

**From Landscapes to Loci: Modeling Climate-Driven Human–Wildlife Interactions and
Improving Genetic Tools for Red Colobus Conservation**

by

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DISSERTATION ABSTRACT

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Doctor of Philosophy in Anthropology

Title: From Landscapes to Loci: Modeling Climate-Driven Human–Wildlife Interactions and Improving Genetic Tools for Red Colobus Conservation

Red colobus (*Piliocolobus*) represent the most endangered genus of monkeys in Africa, with 14 species listed as either Endangered or Critically Endangered by the IUCN (International Union of Conservation). There is a need for improved knowledge on the distribution, abundance, population size, and demography of all red colobus forms in order to accurately assess conservation status and set conservation priorities. In addition, while some conservation challenges have been well-articulated, others remain largely understudied for red colobus populations. In this dissertation, I address broad conservation challenges faced by red colobus, in the form of data deficiencies for conservation planning, as well as understudied challenges for red colobus, in the form of climate change and human-wildlife interactions.

In Chapter II, I optimize a high-throughput amplicon sequencing approach and STR panels for both red colobus and black-and-white colobus to increase accuracy and accessibility of conservation genetics approaches for African colobines. This approach improves allelic richness and discovery of previously cryptic genetic variation as compared to capillary electrophoresis methods, and provides a framework for future integration with genomic approaches like GT-seq.

In Chapter III, I develop a novel approach for exploring the localized impacts of overlapping biodiversity and food insecurity. This is accomplished by examining the spatial nature of agriculturally mediated human-wildlife interactions under climate change scenarios.

The Zanzibar red colobus and the human populations they live among are used as the model system for the work in this chapter. I generate climate projections for the range and probability of occurrence for Zanzibar red colobus, data on climate-resilient subsistence and smallholder crops for Zanzibar, and maps of potential areas of human-wildlife interaction (specifically, crop-raiding) under climate change. In addition, conservation recommendations relevant to the long-term persistence of the Zanzibar red colobus are provided, as well as recommendations for improving smallholder farming production and food security under climate change.

Through this dissertation, I respond to conservation needs for red colobus by increasing the accessibility of genetic methods for generating data, while also generating a novel, integrative method to help us plan for long-term conservation and mitigation of human-wildlife interactions under climate change.

This dissertation includes unpublished co-authored material.

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DEDICATION

For all those who continue to believe in and work for a better world for all.

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CHAPTER ONE

INTRODUCTION

Red colobus (*Piliocolobus*) are one of three major living groups of colobine monkeys found on the African continent. They are distributed across the equatorial forests of Africa from Senegal in the west, to Zanzibar in the east (Struhsaker, 2010). There are 18 distinct forms commonly recognized by various taxonomic authorities, although which of these are distinct enough to merit species status has been a historically contentious issue. Most recently, 17 of the red colobus forms were recognized at the species level, reflecting a high level of species diversity in this group (Linder et al., 2024). Red colobus have highly specialized folivorous diets, preferring to feed on the young parts of plants. Like other folivores, they spend the majority of their time feeding and resting, as their diets provide low amounts of energy and are difficult to digest. They also congregate in large multi-male multi-female social groups that can contain over 100 individuals. Due to their specialized diet, low activity, large social groups, as well as their medium-sized bodies and red pelage, red colobus all over the continent are sensitive to habitat disturbance and can be easy to hunt (Linder et al., 2024). As a result, they represent the most endangered genus of monkeys in Africa, with 14 species listed as either Endangered or Critically Endangered by the IUCN (International Union of Conservation).

In this chapter, I provide a brief overview of the conservation challenges that red colobus monkeys face. I then focus attention on the Zanzibar red colobus, *P. kirkii*, which has long been regarded as one of the more distinct and threatened red colobus forms due to its isolation on an island, small population size, and fragmented habitat. In particular, I introduce how these factors

might combine to make the Zanzibar red colobus particularly threatened by climate change and future human-wildlife interactions. Finally, I introduce how the work of this dissertation helps to meet data and methodological needs to address the above conservation issues.

Red Colobus: Broad Conservation Challenges

Like many tropical species, the primary threats to red colobus are habitat loss and fragmentation, as well as both commercial and subsistence level hunting (Linder et al., 2021). Efforts to conserve red colobus populations are obstructed by several factors. Certain species occur in remote areas which suffer from security issues, making research, tourism, and conservation all difficult. Many entities, even in the conservation community, are not aware of red colobus monkeys, in part because they do not exist anywhere in captivity, thus making support for conservation efforts hard to secure. Perhaps most importantly, there are substantial data deficiencies along multiple axes for red colobus populations. Only a handful of taxa have benefitted from long-term research on natural history and population statuses, and taxonomic uncertainty remains for some populations, particularly those surrounding a hybrid zone in the Eastern Democratic Republic of Congo (Figure 1) (Oates & Ting, 2015; Linder et al., 2024). The Red Colobus Action Plan provides a list of range-wide conservation priorities for these monkeys, and among these is a direct call for improved knowledge on the distribution, abundance, population size, and demography of all red colobus forms (Linder et al., 2021). This information is lacking for most red colobus species and is necessary data for both accurately assessing conservation status and setting conservation priorities.

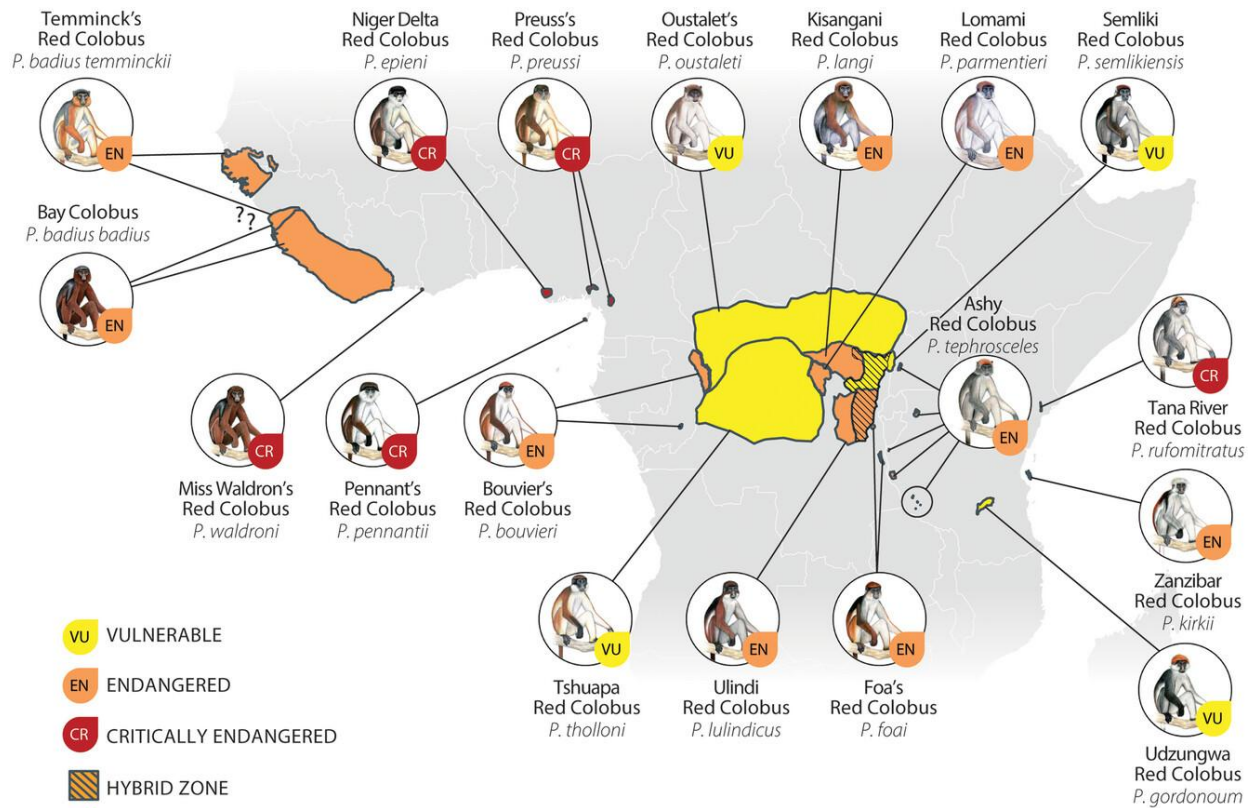


Figure 1: Map of red Colobus distribution and status as currently understood. Taken from Linder et al., 2024, illustrations by Stephen Nash. © 2024 The Authors. Used under Creative Commons Attribution License.

Genetic Approaches for Addressing Data Deficiencies

While data deficiencies relating to population status could be addressed using a number of methods, conservation genetics provides one potential path forward. The conservation community began to discuss the potential for genetics to inform conservation management over 40 years ago, based on the recognition that genetic diversity was important to maintaining species diversity and core ecosystem processes (Hoban et al., 2013a; Taylor et al., 2017). Genetic diversity is now also recognized as crucial to the ability of species to adapt to increasingly modified habitats and climate change, and thus their likelihood of long-term persistence (Hoban et al., 2013a; Taylor et al., 2017). Additionally, despite past disagreement

among some in the field of conservation genetics, there is now strong evidence to support the idea that genetic diversity and inbreeding impact extinction risk (Taylor et al., 2017).

While understanding levels of genetic diversity has long been regarded as important to species conservation, the applications of genetics to conservation have proliferated over the years. Delineation of conservation units, population censusing and monitoring, detecting hybridization, understanding impacts of habitat fragmentation, identifying specific barriers to gene flow, inferring changes in demography, and elucidating familial relations in social species have all been aided by the development of genetic technology (Taylor et al., 2017). Describing distinct units within species allows for more targeted and effective management and monitoring programs (Allendorf et al., 2010; Frankham, 2010). Genetic capture-mark-recapture methods allow researchers to estimate N_c (census size) without needing to physically mark or handle animals, making it an ideal way to estimate population census size for endangered species (Luikart et al., 2010). In addition, genetic studies can provide a wide variety of parameters with implications in wild population management, such as effective population size and measures of kinship. Landscape genetics approaches have gained increased traction in conservation, allowing researchers to explore how specific features in the landscape impact gene flow, genetic drift, and overall genetic variation. This can elucidate patterns of population structuring due to habitat fragmentation and isolation, revealing resulting evolutionary history and allowing for the identification of potential migration corridors (Westphal et al., 2021).

The most ubiquitous approach for obtaining genetic data for conservation has been to use microsatellite markers, specifically short tandem repeats (STRs). STRs are made up of repeated nucleotide sequences, usually of one to six base pairs, and have a high mutation rate (Kelkar et al., 2010). They have utility for population genetics, identification of individuals, and parentage

analyses due to their high levels of allelic diversity, codominant inheritance, and presence throughout the genome (Barbian et al., 2018). Importantly, STRs can be used on samples containing low amounts of endogenous DNA like non-invasive samples (e.g., hair, feces), which has made them a common choice for studying endangered species. However, past STR laboratory and analysis methods (e.g., capillary electrophoresis) used for population genetics studies have been hindered by associated costs. In addition, there are several factors inherent to these methods which can introduce inaccuracy in genotyping. With the advent of next-generation sequencing, however, more time-efficient, cost-effective, and accurate methods for characterizing amplified microsatellites have emerged (e.g., high throughput amplicon sequencing).

Previous work on red colobus populations has overwhelmingly used the traditional capillary electrophoresis approach (Wikberg et al., 2012; Ruiz-Lopez et al., 2016; Minhos et al., 2022; Ruiz-Lopez et al., 2022). There is a need to test and optimize an updated STR workflow for use in red colobus to reduce time and cost barriers, as well as improve accuracy, and standardize methods and genetic markers for better cross-study comparability. A validated, *Colobus* specific STR panel for a high throughput sequencing approach would help address data deficiencies outlined in the Red Colobus Action Plan, making conservation planning and prioritization more feasible.

Zanzibar Red Colobus: Understudied Conservation Challenges

Climate change and human-wildlife interactions are threats known to increase extinction risk for primates (Campos et al., 2017; Carvalho et al., 2019; Kifle & Beehner, 2022; Galán-Acedo et al., 2024), but they are understudied and underarticulated as threats to red colobus

(Galat-Luong & Galat, 2005). In particular, the Zanzibar red colobus has the potential to experience large impacts due to these threats. They are an endangered endemic, existing in a highly fragmented and heterogenous landscape, isolated on a low-lying island (Davenport et al., 2019) which is already experiencing quantifiable climatic shifts. In addition, they live alongside one of the densest human populations in Africa, which has high rates of poverty and food insecurity, depending largely on subsistence and smallholder agriculture. Zanzibar red colobus are known to crop-raid, which has resulted in poisoning and retaliatory killings. Zanzibar red colobus are also the flagship species for Zanzibar, central to ecotourism on the island and an important component of sustainable development plans aimed at poverty relief. For these reasons, Zanzibar provides an excellent system to examine the potential impacts of climate change and human-wildlife interactions on long-term viability of red colobus populations. Here, background for understanding the impacts of climate change and human-wildlife interactions on red colobus, as well as system specific information on Zanzibar important for Chapter Three, are provided.

