR *B. GLOBOSUS* USING RCP8.5

Table D. 4: This study uses AUC and TSS for *B. globosus* for the different climate and ecological models using RCP 8.5.

Climate model	Ecological model	AUC	TSS
Access1-0 (2040-2070)	GLM	0.93	0.76
	MaxEnt	0.95	0.79
	RF	0.98	0.89
	Ensemble	0.99	0.94
	GLM	0.90	0.74
	MaxEnt	0.94	0.78
	RF	0.98	0.89
	Ensemble	0.99	0.94
bcc-csm1-1-m (2040-2070)	GLM	0.89	0.66
	MaxEnt	0.95	0.77
	RF	0.98	0.89
	Ensemble	0.99	0.95
	GLM	0.92	0.74
	MaxEnt	0.95	0.80
	RF	0.98	0.89
	Ensemble	0.99	0.95
hadgem2-cc (2040-2070)	GLM	0.92	0.73
	MaxEnt	0.95	0.79
	RF	0.98	0.89
	Ensemble	0.99	0.94
	GLM	0.92	0.75
	MaxEnt	0.95	0.78
	RF	0.98	0.89
	Ensemble	0.99	0.98

APPENDIX E. AREA UNDER THE CURVE AND TSS SCORES FOR *B. pfeifferi* USING RCP4.5

Table E. 5: This study uses AUC and TSS for *B. pfeifferi* for the different climate and ecological models using RCP 4.5.

Climate model	Ecological model	AUC	TSS
Baseline	GLM	0.92	0.73
	MaxEnt	0.93	0.75
	RF	0.97	0.83
	Ensemble	0.99	0.94
Access1-0 (2040-2070)	GLM	0.89	0.66
	MaxEnt	0.93	0.74
	RF	0.96	0.84
	Ensemble	0.98	0.90
(2070-2100)	GLM	0.87	0.67
	MaxEnt	0.92	0.75
	RF	0.97	0.84
	Ensemble	0.98	0.90
bcc-csm1-1-m (2040-2070)	GLM	0.86	0.64
	MaxEnt	0.91	0.73
	RF	0.96	0.83
	Ensemble	0.97	0.89
(2070-2100)	GLM	0.89	0.69
	MaxEnt	0.92	0.74
	RF	0.97	0.84
	Ensemble	0.98	0.88
hadgem2-cc (2040-2070)	GLM	0.88	0.66
	MaxEnt	0.92	0.75
	RF	0.97	0.85
	Ensemble	0.99	0.91
(2070-2100)	GLM	0.91	0.71
	MaxEnt	0.92	0.75
	RF	0.97	0.84
	Ensemble	0.99	0.91

APPENDIX F. AREA UNDER THE CURVE AND TSS SCORES FOR *B. PFEIFFERI* USING RCP8.5

Table F. 6: This study uses AUC and TSS for *B. pfeifferi* for the different climate and ecological models using RCP 8.5.

Climate model	Ecological model	AUC	TSS
Access1-0 (2040-2070)	GLM	0.92	0.76
	MaxEnt	0.92	0.76
	RF	0.97	0.84
	Ensemble	0.99	0.92
	GLM	0.87	0.68
	MaxEnt	0.92	0.73
	RF	0.97	0.84
	Ensemble	0.99	0.92
bcc-csm1-1-m (2040-2070)	GLM	0.92	0.74
	MaxEnt	0.92	0.74
	RF	0.97	0.83
	Ensemble	0.99	0.91
	GLM	0.89	0.69
	MaxEnt	0.92	0.73
	RF	0.97	0.84
	Ensemble	0.99	0.92
hadgem2-cc (2040-2070)	GLM	0.88	0.70
	MaxEnt	0.93	0.74
	RF	0.97	0.84
	Ensemble	0.99	0.94
	GLM	0.88	0.70
	MaxEnt	0.91	0.74
	RF	0.97	0.84
	Ensemble	0.99	0.95