Climate Change in Zanzibar

The Zanzibar Archipelago is a group of low-lying islands (Unguja, Pemba, Mafia) 35km off the east coast of Tanzania. The largest island, Unguja (1, 658 km²), is often colloquially referred to as ‘Zanzibar’ and is where the Zanzibar red colobus population resides. Zanzibar has a tropical climate, characterized by year-round, fairly stable warm temperature (averaging 80-86 F) and two rainy seasons. *Masika*, the long rainy season, occurs from March to May, and *Vuli*, the short rainy season, occurs from November to December. Climatic conditions in East Africa, particularly related to precipitation, are known for their high levels of inter-annual variability.

Variability is a result of several climatic phenomena such as the ENSO (El-Nino Southern Oscillation), the IOD (Indian Ocean Dipole), and the ITCZ (inter-tropical convergence zone) (Abdalla et al., 2023). On the ground, this variability has resulted in a number of severe drought and flooding events in Zanzibar. Additionally, interannual variability in precipitation increases the degree of vulnerability in subsistence or smallholder-based livelihoods on Zanzibar, as the vast majority of people do not have any additional irrigation inputs (Abdalla et al., 2023).

Several studies have established that climate change has already caused quantifiable shifts in sea level, patterns of precipitation, and soil quality in Zanzibar (Arndt et al., 2012; Suckall et al., 2014; The Hague Institute for Global Justice, 2017; Luhunga et al., 2018). It's expected that climate change in Zanzibar will continue to increase temperatures, increase rainfall variability, and impact wind speeds. Increases in temperature are expected to have impacts on agriculturally based socio-economic development, as it will likely reduce growing seasons for some crops, while also increasing the likelihood of pest and disease emergence. Higher temperatures can also reduce soil moisture which can in turn impact both soil pH and fertility, as well as lead to runoff issues (Luhunga et al., 2018).

Climate Change and Zanzibar Red Colobus

Knock-on impacts from climate change stand to be a large threat for many species, but the interaction of these impacts with several aspects of red colobus natural history stands to make them particularly vulnerable. Changes in plant phenology and physiology due to climatic shifts have been well-documented (Visser & Both, 2005; Richardson et al., 2013; Becklin et al., 2016; Inouye, 2022), and we expect that both the quantity and quality of food sources for primates will be impacted by climate change. These changes are often most problematic for species with

highly specialized diets, such as folivores, due to their lowered dietary flexibility and potential for dietary adaptation. Higher temperatures and lower amounts of rainfall are associated with less palatable leaves due to lower leaf quality (lower protein-to-fiber ratios), lower digestibility, and higher concentrations of secondary compounds (Zverva & Kozlov, 2006; Rothman et al., 2015; Korstjens, 2019). In addition, higher temperatures have been found to lead to smaller livers in mammals (Moore et al., 2015). As larger livers help manage diets with higher levels of toxicity, the impacts from rising temperatures could be particularly troubling for folivores like red colobus who would be left with a more toxic diet, and less physiological capacity to handle it. Although certain red colobus species, such as Zanzibar red colobus, seem to have a certain degree of dietary flexibility, as exhibited by crop-raiding and occasional fruit consumption, they are generally reliant on the young, tender parts of plants, which will likely make them highly vulnerable to climate change (Struhsaker, 1997; Siex & Struhsaker, 1999). Increased fiber content in leaves can also have indirect impacts on survivorship and reproduction. For *Propithecus edwardsi* increases in leaf fiber content due to decreased rainfall resulted in higher levels of tooth-wear, leaving older females unable to produce enough milk for their offspring in drier years, causing increased infant mortality (King et al., 2005; Korstjens & Hillyer, 2016).

Time-budget models have indicated that rising temperatures lead to folivorous primates needing to rest more than frugivores, in turn leading to less time spent on foraging. The full picture is then that rising temperatures associated with climate change could create intense pressure directly related to decreases in energy-intake and nutrition (Korstjens et al., 2010; Korstjens, 2019; Korstjens & Dunbar, 2007). Increased ecological stress due to reduced quality and quantity of food could also have knock-on effects related to social cohesion, and thus reproduction and survivorship. Living in socially bonded groups offers benefits such as

information transfer, reduced predation risk, and access to food. These benefits may be reduced if climate stress via food availability results in increased intra-group competition. Higher levels of competition, and thus a reduction in time available for social bond maintenance, have been shown to result in smaller or more dispersed primate groups (Lehmann et al., 2007; Kortsjens & Hillyer, 2016).

Disease may also become a compounding issue for the red colobus. Novel viral transmission events in areas of high biodiversity and human population density, such as Zanzibar, are becoming increasingly common, as are pathogen transmission events specifically from humans to endangered primates (Dunay et al., 2018; Carlson et al., 2022). A significant contributor to this is climate change, which is expected to lead to continued increases in the prevalence and severity of disease in primates (Nunn & Gillespie, 2016; Kortsjens & Hillyer, 2016). The impacts of climate change on physiological limits, increased disease risk, and interruptions to diet pose direct threats to red colobus. Additionally, climate change directly feeds into and magnifies the impacts of habitat loss and hunting, the two most pervasive threats to red colobus (Estrada et al., 2017). As landscapes are fragmented, the overall proportion of forest ‘edges’ increases. Globally, forest edges have been shown to have higher temperatures than forest interiors, often exceeding optimal temperatures for vegetation productivity (Reek et al., 2025). Some estimates indicate that by 2100, up to 50% of tropical forest areas will be at the forest edge (Fischer et al., 2021). Under these conditions, specialist species with low colonization rates and poor dispersal, such as red colobus, are the most prone to extinction mediated by both habitat loss and climate change (Travis, 2003).

Climate associated impacts from disease, habitat loss, and hunting can also be mediated by habitat range shifts. Climate-change-mediated range shifts have been thoroughly documented

and studied over the past two decades, giving rise to the general prediction that species will track their climatic niches along spatial gradients (Rubenstein et al., 2023). These range shifts can force wildlife into novel environments, which may increase disease risk due to exposure to new vectors or pathogens (Greening et al., 2025). Range shifts may also force species into degraded habitat, resulting in an inability to establish and persist long-term (Holyoak & Heath, 2016). Similarly, if the landscape is already largely fragmented and degraded, it may not even be possible for species to track their climatic niche shifts (Robillard et al., 2015). Climate-driven range shifts also frequently bring wildlife into increased contact with human populations, which exacerbates rates of human-wildlife interactions, and can result in increased negative outcomes for both wildlife (e.g., hunting) and humans (e.g., crop-raiding) (Abrahms et al., 2023). Given that Zanzibar's landscape is already highly degraded and fragmented, and that human-wildlife conflicts in the form of crop-raiding and hunting already exist, range shifts due to climate change could significantly complicate ensuring the long-term viability of the species.

Modeling Approaches for Exploring the Impacts of Climate Change

Ecological niche models (ENMs) are mathematical or empirical approximations of niche, which relate physiological or species occurrence data to environmental variables in an effort to describe and understand the distribution of a species (Guisan et al., 2017; Sillero et al., 2021). ENMs have variable mathematical output, sometimes an equation connecting the dependent variable (species distribution) to the independent variables (environmental predictors), and sometimes a set of response curves which describe how each environmental variable connects to the dependent variable. The output from these models can be translated into maps, creating spatially explicit descriptions of habitat suitability, probability of species occurrence, or

favorability (Sillero et al., 2021). ENMs are applied in a variety of ways, including exploring future distributions under climate change, as has been carried out in Chapter Three of this dissertation. Niche models utilize a variety of approaches and algorithms; here I briefly describe the forms that are relevant to the work of this dissertation. I also provide background on how they can be utilized to study future distributions under various climate change scenarios.

Correlative ENMs

Correlative ecological niche modeling identifies the environmental correlates of a species' current distribution to explore the environmental or climatic niche of the species (Korstjens, 2019). Correlative niche models are generally accepted to be a way of exploring the realized niche of a species, which is the space a species occupies, informed by suitable biotic and abiotic factors (Sillero et al., 2021). Correlative niche models utilize a variety of algorithms, and choice of which model to use is informed by both the driving questions of the study and the types of data available for use in the model. Correlative models are generally grouped by the type of occurrence data being utilized into presence-absence, presence-background, and presence-only models.

Presence-absence models use observed species occurrences and absences to distinguish between the conditions of occupied and non-occupied habitat. However, census datasets often do not contain true absences collected in the field, so in this case, artificially generated pseudo-absences can be used in place of true absences. Within presence-absence modeling, methods include logistic regression, generalized additive models, generalized linear models, random forest, boosted regression trees, multivariate adaptive regression splines, and artificial neural networks (Sillero et al., 2021). In general, these models explore the probability of species

occurrence in a particular habitat, providing a way to examine species distribution which falls in a theoretical space somewhere between the realized and potential niche (Feller, 1968; Guisan & Zimmermann, 2000; Jiménez-Valverde et al., 2008; Sillero, 2011; Sillero et al., 2021).

In contrast, presence-background methods and presence-only methods provide broader predictions of the realized niche. Presence-only methods are not used in this study, but very briefly, they include methods such as envelope modeling and utilize occurrence datasets which only contain presence data. Presence-background approaches to niche modeling include Genetic-Algorithm for Rule-set Production, Ecological Niche Factor Analysis, and the well-known Maximum Entropy, or MAXENT model. These models differ from presence-absence models both in terms of the occurrence data fed into the model, and the type of output they deliver. Instead of needing absences, presence-background sample from the ‘background’ of the entire study area, considering all locations where the species did not occur as available, but unused conditions. In doing so, presence-background models are not assessing the probability of finding a species in any given locale like presence-absence methods but instead differentiating between suitable and unsuitable habitat. It’s important to highlight that habitat being marked as either ‘suitable’ or ‘unsuitable’ does not necessarily ensure presence or absence of the species (Sillero et al., 2021).

For this dissertation, a GLM (generalized linear model) approach was chosen to allow for exploring the potential distribution and probability of occurrence of red colobus in the landscape. GLMs also provide greater insight into the direction and strength of environmental effects, providing the opportunity to examine how much particular environmental variables contribute to niche. In addition, GLMs are generally a more cautious approach, where modeling approaches like MAXENT can be prone to overfitting (Radosavljevic & Anderson, 2013). While many

studies additionally employ what are coined ‘ensemble models’, essentially an average of the differing model algorithms and their predictions, this dissertation does not employ them for several reasons. One is that, quite simply, different types of algorithms provide output which requires differential interpretation. For example, GLMs assess the probability of occupancy while MAXENT assesses habitat suitability, so it makes interpretation of an ensemble model difficult and introduces a high amount of noise and potential error. The other reason is that while ensemble modeling provides a way to capture the breadth of multiple models, the process of averaging them may lead to a final model which is worse in terms of prediction than certain models on their own (Royale et al., 2012).

Mechanistic ENMs

Mechanistic modeling is not widely leveraged because of the kind of data it requires about species’ traits (morphological, physiological, and behavioral data). However, when it can be employed, this type of model has some key advantages. The explicit incorporation of functional traits and processes can produce models which reduce risk of extrapolation under novel environmental conditions. These models also inherently reflect the very processes which shape distribution and influence range-shifts (Sillero et al., 2021). In this dissertation, a mechanistic model referred to as EcoCrop is employed to investigate suitability of subsistence and smallholder crops under climate change on Zanzibar.

EcoCrop is a mechanistic modeling approach which uses climate data and a range of ecological parameters to estimate crop suitability. The simplified required input data makes this modeling approach much more accessible for data-deficient areas, especially with respect to spatially explicit land-use datasets or crop census data (Hijmans et al., 2001; Ramirez-Villegas et

al., 2013). The base EcoCrop model can be expanded to include abiotic factors such as soil pH and type if those data are available. EcoCrop has been found by numerous studies to be an effective way to investigate crop suitability and to provide results consistent with other modeling techniques (Ramirez-Villegas et al., 2013; Vermeulen et al., 2013; Manners & Ettan, 2018).

EcoCrop evaluates crop suitability across an area based on provided crop ecological parameters and climate data. The output from EcoCrop is a suitability score, ranging between fully unsuitable and optimally suitable (0 = no suitability, 1 = perfect suitability). A score that falls somewhere between 0 and 1 indicates that during the crop growth cycle, there are either permissible yet suboptimal temperatures, or precipitation levels are either too low or too high during the optimal growth period (Manners & Ettan, 2018; Heinz et al., 2024). The model achieves this by evaluating crop suitability based on optimal and absolute monthly average minimum temperature, monthly average temperature, and total precipitation over the growth period (Appelt et al., 2023).

A detailed explanation of how EcoCrop computes suitability values can be found in Appendix A. In short, EcoCrop simulates 12 potential crop cycles starting in each month of the year. It calculates the suitability for a crop by assessing how closely the seasonal climate aligns with the crop-specific thresholds for maximum and minimum temperature, as well as rainfall levels (for non-irrigated crops). EcoCrop then automatically selects the crop cycle which results in the highest suitability scores as the output.

The EcoCrop model does have some limitations due to its simplicity; there is no consideration of biotic pressures, such as disease or pests, and no integration of weather variability between years and within months (Manners et al., 2021). The study in Chapter Three is only looking to gain a broad understanding of whether climate change scenarios will increase

or decrease suitability for our suite of crops, so despite the limitations, EcoCrop meets the needs of this research. An additional limitation can arise from relying solely on the original EcoCrop database for crop parameters. The parameters in this database are likely outdated and do not allow researchers to consider different crop varieties (Hijmans et al., 2001; Ramirez-Villegas et al., 2013; Manners et al., 2021). For that reason, the original EcoCrop database was used as a starting point in this study, but other databases as well as primary and grey literature were consulted in order to arrive at the final dataset of crop ecological parameters.

Climate Projection Models

Ecological niche models have become much more widely utilized in conservation research largely because of the ability to project them, both in space and time. Some studies utilize projections to explore the suitability of geographic space novel to species as a way to think about management actions such as translocation, reintroduction, or general restoration. Largely though, ecological niche models are used to examine the impacts of climate change, so researchers are not projecting into new spaces, but rather into time.

The choice of GCM (general circulation model) is important when performing predictive modeling, as different GCMs often disagree in certain ways due to differences in inputs such as forcing and feedback. Certain GCMs may also be better than others at capturing natural atmospheric processes important for driving the climate in certain regions. In general, models vary both spatially and temporally and good predictive ability in one variable or region does not necessarily mean good ability in other variables or regions (Beaumont et al., 2008; Beaumont et al., 2019). When creating projections, researchers will often take an average of several GCMs. This approach is widely considered a way to improve the predictive power of model projections,

as it captures a wider range of possible climatic variation in the input. It can also be thought of as a way to reduce error in projections, as a GCM less suited for a particular region will not solely drive the results. This approach, though, may be inadvisable in certain situations, as averaging may swamp out small changes in variables or important regional atmospheric patterns.

East Africa has very specific bimodal rainfall patterns associated with the intertropical convergence zone, and temporal variability linked to the ENSO and Indian Ocean Dipole atmosphere-ocean modes (Nicholson, 2015; Pickler & Molg, 2021). This rainfall pattern is very important to the natural diversity and abundance of vegetation in East Africa, as well as a key input to the structure of small-scale agricultural systems in this region. For these reasons, it was important to choose GCMs that perform well in East Africa and reliably capture regional climate patterns.

Originally, I had planned to use a single model family found to be very reliable for the East African region, but the data necessary for our paired mechanistic modeling of crops were not available for this GCM at the time steps and SSPs necessary. For this reason, I elected to utilize multiple GCMs in an ensemble projection approach. Under the previous CMIP (coupled model intercomparison project; CMIP5), some of the chosen GCM families performed very well in the East African region, while others performed more moderately (Kelley et al., 2020; Pickler & Molg, 2021). The data utilized in this study, however, is derived from CMIP6 which in general has better performing GCMs due to improvements in spatial resolution, improved atmospheric and land surface parameterizations, and updated forcing datasets. CMIP6 also integrates the SSPs (Shared Socioeconomic Pathways) whereas CMIP5's GCMs were based on only RCP (Representative Concentration Pathways) (IPCC 2023).

RCPs and SSPs are climate change scenarios created by the IPCC (Intergovernmental Panel on Climate Change) as input for climate models. IPCC has long utilized RCPs for the climate Assessment Reports they publish, but they began integrating SSPs in the sixth assessment report (IPCC, 2023a,b). RCPs as a framework revolve around levels of radiative forcing (watts/m^2) expected at the year 2100, with higher numbers indicating higher levels of anthropogenically driven GHG (greenhouse gas) emissions and thus greater warming (RCPs 1.9, 2.6, 4.5, 6.0, 7.0, 8.5). SSPs incorporate the impacts of socio-economic development on climate change mitigation, adaptation and land-use. There are five SSPs, described in brief below.

- SSP1 is considered a ‘sustainable’ pathway, with low challenges to climate mitigation and adaptation. It features a peak and then decline in global population (roughly 7 billion in 2100), reductions in inequality and resource consumption, sustainable agricultural practices, effective land-use regulation, free trade, and increased income levels.
- SSP2 is considered a ‘middle of the road’ pathway, with medium challenges to climate mitigation and adaptation. It features medium global population growth (about 9 billion in 2100), continued current resource consumption patterns, technological progress, medium income levels, and only a slight reduction in inequality.
- SSP3 is considered the ‘regional rivalry’ pathway, with high challenges to both climate mitigation and adaptation. It features high global population growth (about 13 billion in 2100), material-intensive production and consumption patterns, barriers to trade, slow rates in technological advances, stagnant levels of inequality, and low income.
- SSP4 is considered the ‘inequality’ pathway, with low challenges to climate mitigation but high challenges to adaptation. It features medium population growth (about 9 billion

in 2100), significant inequality both within and across global regions, and medium income levels.

- SSP5 is considered the ‘fossil-fuel development’ pathway, with high challenges to climate mitigation and low challenges to adaptation. It features a peak and then decline in global population (about 7 billion in 2100), resource-intensive production and consumption patterns, free trade, reduced inequalities, and high-income levels.

As mentioned, in the IPCC’s sixth assessment, integration of the RCP and SSP frameworks began, and that has been reflected in climate modeling and research. The combination of different SSPs with varying RCPs implies differing levels of mitigation, which has impacts on adaptation, and can be consistent with differing levels of global mean surface temperature rise. That said, some SSP-RCP combinations are not possible. Lower concentration pathways, like RCP 2.6, and thus lower levels of temperature rise are not possible in the SSP3 pathway (Riahi et al., 2017; IPCC, 2023a,b). The combined SSP-RCP Scenarios used in Chapter Three of this dissertation are SSP1-2.6, SSP3-7.0, and SSP5-8.5, as these were the SSP-RCP scenarios available for the chosen climate dataset.

Human Livelihoods & Human-Wildlife Interactions in Zanzibar

Poverty, Land Tenure, and Agriculture in Zanzibar

Small-scale agricultural livelihoods are exposed to risk along multiple axes due to changes in climate, ecosystem services, and economic markets. In addition, rates of poverty are often higher than national averages among subsistence and smallholder farmers (FAO, 2015) and can be directly connected to food insecurity (Molotoks et al., 2017). For these reasons,

examining patterns of poverty and small-scale agriculture can guide our understanding of risk to food security and livelihoods. Here, I provide background on poverty rates and alleviation efforts, as well as general information on the economy and agricultural sector in Zanzibar to provide additional context for Chapter Three.

Zanzibar's current national development plan (Zanzibar Development Vision 2050) is focused on raising the economy to meet upper-middle income status by 2050. A large part of achieving this goal is poverty reduction achieved through equitable, sustainable, and balanced improvements in the standard of living. While overall poverty rates in Zanzibar have dropped since 2009 (from 34.9% in 2009 to 30.4% in 2019), Zanzibar's population has continued to increase at roughly 2.8% a year, meaning population growth is still high relative to poverty reduction. In addition, the pace of poverty reduction has been greatly skewed towards urban areas, with rural populations carrying the largest share of the poverty burden. Basic needs poverty rates in urban areas from 2009-2019 dropped from 28.5% to 15.5%, while reduction in rural areas was only 39.5% to 33.7% (The World Bank 2022).

Despite a large part of the government's development plans focusing on the tourism sector, tourism itself has yet to make a large impact on poverty reduction. From 2014 to 2021, there was a large shift of people out of smallholder agriculture into the tourism sector, but decomposition analysis by The World Bank (2022) demonstrates that these shifts barely contributed to poverty reduction. Interestingly, the poverty profile of people living on Pemba differs from those on Unguja; while the largest portion of the poorest people are still in the agricultural sector on Pemba, the largest share on Unguja are now in the services/tourism sector (The World Bank, 2022).

Agriculture currently contributes to a significant portion of Zanzibar's GDP, but the sector is overwhelmingly subsistence based and food insecurity is pervasive (Zanzibar Food Security and Nutrition Monitoring, 2017; Zanzibar Planning Commission, 2020). The government links these realities to erratic production trends and limited productivity, due to lack of agricultural technical knowledge related to irrigation, fertilizing, pests, and disease control. The government also acknowledges that resilience to climate change within their agricultural sector is becoming increasingly crucial to both addressing food insecurity and creating better linkages between smallholder growers and the economy (Zanzibar Planning Commission, 2020). They list a number of activities to help meet these goals, but the one of most interest to this research is creating 'climate-smart agriculture.' They approach this mainly through financial and sector-specific risk-management strategies, but there are additional avenues which could boost efforts to create 'climate-smart agriculture' on Zanzibar.

It is also important to note that within the specific context of smallholder farms in Africa, analyses suggest that the typical paradigm of intensification focused on precision agriculture, soil quality, and yield potential may not lead to significant progress in closing poverty gaps (Tittonell & Giller, 2013). Higher yields offered by improvements in crop strain are likely out of reach for many smallholder farms which cannot access the necessary nutrient input to maintain soil quality. Improper proper soil management may therefore act as a chronic poverty trap for many smallholder farms in Africa (Tittonell & Giller, 2013).

Most farming on Zanzibar is either smallholder or subsistence, with farmers growing a wide variety of annual and perennial crops. Cash crops, where grown, are primarily grown by either large scale commercial farms or smallholder farms for commercial export (NBS, 2021a,b). Agricultural census data collected by the government is available for Zanzibar for the years

2002-03, 2007-08, 2016-17, and 2019-20 (Office of the Chief Government Statistician, 2012; Ministry of Agriculture and Natural Resources, 2012; National Bureau of Statistics, 2017; National Bureau of Statistics, 2021a,b). Together, these censuses reveal a few patterns. Agriculture, specifically crop-focused, is practiced by large swaths of censused households and the numbers have grown since 2003. In the 2002-2003 period, roughly 96,522 censused households were engaged in crop production. By the 2007-2008 period this had increased to 130,353 households, and to 180,220 households by the 2019-2020 period. The number of households active in crop production is seasonally dependent, with about 84% of households engaging during the long rainy season versus about 34% during the short rainy season (Office of the Chief Government Statistician, 2012). Over the years, the number of individuals working full-time on crop production has decreased, from 68% in 2002-2003 to 37% in 2019-2020. This is likely reflective of overall shifts in sectors of the economy, as well as the government's concerted investment in expanding the tourism sector over the last couple of decades. It seems like households may be relying on younger members to carry out crop production as adults shift to other sectors, as a large portion of household members working in crop production (55%) are students.

Overall land use for agriculture, particularly smallholders, has also increased over the last decade. 80.5% of the total arable land on Zanzibar (roughly 20, 774, 267 hectares) was being utilized for smallholder agriculture in the 2019-2020 period. While that would roughly equate to 2.7 hectares of available land per household, the actual picture on the ground is more complex owing to Zanzibar's complicated history of land tenure structures. Research has shown that landholding amounts can differ wildly. While most landholders on Unguja have between one and four acres of land, it can range anywhere from one to 350 acres (Singer, 1996).

Past landholding rights were influenced by Shirazi land tenure traditions, and land tenure systems focused on large plantations under Omani and British colonial rule. These systems were a patchwork of foreign and native land ownership, with large plantations mostly owned by colonial entities and worked by enslaved people. Eventually, with the abolition of slavery in Zanzibar, squatting rights popped up, where individuals could grow crops under trees, most often owned by plantation owners (Torhonen, 1998). All plantations and foreign land holdings were reclaimed by the government following the revolution in 1964, after which they tried a scheme of dispensing agricultural land in three-acre parcels. These parcels were owned by the government and considered public land, but essentially ‘leased’ to individuals. This existed alongside customary land holding (Torhonen, 1998). The Land Tenure Act of 1992 enshrined a patchwork of land rights based on both legislative and religious laws, including right to occupancy, provisional right to occupancy, leasehold, easement, right to trees, and Waqf (an interest in land according to Islamic religious laws) (Bjorken & Blixt, 2005).

For the purposes of this dissertation, it is most important to understand how landholdings operate for subsistence and smallholder farmers. Farms of these types in Zanzibar are referred to as Shambas, the Swahili word for ‘farm.’ Generally, Shambas have been plots in fertile, deep-soil, former plantation areas. That definition has, however, expanded as the population of Zanzibar has continued to grow. Some farmers are ‘dislocated’ individuals, working land in areas where they were not born. More often than not, these ‘dislocated’ farmers are working shambas in coral rag areas, where soil is semi-fertile and agricultural productivity tends to be lower (Singer, 1996).

Shamba land is generally acquired through either inheritance, purchasing, clearing or borrowing. Inheritance has typically been patrilineal, and borrowing is the lending of land, often

among family members who have plots in highly fertile areas (Singer, 1996). Clearing occurs when there is an overgrown, unused plot; the person wanting to work the land will generally ask surrounding plot-holders if they may clear and use the land. These lands are still considered public lands held by the government, and most shambas are informal land holdings in the sense that there is no documentation tracking the land tenure history (Singer, 1996).

Between persistent rates of poverty, a large amount of the population relying on small-scale agriculture, and a complicated system of land tenure, there is already a high degree of risk inherent to many livelihoods in Zanzibar. As mentioned previously, climate change introduces an additional layer of risk, especially where agriculture and food security are concerned. It also poses a threat to the national development plan's attempts to reduce poverty through growth in the tourism sector. Climate change poses risks to the tourism sector in a multitude of ways, but most relevant to this dissertation is that it directly threatens the red colobus population, which is the primary ecotourist draw to Zanzibar. All of these factors create a complex web of risk to livelihoods and food security in Zanzibar, which is further complicated by human-wildlife interactions.

Human-Wildlife Interactions

Human-wildlife interactions exist on a continuum from positive to negative, varying in severity from minor to severe and in frequency from rare to common. Negative interactions, also referred to as 'human-wildlife conflict,' can have significant consequences for human health and safety, and for ecosystem health and biodiversity writ large (Nyhus, 2016). Humans can incur health related costs through direct attacks, collisions, or transmission of disease. Human-wildlife conflict can also result in direct impacts to economic stability due to damage to crops, livestock,

and property (Woodroffe et al., 2005). While indirect impacts are more difficult to measure, we know that human-wildlife conflict also carries opportunity costs tied to guarding crops, reduced psychosocial wellbeing, and interruptions to livelihoods and food security (Linnell et al., 2010; Barua et al., 2013; Nyhus, 2016).

As with other species, interactions between humans and red colobus take a multitude of forms, but they are largely mediated by factors such as agriculture, poverty, tourism, and resource use. Not all interactions have negative consequences, but it is common for one or both parties to experience negative outcomes. Hunting, as an interaction, has an obvious negative outcome for red colobus, and constitutes one of the largest current threats to red colobus. Red colobus are considered by many hunters to be the easiest African primate to hunt, given their conspicuous nature and low perceptivity of humans (Struhsaker, 1999). *P. waldroni* is an excellent example of how impactful unchecked hunting can be for red colobus. The species was extirpated from several small West African forests via hunting over a 15-year period, and is now considered functionally, if not truly, extinct (Struhsaker, 2010). Red colobus are hunted across their range, usually for subsistence or economic purposes, but they are also killed due to negative perceptions or out of retaliation. In Zanzibar, perceived impacts of crop-raiding have led to instances of retaliatory killing and lethal control, with reports of one sub-population being reduced from 200 to 30 (in 2000) by farmers (Zanzibar Commission for Natural Resources & CARE, Tanzania 2000; Saunders, 2011).

While perceptions of wild primates vary greatly globally, they are often viewed as ‘problem’ animals, particularly in places where agriculture is important to livelihoods and the economy. Crop-raiding and mechanical damage to crops tend to be at the heart of negative perceptions in these systems, with primates being cited as causing considerable damage to both

tree and field crops (Hill et al., 2010). Zanzibar red colobus seem to suffer from similar negative perceptions, although it is unclear how pervasive these attitudes are across their range. Research on crop-raiding and perceptions from farmers has been conducted mostly in the Jozani-Chwaka Bay National Park (JCBNP) area, and from these studies it appears that attitudes towards the colobus may have worsened since the 1990s (Siex & Struhsaker, 1999; Saunders, 2011). Older work states that less than half of the farmers interviewed saw the colobus as agricultural pests, while more recent work states negative attitudes are more prevalent. The creation of JCBNP has likely had some influence on overall perceptions of red colobus, as its primary draw for tourism is the large red colobus population. The national park is surrounded by shambas, creating an area with high potential for human-wildlife interactions mediated by agriculture. Saunders' (2011) research indicates that at the formation of the park, some of the compensation schemes offered for crop damage by the colobus were met with dissatisfaction by surrounding communities and may have engendered negative views of the JCBNP project.

Apart from the crop-raiding and crop-destruction behaviors, there are other factors which may influence perceptions of red colobus. Zanzibar red colobus, for example, live sympatrically with Skyes' monkeys, which as cercopithecines, have a much wider dietary breadth and thus generally do more crop-raiding (Siex & Struhsaker, 1999). Cultural construction can also influence perceptions. Zanzibar red colobus are known as '*kima punju*' or 'poison monkey.' Several origin stories for the Swahili name have been suggested, including connection to a reptile-based poison used by 'evildoers' called *punju*, the idea that when monkeys feed in an area the trees and crops die, and that if a dog eats a colobus it will lose its fur. It has also been suggested that the origin may stem from the fact that colobus feed on immature fruit and leaves, which are higher in tannins, meaning the colobus are consuming 'poison' (Saunders, 2011).

Tourism also directly increases the frequency of human-wildlife interactions for many primate species. The inability of tourists to adhere to safety standards when viewing animals can greatly increase risk of disease transmission and animal bites. Infrastructure changes necessary for tourism also often incur direct costs. In Zanzibar, the main road that passes through Jozani was paved, enabling vehicles to travel at much faster speeds, resulting in Zanzibar red colobus getting hit and killed (Struhsaker, 2010). These mortality events have decreased since the installation of speedbumps along the road, but the situation reflects how changes in infrastructure can impact the frequency and severity of human-wildlife interactions (Olgun et al., 2022).

It's also important to note that human-wildlife interactions, like many conservation challenges, are complicated by extrinsic factors like climate change. Climate change is an often-underappreciated amplifier of human-wildlife conflict, specifically, due to how it decreases resource availability, alters human and animal behavior, and influences animal range and distributions (Abrahms et al., 2021). As previously mentioned, red colobus are inherently vulnerable to climate change given their ecology and tropical distributions. The additional synergy between climate change and human-wildlife conflict could worsen perceptions of red colobus and thus put even more pressure on populations.

Dissertation Outline

The throughline of this dissertation is understanding and addressing outstanding challenges to red colobus conservation. Chapter Two seeks to fulfil the Red Colobus Action Plan's call to improve knowledge concerning red colobus population ecology and status by improving the accuracy and accessibility of conservation genetics approaches in African colobines (Linder et al., 2021). Chapter Three addresses the need to better understand the threats

of climate change and human-wildlife interaction for red colobus, providing a better understanding of Zanzibar red colobus ecological needs and identification of important areas to consider for protection in the future. Chapter Three also generates data pertaining to crop suitability under climate change and food security in Zanzibar, as well as a novel approach for understanding the spatial nature of human-wildlife interactions under climate change.

In this dissertation, I produce and test methods that enable the generation of data necessary for effective, long-term conservation of red colobus populations. Specifically, my work:

- 1) Optimizes and standardizes a conservation genetics approach for *Piliocolobus* (and *Colobus*) which leverages next-generation sequencing technologies to improve the accuracy of findings, while reducing associated time and costs.
- 2) Examines how climate change will impact the range and occurrence of Zanzibar red colobus monkeys.
- 3) Generates a novel approach for elucidating spatial patterns of agriculturally mediated human-wildlife interactions under climate change.
- 4) Produces conservation recommendations relevant to the long-term persistence of the Zanzibar red colobus.

In Chapter Two, I optimize and test a high-throughput amplicon sequencing approach and compare it to past approaches used in red colobus and black-and-white colobus population genetics studies. This chapter is titled “Improving Accuracy and Accessibility of Conservation Genetics Approaches for African Colobines.” In addition to myself, this work is co-authored by Nelson Ting. This chapter provides an optimized and standardized workflow for genetic research in *Piliocolobus* and *Colobus* using high throughput amplicon sequencing. The described approach reduces associated costs and time while improving accuracy and cross-study

comparability, allowing for easier uptake of conservation genetics methods to address areas of data deficiency in colobus monkeys.

In Chapter Three, I describe a novel approach for understanding the impacts of climate change on the ‘wicked problem’ of conservation conflicts originating from the overlap of food insecurity with high levels of biodiversity. This is accomplished through exploring spatial distributions of human-wildlife interaction under climate change, utilizing niche modeling and climate projections. My study uses Zanzibar as a model system, focusing on the endangered Zanzibar red colobus monkey, as well as subsistence and smallholder crops crucial to livelihoods in Zanzibar. This chapter is titled “Islands of Change: Zanzibar Red Colobus, Food Security, and Human-Wildlife Interactions Under Climate Change.” In addition to myself, this work is co-authored by Nelson Ting and Tim Davenport. This chapter generates knowledge relevant to managing the Zanzibar red colobus population for long-term viability under climate change, including specific conservation recommendations.

Chapter Four distills the findings from both data chapters and contextualizes their relevance for conservation prioritization and planning for red colobus across Africa.

CHAPTER TWO

IMPROVING ACCURACY AND ACCESSIBILITY OF CONSERVATION GENETICS

APPROACHES FOR AFRICAN COLOBINES

Contributions

This chapter was co-authored by Jenneca McCarter and Nelson Ting. Jenneca McCarter was responsible for lab work, data analysis, and writing of the manuscript. Nelson Ting provided intellectual guidance and assistance editing the manuscript.

Introduction

Since the 1970s, the use of genetic methods to examine the issues facing small and fragmented populations has gained continued traction in conservation biology, giving rise to the subfield of conservation genetics. Conservation genetics offers tools for addressing a multitude of common questions at the center of conservation planning and action. For example, measures of effective population size and census population size can be estimated using genetic data and represent crucial baseline information for establishing population trends and future viability. We can also explore the impacts of landscape change such as habitat fragmentation on migration, recruitment, and gene flow. Genetic data can help inform on taxonomic identity and/or assist in delineating conservation units (Allendorf et al., 2010; Frankham, 2010; Funk et al., 2012). In addition, genetic information can identify individuals, make inferences about kinship, and inform on wildlife forensic cases (Luikart et al., 2010; Taylor et al., 2017). Over the last decade, there have been increased calls for the integration of genomic technologies and approaches in conservation genetics (Hogg, 2024). Numerous papers have already highlighted the challenges with utilizing genomics in the study of endangered species, chiefly the difficulties presented by

low-quality, non-invasive samples (Arandjelovic & Vigilant, 2018; Oklander & Soto-Calderon, 2024). While we continue to work on resolving these challenges, there is a need for modifying conservation genetics workflows for next-generation platforms as an intermediate step. In doing this, we can improve the accuracy of the conservation genetics data we currently produce, while preparing for a future where our workflows can be immediately integrated into genomics projects.

African colobines (*Colobus*, *Piliocolobus*, *Procolobus*) include some of the most endangered primates on the African continent. Red colobus monkeys are the most threatened genus (*Piliocolobus*) of monkeys in Africa, with over 75% (14 of 18 taxa) listed as either Endangered or Critically Endangered (Linder et al., 2024). Black-and-white colobus are doing slightly better, with 30% of taxa listed as Endangered or Critically Endangered. However, two black-and-white colobus species (*C. vellerosus*; *C. polykomos*) face significant threats, with population sizes reduced by 50-80% over the last three generations (Gonedelé et al., 2020; Matsuda et al., 2020). Due to their highly threatened status, this group of primates should be a high priority for conservation action, but conservation efforts have hindered by multiple factors. A large impediment to conservation planning and action for African colobines is a thorough understanding of conservation status. While some red colobus species have well-defined distributions owing to long-term research, several taxa are highly data deficient with regards to both natural history and population status (Linder et al., 2024). The *Colobus* genus is less data deficient, but some of the more endangered species (e.g., *C. polykomos*) lack crucial information about population status as well (Gonedelé et al., 2020; Fashing, 2022). Due to these data deficiencies, improving knowledge on colobus distribution and population size is a high

conservation priority (Linder et al., 2021). One avenue to aid in securing the necessary data is by leveraging conservation genetics approaches.

Past population genetics studies on colobus have primarily utilized capillary electrophoresis to genotype small sets of microsatellite markers (STRs, short tandem repeats) (Harris et al., 2009; Wikberg et al., 2012; Ruiz-Lopez et al., 2016; Minhos et al., 2022; Ruiz-Lopez et al., 2022). STR loci have been widely used for population genetics, as well as parentage analysis and identification of individuals, given their codominant patterns of inheritance, high rates of allelic diversity, and general ubiquity across the genome (Balloux & Lugon-Moulin, 2002; Selkoe & Toonen, 2006; Barbian et al., 2018). Importantly, STRs can be utilized on samples with low amounts of endogenous DNA, such as hair and feces. Population genetics work on endangered primates is overwhelmingly conducted using non-invasive sampling, so STRs are highly applicable. However, STR analysis via capillary electrophoresis can be cost-prohibitive at large scales and laborious due to limitations in the number of loci which can be analyzed simultaneously (Barbian et al., 2018). Additionally, genotyping is often found to be imprecise and inconsistent both within and across studies (Pasqualotto et al., 2007). These issues arise because capillary electrophoresis determines the size of alleles by comparing mobility of fluorescently labeled PCR products to standardized control fragments, providing only approximate size results. Researchers must manually adjust these size ambiguities, which can lead to inconsistent allele calls between experimental replicates and researchers (Weeks et al., 2002; Barbian et al., 2018). PCR artifacts, such as stutter and artifactual peaks, are also often generated in STR work, and they can be hard to identify on the electropherograms produced by capillary electrophoresis (Shinde et al., 2003; Guichoux et al., 2011).

One avenue to improve the validity and reproducibility of STR genotyping is to utilize short-read sequencing technologies (e.g., Illumina). High throughput amplicon sequencing on these platforms results in unambiguous allele lengths, irrespective of sequencing platform or differences in protocols, as well as discovery of allelic diversity which might be missed by capillary electrophoresis. This includes alleles which differ in size by only one nucleotide, and those which are the same size and differ by sequence (Adams, 2004). Multiplexing approaches are also more accessible using these techniques. This allows researchers to tag amplicons in parallel and pool samples, greatly increasing overall throughput on a single sequencing run and making it feasible to sequence larger panels of loci (Zavonda et al., 2013). Larger panels of loci provide higher levels of resolution, enabling stronger inference of population history and species identity. On the back end, pipelines which greatly speed up analyses now exist, some of which allow researchers to detect and filter erroneous alleles (Barbian et al., 2018; Jønck et al., 2020; Wang et al., 2020; Halman et al., 2022; Zhang et al., 2025). Previous studies have demonstrated that deriving STR genotypes using high throughput amplicon sequencing significantly increases accuracy, while simultaneously reducing associated costs and time. With all of this in mind, reducing data deficiencies for African colobines would likely be improved by a transition to high throughput amplicon sequencing.

Our study aims to test, optimize, and standardize an STR panel and high throughput amplicon sequencing protocol which can be utilized using fecal samples for colobus population genetics. The driving impetus is to produce a reliable and easily reproducible approach for non-invasive samples, as high-quality samples can be a limiting factor in leveraging conservation genetics. This will not only make population genetics work more accessible for research groups studying colobus but will also ensure that we have higher cross-study comparability owing to

using shared genetic markers. Additionally, this approach may allow us to capture previously invisible allelic diversity and patterns, such as allelic dropout, with higher precision, improving the accuracy of our data. As mentioned earlier, this work constitutes an intermediary step between conservation genetics and genomics. In the future, any STRs found to be effective here can be added to other sequencing panels, for example integrating both STRs and SNPs (single nucleotide polymorphisms) for a greater number of loci and increased resolution when making inferences from genetic data.

Here, we test twenty human-derived STR markers utilized across previous red colobus and black-and-white colobus studies (Wikberg et al., 2012; Ruiz-Lopez et al., 2022), as well as thirty-six markers recently developed using high-quality DNA for use across catarrhine primates (Trede et al., 2020). Trede et al., (2020) included one high-quality *Colobus guereza* sample in the tests of their panel, but this panel has not previously been optimized for use in non-invasively acquired African colobine samples. We genotype individuals and explore basic measures of diversity for a population of Ashy red colobus (*Piliocolobus tephrosceles*) monkeys in Kibale National Park, Uganda and White-thighed colobus (*Colobus vellerosus*) in Boabeng-Fiema Monkey Sanctuary, Ghana. We then compare our results to previous STR genotyping done via capillary electrophoresis for the same populations. By directly comparing to previous genotypes and measures of genetic diversity, we hope to demonstrate that our approach provides commensurate if not better results, with the benefit of greater reproducibility between studies.

Methods

Study Sites and Samples

The full initial set of samples used for testing and optimizing the STR panel contained six red colobus tissue samples (*P. outstaleti*, *P. parmentieri*, *P. preussi*, *P. pennatii*, *P. temminckii*, *P. tephrosceles*) and six fecal samples from the Udzungwa red colobus (*P. gordonorum*) collected in 2009 in the Udzungwa Mountain National Park, Tanzania. Samples used for validation and analysis came from the Ashy red colobus (*P. tephrosceles*; 21 samples) and the white-thighed black-and-white colobus (*C. vellerosus*; 20 samples). Ashy red colobus (*P. tephrosceles*) samples were collected during a previous study conducted from 2011 – 2015 in Kibale National Park, a 795 km² semi-deciduous protected area located in Western Uganda (0°13'–0°41'N and 30°19'–30°32' E) (Ruiz-Lopez et al., 2022). These samples came from two sites within Kibale National Park (Kanyawara, Sebitoli), and two forest fragments (Lake Nkururba, Lake Kasenda) that exist in the agricultural matrix just outside the park. The black-and-white colobus (*C. vellerosus*) samples were collected during a previous study conducted from 2019 – 2020 at Boabeng-Fiema Monkey Sanctuary, in central Ghana (7° 43' N and 1° 42'W) (Christie, 2023). Boabeng-Fiema is a 1.92 km² semi-deciduous forest connected to surrounding forest fragments by riparian corridors.

Genetic Analysis

All lab work was performed in the Ting lab at the University of Oregon. Tissue DNA extractions were carried out using the DNeasy Blood & Tissue Kit (Qiagen) following the manufacturer's protocol. Fecal DNA extractions were carried out using the QIAamp Fast DNA

Stool Mini Kit (Qiagen), with modifications to the manufacturer protocol. These modifications include: 1) 800uL of fecal slurry digested for 12-18 hours in 1mL buffer ASL and 1mg Proteinase K in an incubator at 55°C, shaking at 300rpm; 2) an increased volume of 1,800uL of lysate was centrifuged through each spin column; 3) prior to final elution, 100uL of buffer AE was incubated on the spin column at room temperature and then centrifuged through, twice.

An initial set of samples (five red colobus tissue, fourteen red colobus fecal, four black-and-white colobus fecal) were genotyped for all 56 microsatellite loci in four pools. The markers for these loci come from previous studies on colobus monkeys (Wikberg et al., 2012; Ruiz-Lopez et al., 2016; Ruiz-Lopez et al., 2022) and from a study which utilized catarrhine primate genomes to develop new STR primers (pools 2-4) (Trede et al., 2020). The initial pools were: Pool one(C19a, D1S548, D3S1229, D3S1766, D4S243, D4S2408, D5S1457, D6S311, D6S474, D6S493, D6S1056, D7S503, D8S165, D8S260, D10S676, D11S2002, D12S67, D13S321, D14S306, FESP); Pool two (DXS571.2, D1S2797, D2S391, D3S1768, D4S403, D5S1457, D6S493, D7S503, D8S271, D9S160, D9S1796, D12S372, D13S1291, D16S3106, D17S791, D17S1304, D18S57); Pool three (D1S207, D1S1675, D2S146, D4S2430, D6S264, D6S287, D10S587, D13S280, D14S66); Pool four (D3S1614, D8S505, D10S179, D14S61, D15S649, D16S403, D16S3089, D17S261, D18S861, D20S189). Genotyping was carried out using a two-step, high-throughput amplicon (HTAS) approach (Barbian et al., 2018; Dolotovskaya et al., 2020; Trede et al., 2020; Barrett et al., 2022; Goodfellow, 2023). All primers were ordered with an Illumina sequencing tag attached to the 5' end of both the forward and reverse primers (FW primer overhang: 5' TCGTCGGCAGCGTCAGATGTGTATAAGAGACAG 3'; RV primer overhang: 5' GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAG 3').

Loci were amplified in the four pooled reactions per sample in 25uL volumes consisting of 7.5uL Qiagen Multiplex Mastermix, 0.5uL BSA (50mg/mL), 7uL DNA, 10X primer pools (concentration: pools 1 & 2, 0.11uM; pools three & four, 0.17uM), and H₂O. PCRs were performed in a Nexus Gradient thermocycler. Cycling conditions consisted of 15 min at 95°C, 50 cycles each with denaturation at 94°C for 30 s, annealing at 58°C for 90 s and extension at 72°C for 90 s, and a final extension step of 10 min at 72°C. After amplification, samples were subjected to a 1.8X cleanup following the MagBind RxNPure Plus manufacturer's protocol and diluted 1:100 into H₂O. Ligation of dual-indexed adapters was carried out via a second PCR. This barcoding PCR was done in 10uL volumes consisting of 4 uL Qiagen Multiplex Mastermix, 0.5 uM i5 and i7 adaptors (Nextera XT Index Kit v2; Illumina), and 5 uL diluted amplicon pool (Lepais et al., 2020). For the second PCR, cycling conditions consisted of 10 min at 95°C, followed by 12 cycles of 95°C for 30 seconds, 59°C for 90 seconds, and 72°C for 30 seconds, and a final extension step at 68°C for 10 minutes. Libraries were then cleaned a second time at 1.4X following the MagBind RxNPure Plus manufacturer's protocol and quantified using the Quant-IT dsDNA HS kit (Thermofisher). The unique dual-indexed libraries were pooled equimolarly per run and sequenced on an Illumina MiSeq at the University of Oregon Genomics & Cell Characterization Core Facility (GC3F) using v3 chemistry at 375 forward read cycles (Barbian et al., 2018).

After initial sequencing runs, loci which did not reliably and effectively amplify across fecal samples and PCR replicates were dropped. This reduced the red colobus STR panel to 17 loci, and the black-and-white colobus panel to 21 loci. The new pools for black-and-white colobus consisted of: Pool one (C19a, D4S243, D6S311, D8S260, D10S676, D14S306); Pool two (DXS571.2, D2S391, D12S372, D13S1291, D17S791, D18S57); Pool three (D1S1675,

D2S146, D4S2430, D6S264, D6S287, D10S587); Pool four (D16S403, D20S189). The new pools for red colobus consisted of: Pool one (C19a, D4S243, D6S311, D8S260, D10S676, D14S306); Pool two (DXS571.2, D2S391, D13S1291, D17S791, D18S57); Pool three (D1S1675, D2S146, D4S2430, D6S287); Pool four (D16S403, D20S189). These reduced pools were then carried through the above protocol for 21 ashy red colobus fecal samples and 20 white-thighed black-and-white colobus fecal samples at 5-8 replicates.

Population Genetic Analyses

Sequencing reads were demultiplexed per sample, and adapters were trimmed and filtered for quality using cutadapt v3.5 (Martin, 2011). All samples were demultiplexed by locus. Genotyping was then carried out using CHIIMP (Barbian et al., 2018). Parameters within CHIIMP were set to utilize a length of 100bp for locus demultiplexing, minimum read depth of 100 reads per locus, a stutter ratio count of 0.70, and at least 10 reads per allele for genotype calling (Trede et al., 2020; Salado et al., 2021). The average matched reads per locus for a single sequencing run can be found in table 1; the range of matched reads per locus ranged from 418 – 6,649. Currently, CHIIMP cannot automatically account for wobble positions, so any primer sequences with wobble positions were included twice, in the varying forms. Additionally, STR motifs must be specified in CHIIMP, but as these can vary by species, we checked raw data to confirm STR patterns in *Piliocolobus* and *Colobus* before setting parameters in CHIIMP (Trede et al., 2020). As some stutter is potentially mis-called as alleles in CHIIMP, genotypes were validated through visual inspection of read length histograms using a custom python script

(Goodfellow, 2023). Consensus genotypes for this study had to be confirmed in a minimum of two replicates for heterozygous calls, and at least three replicates for homozygous calls.

We tested for deviations from Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium (LD) for populations in GENEPOP v4.7. Standard metrics of genetic diversity (H_o , H_e , F_{st}) were generated with GenAlEx v.6.51b2 (Peakall & Smouse, 2012). Mean allelic richness adjusted for sample size using rarefaction was calculated using HP-RARE v1 (Kalinowski 2004). We conducted these analyses for our full sample sets, and then also conducted a subset of analyses on matched individuals at matched loci with two previous studies in the same red colobus (Ruiz-Lopez et al., 2022) and black-and-white colobus populations (Wikberg et al., 2012). We were able to do so owing to population and genotyping metadata shared with us by these authors.

Locus	Reads
C19a	893
D1S1675	1452
D2S146	1503
D2S391	1126
D4S243	2765
D4S2430	2881
D6S264	2335
D6S287	682
D6S311	857
D8S260	1969
D10S587	1722
D10S676	418
D12S372	559
D13S1291	1642
D14S306	1579
D16S403	6649
D17S791	751
D18S57	2312
D20S189	3100
DXS571.2	843

Table 1: Average matched reads per locus for a single Illumina MiSeq sequencing run.

Results

Genotypes

All red colobus and black-and-white colobus samples returned unique genotypes. For the 5 loci shared between our red colobus STR panel and Ruiz-Lopez et al's (2022) past work, we had 92% consensus genotyping. Two individuals differed at D4S243, which can be attributed to our method catching allelic dropout. Four individuals differed at D10S676, perhaps due to this locus sometimes only having 3 successful replicates and thus affected by allelic dropout. Lastly, we captured previously hidden allelic diversity at two loci (C19a, D14S603). At these sites, some individuals had been previously genotyped as homozygotes using capillary electrophoresis, however in our study we found they were heterozygotes with unique alleles of the same length.

For the four loci shared between our black-and-white colobus samples and Wikberg et al's (2012) past work, we had 83% consensus genotyping. Two individuals differed at C19a and D14S306, both of which can be attributed to our method catching allelic dropout. Similar to the red colobus, five individuals differed at 10S676. We also captured hidden allelic diversity at the same two loci (C19a, D14S306) for black-and-white colobus.

We were able to reliably capture instances of allelic dropout with our approach. Across all of our samples, we found instances of allelic dropout (ADO) at all but one locus in our STR panels. Per locus, we captured ADO in 13-50% of observed heterozygotes across all samples in at least one sequencing replicate. Generally speaking, we saw higher rates of ADO in our red colobus samples, which is unsurprising given that they are anywhere from 4-9 years older, and come from populations which are less habituated than the black-and-white colobus population. Rates of per locus ADO can be found in supplementary Table 1.

Genetic Diversity

For red colobus, the number of alleles per locus across the population ranged from two to seven. Across the full population, 100% of loci were polymorphic. On average, there were 4.53 ± 0.49 SE unique alleles per locus. Across the full sample, three loci deviated significantly from HWE (D10S676, D13S1291, D17S791). At D10S676, this may simply be an artifact of lower sequence depth, but for the other loci this may be an indication of biological processes like non-random mating or sub-structuring in the population. For both the full sample and per site, no loci showed significant evidence of linkage disequilibrium. Inbreeding coefficient (F) values were negative at 5 of 17 loci without significant HWE deviations, indicating moderate heterozygote excess consistent with high allelic diversity and locus-specific variation. General measures of genetic diversity for the full population can be found in Table 2.

We also directly compared the five markers used in previous red colobus work (C19a, D4S243, D8S260, D10S676, D14S306), with the same subset of 17 red colobus individuals (Tables 3-4). Our approach retrieved a higher average number of alleles ($CE = 4.00 \pm 0.63$; $HTAS = 5.40 \pm 0.68$) and thus increased average allelic richness ($CE = 3.59 \pm 0.42$; $HTAS = 4.54 \pm 0.50$).

Locus	Na	Ne	Ho	He	uHe	F	HWE
C19a	5.00	2.27	0.43	0.56	0.57	0.23	ns
D1S1675	6.00	2.33	0.48	0.57	0.58	0.17	ns
D2S146	3.00	2.88	0.57	0.65	0.67	0.13	ns
D2S391	3.00	1.98	0.57	0.50	0.51	-0.15	ns
D4S243	7.00	5.10	0.76	0.80	0.82	0.05	ns
D4S2430	2.00	1.05	0.05	0.05	0.05	-0.02	ns
D6S287	2.00	1.54	0.25	0.35	0.36	0.28	ns
D6S311	3.00	1.16	0.14	0.13	0.14	-0.06	ns
D8S260	3.00	1.56	0.29	0.36	0.37	0.20	ns
D10S676	6.00	1.98	0.33	0.49	0.51	0.33	**
D13S1291	7.00	2.02	0.38	0.50	0.52	0.24	**
D14S306	7.00	3.83	0.86	0.74	0.76	-0.16	ns
D16S403	3.00	2.00	0.43	0.50	0.51	0.14	ns
D17S791	7.00	3.57	0.67	0.72	0.74	0.07	**
D18S57	3.00	2.28	0.57	0.56	0.57	-0.02	ns
D20S189	3.00	1.27	0.14	0.21	0.22	0.33	ns
DXS571.2	7.00	4.01	0.67	0.75	0.77	0.11	ns
MEAN	4.53	2.40	0.45	0.50	0.51	0.11	ns
SE	0.49	0.27	0.06	0.05	0.05	0.04	ns

Table 2: Genetic diversity using high throughput amplicon sequencing for red colobus at Kibale National Park, Uganda. Generated by GenAlEx v6.51b2. *Na* - Number of unique alleles; *Ne* - Effective number of alleles; *Ho* - Observed heterozygosity; *He* - Expected heterozygosity; *uHe* - Unbiased expected heterozygosity; *F* - Inbreeding coefficient; *HWE* - Deviations from Hardy Weinberg Equilibrium.

Locus	Na	Ne	Ac	Ho	He	uHe	F
C19a	3.00	1.73	2.88	0.47	0.42	0.43	-0.12
D4S243	3.00	2.82	3.00	0.71	0.65	0.66	-0.09
D8S260	3.00	1.82	2.88	0.41	0.45	0.47	0.09
D10S676	6.00	2.64	4.77	0.65	0.62	0.64	-0.04
D14S306	5.00	3.32	4.43	0.71	0.70	0.72	-0.01
Mean	4.00	2.47	3.59	0.59	0.57	0.58	-0.04
SE	0.63	0.30	0.42	0.06	0.06	0.06	0.04

Table 3: Genetic diversity at matched loci using capillary electrophoresis for Kibale National Park, Uganda. *Na* - Number of unique alleles; *Ne* - Effective number of alleles; *Ac* - allelic richness corrected by sample size; *Ho* - Observed heterozygosity; *He* - Expected heterozygosity; *uHe* - Unbiased expected heterozygosity; *F* - Inbreeding coefficient.

Locus	Na	Ne	Ac	Ho	He	uHe	F
C19a	5.00	2.29	4.14	0.47	0.56	0.58	0.17
D4S243	6.00	4.55	5.36	0.71	0.78	0.80	0.10
D8S260	3.00	1.73	2.88	0.35	0.42	0.43	0.16
D10S676	6.00	2.35	4.63	0.41	0.57	0.59	0.28
D14S306	7.00	3.96	5.68	0.82	0.75	0.77	-0.10
Mean	5.40	2.98	4.54	0.55	0.62	0.64	0.12
SE	0.68	0.54	0.50	0.09	0.07	0.07	0.06

Table 4: Genetic diversity at matched loci using high throughput amplicon sequencing for Kibale National Park, Uganda. *Na* - Number of unique alleles; *Ne* - Effective number of alleles; *Ac* - allelic richness corrected by sample size; *Ho* - Observed heterozygosity; *He* - Expected heterozygosity; *uHe* - Unbiased expected heterozygosity; *F* - Inbreeding coefficient.

For black-and-white colobus, the number of alleles per locus across the sample ranged from 1 at DS14306 to 7 at D1S1675. On average, there were 4.200 ± 0.401 SE unique alleles per locus. 95% of loci were polymorphic across the population, except for D16S403, which was monomorphic. Three loci deviated significantly from HWE (D1S1675, D10S676, D17S791), but no loci showed significant evidence of linkage disequilibrium. Here again, this may simply be an artifact of lower sequence depth at D10S676, but for the other loci may be an indication of biological processes like non-random mating or sub-structuring in the population. Inbreeding coefficient (F) values were negative at 12 of the 20 loci, which may reflect heterozygote excess due to gene flow, potential admixture, or other biological and technical factors. General measures of genetic diversity for black-and-white colobus can be found in Table 5.

Locus	Na	Ne	Ho	He	uHe	F	HWE
C19a	6.000	4.624	0.800	0.784	0.804	-0.021	ns
D1S1675	7.000	3.343	0.316	0.701	0.720	0.549	P<0.001
D2S146	2.000	1.280	0.250	0.219	0.224	-0.143	ns
D2S391	2.000	1.835	0.600	0.455	0.467	-0.319	ns
D4S243	5.000	3.021	0.737	0.669	0.687	-0.101	ns
D4S2430	3.000	1.504	0.250	0.335	0.344	0.254	ns
D6S264	6.000	2.694	0.550	0.629	0.645	0.125	ns
D6S287	2.000	1.600	0.400	0.375	0.385	-0.067	ns
D6S311	5.000	3.524	0.800	0.716	0.735	-0.117	ns
D8S260	4.000	2.388	0.600	0.581	0.596	-0.032	ns
D10S587	4.000	1.918	0.350	0.479	0.491	0.269	ns
D10S676	6.000	4.599	0.526	0.783	0.804	0.327	P<0.001
D12S372	3.000	1.559	0.450	0.359	0.368	-0.254	ns
D13S1291	3.000	2.062	0.750	0.515	0.528	-0.456	ns
D14S306	7.000	5.405	0.900	0.815	0.836	-0.104	ns
D16S403	1.000	1.000	0.000	0.000	0.000	-	-
D17S791	6.000	2.484	0.400	0.598	0.613	0.331	P<0.01
D18S57	3.000	2.658	0.700	0.624	0.640	-0.122	ns
D20S189	5.000	2.402	0.450	0.584	0.599	0.229	ns
DXS571.2	4.000	3.524	0.800	0.716	0.735	-0.117	ns
MEAN	4.200	2.671	0.531	0.547	0.561	0.012	-
SE	0.401	0.268	0.053	0.047	0.048	0.057	-

Table 5: Genetic diversity using high throughput amplicon sequencing for black-and-white colobus at Boabeng-Fiema, Ghana. Generated by GenAlEx v6.51b2. *Na* - Number of unique alleles; *Ne* - Effective number of alleles; *Ho* - Observed heterozygosity; *He* - Expected heterozygosity; *uHe* - Unbiased expected heterozygosity; *F* - Inbreeding coefficient; *HWE* - Deviations from Hardy Weinberg Equilibrium.

Discussion

Despite continued calls for the application of genomics to conservation, these methods are still not feasible for many natural populations of endangered species, particularly when researchers are limited to non-invasive sampling and thus more degraded samples. In addition, while genomic approaches offer better resolution to addressing questions of conservation interest, for certain questions a genetic approach with a smaller number of loci can sufficiently meet needs, such as addressing data deficiencies and questions of conservation status.

Population genetics analyses utilizing microsatellites are a proven method for generating data and knowledge useful for conservation prioritization (Hauser et al., 2021). These

approaches have been successfully leveraged in numerous wild primate populations (Oklander & Soto-Calderon, 2024); however, traditional genotyping methods have some caveats that can hinder their utility for conservation applications. Conservation efforts are often limited by access to funding. Any reduction in costs associated with research makes an approach more feasible, and while capillary electrophoresis may be more affordable when handling a very small number of samples, next-generation sequencing allows researchers to process the higher number of samples associated with population genetics studies in a cost-effective manner due to multiplexing and pooling of replicates (Darby et al., 2016). Additionally, capillary electrophoresis instruments are now less commonly available than next-generation instruments, making the former a less accessible approach. Genotyping using capillary electrophoresis is also imprecise and easily open to the introduction of error both within and between researchers (Pasqualotto et al., 2007). A high throughput amplicon sequencing approach makes data sharing and analysis methods easier to standardize.

While we work towards genomics workflows which perform well in non-invasive samples, there is a need to update conservation genetics methods in a way which leverages next-generation technologies, making them easy to integrate with genomics approaches in the future. Adapting STR panels for a high throughput amplicon sequencing approach allows us to genotype in a more accurate and accessible manner, which has direct implications for utility in conservation applications.

Genotyping

This work comprises the first deployment of a high throughput amplicon sequencing approach on fecal samples from wild red colobus and black-and-white colobus populations. It follows the patterns found in previous studies, which show that sequence-based genotyping methods tend to reveal higher proportions of cryptic alleles as compared to purely length-based assignments (Darby et al., 2016; Vartia et al., 2016). At the loci shared between studies, we located cryptic alleles at 40-50% of loci. The discovery of these alleles alone altered genotypes for 13% of the red colobus and 15% of the black-and-white colobus individuals. These were individuals who had previously been genotyped as homozygous due to having two alleles of the same size, which were revealed to be different by sequence.

Allelic dropout (ADO) is often a particularly thorny problem for studies utilizing non-invasive, degraded samples (Gagneux et al., 1997; Dai et al., 2015; Forgacs et al., 2019). The general approach to handle this issue is to perform multiple replicates so that homozygotes can be confirmed across experiments (Morin et al., 2001). In capillary electrophoresis, replicates must be performed independently in order to establish true alleles from nonspecific signals, while next-generation platforms allow researchers to combine products from multiple PCR reactions (Barbian et al., 2018). This makes successfully capturing patterns of allelic dropout, again, much more time and labor intensive using a CE approach. We were able to reliably capture patterns of allelic dropout across all our loci and picked up ADO rates of 0 – 50% among observed heterozygotes. Given that studies on endangered species may more often contain small sample sizes, this kind of improved accuracy when genotyping via high throughput amplicon sequencing as compared to capillary electrophoresis may be particularly impactful. This approach also provided greater confidence that we are capturing true allele size, since we have

sequences, as opposed to the estimated peak sizes obtained by capillary electrophoresis. When assessing genotypes at matched loci from previous work for both red colobus and black-and-white colobus, we frequently found sequence lengths in previous studies were off, most often by 1 – 3 base pairs.

This study also represents one of the first independent tests of Trede et al's (2020) universal catarrhine microsatellite panels using non-invasively collected samples from wild populations. In the process of optimization, we dropped 22 of the loci originally included in the panels due to poor amplification or reliability across replicates. Non-invasive samples are notoriously difficult to genotype and yield heterogeneous results due to varying levels of degradation related to behavioral, environmental, and storage factors (Schultz et al., 2021). The fecal samples used in the bulk of this work, from Kibale National Park and Boabeng-Fiema Monkey Sanctuary, are anywhere from 5-14 years old and represent wild populations with varying degrees of habituation, from unhabituated to well-habituated. We feel our samples are a good reflection of the degradation levels fellow researchers studying African colobines may be faced with when undertaking population genetics studies. With this in mind, we feel our optimization steps will lead to more efficient sequencing for populations of conservation concern.

Genetic Diversity

Measures of genetic diversity captured for the red colobus population using the new STR panel and high throughput amplicon sequencing were roughly on par with values reported from a past study using capillary electrophoresis and a different panel (Na: $CE = 3.98 \pm 0.44$, HTAS =

4.53 ± 0.49 ; Ne: $CE = 2.76 \pm 0.19$, HTAS = 2.40 ± 0.27 ; uHe: $CE = 0.61 \pm 0.01$, HTAS = 0.51 ± 0.05 ; F: $CE = 0.01 \pm 0.07$; HTAS = 0.11 ± 0.04) (Ruiz-Lopez et al., 2022). When we tested only the shared markers for the 17 matched samples between Ruiz-Lopez et al.'s (2022) study and our work, we captured higher levels of allelic richness at the same loci. This also resulted in the inbreeding coefficient dropping from indicating an excess of homozygotes at 4 of 5 loci in the previous study (Ruiz-Lopez et al., 2022), to only 1 of 5 loci in our study. The black-and-white colobus STR panel captured a moderate level of genetic diversity ($N_a = 4.2$, $N_e = 2.671$, $uHe = 0.561$) and little to no evidence of inbreeding ($F = 0.012$). Our results suggest that our approach catches roughly equivalent levels of diversity as past STR panels using capillary electrophoresis methods in colobus, while improving the captured allelic richness at previously used markers (Ruiz-Lopez et al., 2022).

Considerations for Application

We believe the application of this STR panel using a high throughput amplicon sequencing approach has the ability to make population genetics work for colobus more accessible and results more comparable cross-study. Resulting data would fill key knowledge gaps necessary for targeted conservation prioritization and action in several highly threatened colobus species. There are some specific recommendations about how to utilize these panels generated by our work.

If researchers have the means, it would be advantageous to initially quantify endogenous DNA, particularly if samples are known to have been exposed to conditions likely to increase degradation. This way, resources can be allocated towards samples with the best potential for

amplification. We recommend at least three replicates of each pool per sample to be able to correctly identify homozygous individuals. We consider this a bare minimum, and if front-end quantification of samples is not performed, researchers may need additional replicates to correctly genotype individuals and catch allelic dropout. One locus in our first pool (D10S676) showed a higher rate of stochasticity with respect to sequencing depth. On sequencing runs which were very full, it was often the first locus to lose a considerable amount of read depth. It may be advantageous to add depth for this locus by singleplexing, where necessary. During data analysis, we found that CHIIMP's allele calls needed to be checked visually. Often, stutter was called as an allele in heterozygotes, when the true second allele was labeled as a 'prominent sequence.' By visually examining all calls per locus across replicates and samples, we were able to glean locus specific stutter patterns and adjust allele calls where necessary.

Conclusions

Conservation of colobus in Africa is often impeded by the lack of data necessary for assessing conservation status, such as population metrics, distributions, and population history. Population genetics allows us to generate these data in an efficient and accurate manner. However, older technologies and methods for genotyping, such as capillary electrophoresis, can be inaccessible and even inaccurate at times. High throughput amplicon sequencing increases identification of cryptic diversity and accuracy of genotyping via a conservation genetics approach, while generating the scaffolding necessary to integrate these methods with future genomics approaches. The STR panels tested and optimized here represent an opportunity to make these approaches more accessible for colobus research, as they remove the time and costs

associated with testing markers for future studies, and leverage next-generation sequencing platforms. A standardized set of markers and workflow also provides the basis for better cross-study comparison, which could be particularly useful for tracking populations long-term. These panels produce diversity metrics roughly equivalent to previous colobus genetics studies while increasing genotyping accuracy and revealing previously cryptic variation. This study offers an updated workflow to studying African colobine population genetics, which allows us to fill currently pressing data gaps, while also looking forward to potential integration with future genomics approaches.

CHAPTER THREE

ISLANDS OF CHANGE: ZANZIBAR RED COLOBUS, FOOD SECURITY, AND HUMAN-WILDLIFE INTERACTIONS UNDER CLIMATE CHANGE

Contributions

This chapter was co-authored by Jenneca McCarter, Nelson Ting, and Tim Davenport. Jenneca McCarter was responsible for study design, data analysis, and writing of the manuscript. Nelson Ting provided intellectual guidance and assistance editing the manuscript. Census data for Zanzibar red colobus were provided by Tim Davenport.

Introduction

Conservation often requires us to consider threats to both biodiversity and human populations in tandem, presenting us with ‘wicked problems’: complex situations with differences in stakeholder values and no straightforward solutions without impacts to one or more involved parties (Mason et al., 2018). One such wicked problem is the global overlap of highly biodiverse regions with areas of high food insecurity. Conserving biodiversity and addressing food insecurity are intrinsically linked, as approaches to address one almost always involve making decisions which will impact the other (Chappell & LaValle, 2011).

Food security is defined as ‘existing when all people, at all times, have physical and economic access to sufficient, safe, and nutritious food that meets their dietary needs and food preferences for an active and healthy life’ (FAO, 2008). The people most impacted are rural communities working in agriculture, reflecting that the availability of food does not necessarily equate to access due to economic and market barriers (Pinstrup-Anderson, 2009; Brussard et al.,

2010). Poverty is the driving force behind food insecurity, often leading to increased reliance on ecosystem services, as there are generally no alternatives, particularly in rural areas (Fisher & Christopher, 2007; Poppy et al., 2014). This is especially true given that current international food price increases are comparable to historical food crises seen in 1973-1974 and 2007-2008 (FAO, 2025). Biodiversity is a key element of food security in these situations because it serves as a safety net and provides dietary diversity which would be otherwise inaccessible. In addition, biodiversity supports ecosystem services and ecological processes which improve agricultural productivity, soil fertility, water quality, and mitigates pollution (Snel, 2004; Dannenberg et al., 2024). Food security is also supported by the economic gains biodiversity can confer. Tourism is a common element of sustainable development and poverty alleviation plans, but ecotourism in particular can integrate rural households into the market economy (Snyman, 2014). Given the interconnected nature of food security and biodiversity, we have no choice but to try and find solutions which, at least in part, attempt to address both. This ‘wicked problem’ is likely to only get thornier due to the compounding impacts of climate change on both food production and ecosystem stability (Malhi et al., 2020; Hultgren et al., 2025).

Climate change is expected to worsen food insecurity in many regions, as it reduces crop productivity through affecting water availability, causing heat stress, altering phenology, and increasing likelihood of pests and disease (Mirzabaev, et al., 2023). Due to this, fluctuations in yields are expected to create interruptions to our food systems and raise food prices globally (Mbow et al., 2019). In rural, low-income regions, this will inevitably put even more pressure on land-use practices and biodiversity. Agricultural expansion necessitates habitat degradation and destruction, which are major drivers of species extinctions (Molotoks et al., 2017). The impact of climate change on agricultural productivity may mean that conservation is left with a dual-

pronged problem: agricultural expansion to address shortfalls due to climate change, together with increased reliance on biodiversity to help meet resulting resource and economic needs.

As climate change continues to impact agricultural productivity, conflict stemming from improving both food security and biodiversity protection will presumably arise. With this in mind, there is a need to better understand these risks at localized scales for long-term conservation planning. One way of doing this is to explore how spatial dimensions of human-wildlife interactions mediated by agriculture may shift under climate change. Crop-raiding is of particular concern as it is the most common human-wildlife interaction mediated by agriculture and has the potential for negative impacts for both human and non-human parties. Loss of crops directly reduces the security of human agricultural livelihoods, particularly at subsistence and smallholder farming levels (Raphela & Pillay, 2021), while crop-raiding often engenders negative perceptions of species and can result in retaliatory killings. Retaliatory killings can be particularly problematic, for both the wildlife and human populations involved, when species are endangered and of economic significance. Obtaining a clearer picture of how the spatial dimensions of this interaction will shift with climate change is thus of crucial conservation importance, as it may provide an opportunity to develop conservation plans that mitigate future negative outcomes.

In this study, we demonstrate such an approach by assessing the future of human-wildlife interactions under various climate change scenarios on the island of Unguja, which is part of the United Republic of Tanzania and the Zanzibar archipelago off the coast of East Africa. Unguja is a low-lying island where large swaths of the population are dependent on subsistence and smallholder agriculture (The United Republic of Tanzania, 2022). Overall forest cover on the island has decreased sharply since 1996 (566.9 km² to 537 km²) alongside large population

growth (1988 = 640,685; 2012 = 1,303,569) (Kukkonen & Käyhkö, 2014; Office of the Chief Government Statistician Zanzibar, 2025). Food insecurity in Zanzibar is pervasive, with a 2017 Food Security & Nutrition Analysis report putting large portions of the population into food security categories such as ‘stressed’ (69%), ‘crisis’ (12%), and ‘emergency’ (2%) (Zanzibar Food Security and Nutrition Monitoring 2017). In addition, Unguja farmers have already reported needing to adjust their practices due to quantifiable shifts in sea levels, patterns of precipitation, and soil quality (Geere, 2014; Zhang & Baker, 2017; The Hague Institute for Global Justice, 2017). Meanwhile, Unguja is also home to an endangered primate endemic; the Zanzibar red colobus monkey (*Piliocolobus kirkii*). This species has a population of roughly 5,862 individuals distributed across roughly 21 sites (Davenport et al., 2019). It has a highly specialized folivorous diet, slow reproduction rate, and low survivorship and recruitment, all of which leave it highly vulnerable to the impacts of climate change (Davies & Oates, 1994; Estrada et al., 2016; Korstjens & Hillyer, 2016; Korstjens, 2019; Alexio-Pais et al., 2023). While reports of how much crop-raiding Zanzibar red colobus engage in varies, perceived impacts have led to instances of retaliatory killing, with reports of one sub-population being reduced from 200 to 30 (in 2000) by farmers (Zanzibar Commission for Natural Resources & CARE Tanzania, 2000; Saunders, 2011). It is also important to note that the Zanzibar red colobus is the flagship species for Zanzibar and central to ecotourism, as well as an important component of sustainable development plans aimed at poverty relief in Zanzibar. Jozani–Chwaka Bay National Park brought in \$334,700 USD in 2016, primarily from tourists viewing the red colobus (Davenport et al., 2019). The long-term health of the Zanzibar red colobus population is therefore not simply of importance for conservation of biodiversity and protection of Zanzibar’s natural history, but also for the well-being of the human population.

Our study thus uses this system to explore relationships between biodiversity conservation and food security at a localized scale, specifically considering the role of climate change. We do this by 1) examining the impacts of climate change on the range and occurrence of an endangered endemic primate (*P. kirkii*), 2) isolating a suite of crops key to livelihoods in Zanzibar that remain productive under climate change, examining their spatial patterns of suitability, and 3) intersecting these results to investigate the spatial nature of human-wildlife interactions mediated by agriculture under climate change (e.g., potential for crop-raiding by colobus). By doing this, we hope to demonstrate a novel approach for moving from generalized understandings of the ‘wicked problem’ of overlapping biodiversity and food security crises to directly considering these issues in tandem as part of long-term, localized conservation planning.

Methods

Study Area

The spatial extent of this study includes the entire area of Unguja, the largest island in the Zanzibar Archipelago, 35km off the East coast of the United Republic of Tanzania (5 to 6 °S; 39°E). Unguja, colloquially and hereafter referred to as ‘Zanzibar,’ has an area of approximately 1,658 km². Zanzibar is low-lying, with its highest point of elevation at only 110m above sea level and has a tropical monsoon climate consisting of two rainy seasons (the long rains/*masika*; the short rains/*vuli*) and two drier seasons (summer/*kiangazi*; winter/*pupwe*) (Makame 2013). The mean annual precipitation ranges from 1,400 to 2,000mm, with the Eastern coast typically receiving less precipitation, particularly during the short rainy season. Temperatures on Zanzibar do not fluctuate much across the year, with mean monthly maximums between 28-32 °C and mean monthly minimums between 18-22 °C. Zanzibar’s landscape is highly heterogeneous with

a mixture of mangrove, thicket, coral rag, groundwater forest, and agricultural plots of varying size (Davenport et al., 2019).

Species Occurrence Data

Species occurrence data utilized in this project come from the most recent census of *P. kirkii* conducted between 2013 and 2015 (Davenport et al., 2019; Figure 1).

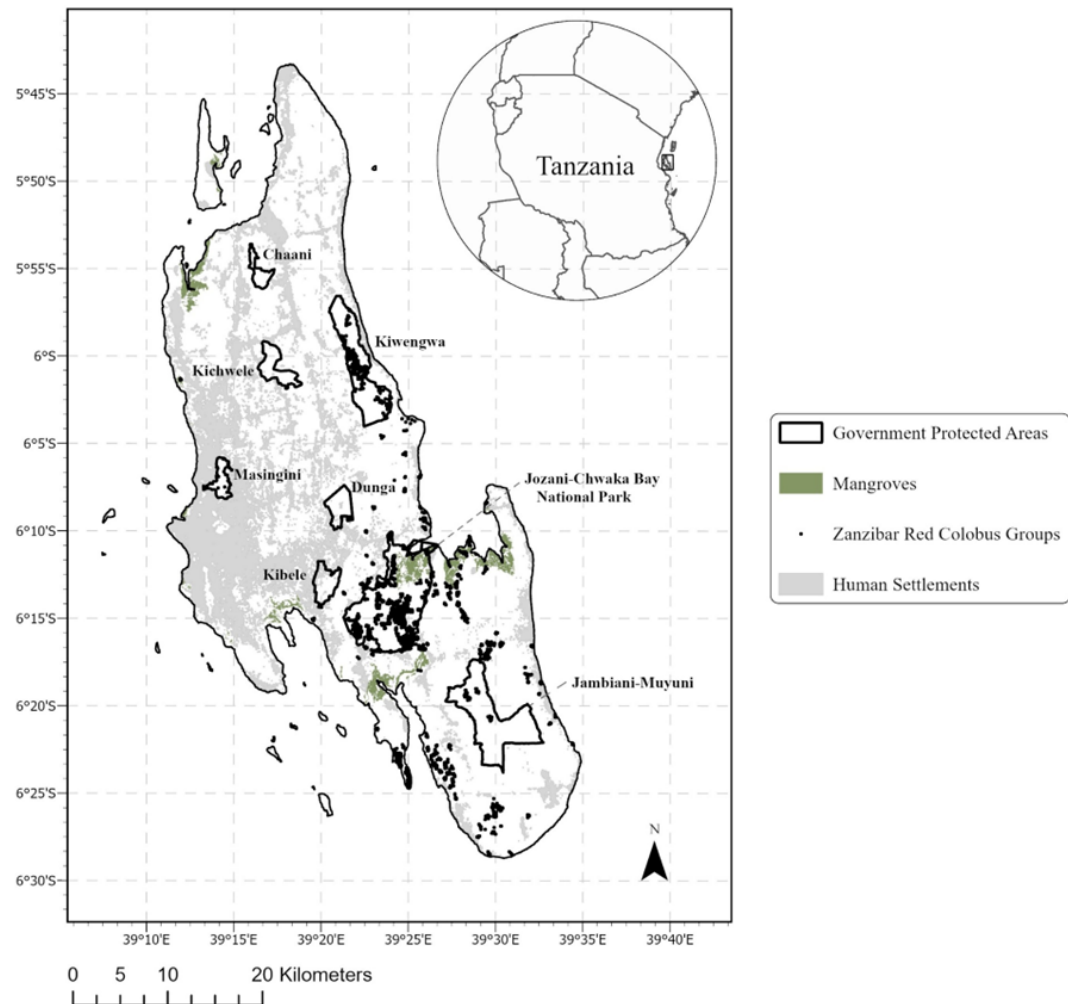


Figure 1: Map of distribution of *P. kirkii* across Unguja from the Davenport et al., (2019) census. Map includes human settlements across the island, important mangrove habitat, and government protected areas (Chaani Forest Reserve Plantation, Kichwele Forest Reserve Plantation, Kiwengwa Forest Reserve, Masingini Forest Reserve, Dunga Forest Reserve Plantation, Kibele Forest Reserve Plantation, Jozani-Chwaka Bay National Park, Jambiani-Muyuni Proposed Forest Reserve).

The census estimated the population to be roughly 5,862 individuals across 21 sites, with a large portion of the population (~51%) located in Jozani-Chwaka Bay National Park and its surrounding farms (*shambas*). This census was carried out systematically over the entire natural extent of *P. kirkii*, providing an excellent starting point for constructing an Ecological Niche Model (ENM).

After cleaning the raw census data for any repeated locations and points with missing or erroneous geospatial tags, there were 8,743 species occurrence points. Due to the small area of the island and the fact that much of the island is transformed, many of the occurrence points were very close to one another (under 1km). Also, while the much higher density of *P. kirkii* in and around Jozani-Chwaka Bay National Park is a very real phenomenon due to it being a protected area with much more natural vegetation than any other site on the island, the time spent sampling in and around Jozani Forest was significantly higher than at any other site (Jozani Forest censused over ~95 days; all other sites were censused anywhere from ~3-32 days). We performed an initial round of thinning in ArcMap, so that all records were separated by a distance of at least 1km, being careful to preserve patterns of spatial distribution across the island. It's important to point out that this thinning was a way to adjust for unequal sampling at sites, not a way to reduce spatial autocorrelation, even though many ENM studies will equate thinning or filtering with 'reducing autocorrelation.' Spatial autocorrelation mirrors the structure of environmental variables and species distribution in the landscape owing to the First Law of Geography ("Everything is related to everything else, but near things are more related than distant things") (Sillero & Barbosa, 2021). Therefore, spatial autocorrelation is a natural property and something we want to preserve in our models. After processing the census data fully, 136 occurrence records were isolated from the original dataset to use in the models, which is

considered a robust number of records for modeling island endemics as compared to other studies (Benavides Rios et al., 2024). Beyond this initial round, additional thinning of the data was conducted using the package *spThin* in RStudio (Aiello-Lammens et al., 2015). This package allows the user to thin their data based on a chosen distance between occurrence points, employing a nearest-neighbor approach which produces several new subsets of thinned data. The user can then select the subset which both meets their distance thinning parameter and allows them to keep the most data possible for use in their ENM.

Crop Data

Crop selection was based on agricultural census data from multiple census efforts for both the United Republic of Tanzania and the Revolutionary Government of Zanzibar (2002/03, 2007/08, 2016/17, 2019/20)(Office of the Chief Government Statistician, 2012; Ministry of Agriculture and Natural Resources, 2012; National Bureau of Statistics, 2017; National Bureau of Statistics, 2021a,b). An initial suite of approximately 40 crops was selected and then reduced to 35. As this study is concerned with crops associated with food security, selected crops were either high in planted amounts and yields, or those which could be found across multiple censuses. Not all the selected crops have been planted in high amounts or produced high yields, but as this study is concerned with primarily subsistence and smallholder crops, we took low-area crops that were present across multiple censuses to be a good sign that these may be subsistence level agricultural efforts. In addition, some crops found in the censuses were specifically included as they have been proposed by other research to be climate-resilient crops, or alternative crops which may fill the same niche as currently ubiquitous crops that may not grow well under certain climate scenarios (e.g., substituting sorghum for other cereals) (Snapp et

al., 2003; Thiele et al., 2017; Boakye et al., 2018; Tan et al., 2020; Mwamahonje et al., 2021; Adiele, 2023; Heinz et al., 2024). The final suite of crops (Table 1) ended up being slightly smaller (30) due to findings during modeling (see below in the ‘mechanistic niche modeling’ section).

Crop	Planted Area (ha)	Harvest Area (ha)	Quantity Harvested (tons)	Yield (tons/ha)
<i>Cash</i>				
Sugarcane	1,008	654	12,313	18.8
Total	36,767	26,835	54,615	1.6
<i>Cereals</i>				
Paddy Rice	33,155	24,554	50,421	2.1
Bulrush Millet	110	64	150	2.4
Finger Millet*	18	19	13	0.7
Maize	3,363	2,106	3,951	1.9
Sorghum	121	92	80	0.9
Total	36,767	26,835	54,615	1.6
<i>Beans & Pulses</i>				
Bambara Nut*	26	24	17	0.7
Cowpea	2,022	1,316	3,675	2.8
Green Gram	496	392	155	0.4
Groundnut	1,231	1,017	690	0.7
Pigeon Pea	1,116	655	931	1.4
Total	4,891	3,404	5,468	1.2
<i>Fruits & Vegetables</i>				
Cabbage	2	2	2	1.1
Chili*	98	96	125	1.3
Cucumber*	286	282	819	2.9
Okra	1,593	1,110	11,004	9.9
Pumpkin*	506	505	4,443	8.8
Tomato	2,408	1,739	10,647	6.1
Watermelon	1,907	694	10,897	15.7
Total	6,800	4,428	37,937	6.54
<i>Permanent Fruits</i>				
Banana	30,016	25,019	88,085	3.5
Mango	2,830	1,157	17,313	15
Orange	1,353	773	7,985	10.3
Starfruit*	1	0	0	0.1
Total	34,200	26,949	113,383	7.23
<i>Permanent Cash</i>				
Clove	8,830	231	2,355	10.2
Coconut	7,607	5,446	13,233	2.4
Total	16,437	5,677	15,588	6.3
<i>Pseudocereal</i>				
Amaranth*	271	268	1,258	4.7
Total	271	268	1,258	4.7
<i>Roots & Tubers</i>				
Cassava	62,794	35,696	183,971	5.2
Sweet Potato	7,144	3,455	38,180	11
Yam	1,913	659	1,409	2.1
Total	71,851	39,810	223,560	6.1
<i>Spices & Herbs</i>				
Kothmir*	2	2	2	1.1
Turmeric*	191	199	139	0.7
Total	193	201	141	0.9

Table 1: Measures of productivity for the final suite of chosen crops from past agricultural censuses on Zanzibar. (From: Office of the Chief Government Statistician 2012*; National Bureau of Statistics 2021a,b).

Data on ecological parameters for crops included in this study were obtained from a variety of sources. The FAO's (Food and Agriculture Organization of the United Nations) GAEZ (Global Agro-Ecological Zones) data portal (<https://gaez.fao.org/pages/ecocrop>) was used as a starting point for collating information on ecological parameters for our suite of crops (Ramirez-Villegas, 2013; FAO Global Agro Ecological Zones, 2024). These data were then checked against primary and grey literature focused on agricultural research and standards for these crops within the African continent, and specially within East Africa, where possible. Ecological parameters were updated for crops where information on more specific varieties grown in the study region were available.

Environmental Data

Global current land-use/land-cover data were downloaded from (<https://zenodo.org/record/3986872>; Liu et al., 2020) at a resolution of 30-m. Future land-use/land-cover data were downloaded from (<https://zenodo.org/record/4584775>; Chen et al., 2022) at a resolution of 1-km. The future land-use/land-cover dataset follows the SSP-RCP scenarios for climate change, with separate projections for each scenario at different timesteps. Topographic data for this study were downloaded using the USGS EarthExplorer (<https://earthexplorer.usgs.gov/>). The digital elevation model chosen for this study comes from the global Shuttle Radar Topography Mission (SRTM) flown in February 2000 at a scale of 1 arc-second. Historical climate data were downloaded from Climatologies at High Resolution for the Earth's Land Surface Areas (CHELSA version 2.1, <https://chelsa-climate.org/>) (Brun et al., 2022). CHELSA's bioclimatic datasets are comprised of 19 variables which address trends, seasonality, and extreme or limiting factors across annual, quarterly, and monthly timesteps.

CHELSA also provides a wide range of other climate data, including monthly precipitation, mean daily temperature, and mean daily minimum temperature. The datasets utilized as current climate in this study is an average across the years 1981 – 2010. The finest scale available was selected (30 arc-seconds). Future climate data were also provided through CHELSA for the same variables listed above, which were downscaled from the CMIP6 future climate projections.

GCMs (global climate models) are available over three 30-year periods (2011-2040, 2041-2070, 2071-2100) for three SSPs (shared socioeconomic pathways; SSP1-2.6, SSP3-7.0, SSP5-8.5).

Five GCMs (general circulation models) were selected to use in an ensemble approach to modeling (GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-HR, MRI-ESM2-0, UKESM1-0-LL).

Predictor variables for Zanzibar red colobus distribution were chosen based on a combination of statistical analysis and what has been found to be of high importance in previous primate studies (Dunbar et al., 2009; Gouveia et al., 2014; Korstjens, 2019; Wang et al., 2013; Williams et al., 2021). Principal components analysis (PCA) was used to first explore which variables best explained Zanzibar red colobus occurrence in environmental space. This set of variables was compared to past work on *Colobus* which investigated the importance of these same 19 bioclimatic variables, as well as measures of vegetation, in explaining distribution (Korstjens, 2019; Williams et al., 2021). The variables previously noted as being most important to explaining *Colobus* distribution were also found to be of high importance for *P. kirkii* in the PCA. However, we removed vegetation class (land-use/land-cover) from our dataset as it ranked as one of the lowest predictors for Zanzibar red colobus occurrence. It's unclear if this is a true relationship between LULC classification and red colobus occurrence, or if this is simply an artifact of how accurate these LULC datasets are. When compared to high-resolution drone imagery, certain classifications seemed inaccurate or simply too broad.

From this point, the objective was to keep as many of the highly explanatory variables as possible while reducing multicollinearity among environmental predictors. This was accomplished by examining the PCAs, and calculating Pearson coefficients and Variable Inflation Factors (VIF). In the end, the goal was to have a set of variables which when taken together, had the lowest combination of VIF scores possible without removing all highly explanatory or biologically relevant variables, while remaining cognizant of the ratio between occurrence points and predictors. When too many variables for the number of occurrence records are utilized, it can result in model overfitting, which we must pay particular attention to in small island systems (Benavides Rios et al., 2024). This selection process resulted in a final variable set of four bioclimatic variables and one DEM-derived variable, with VIF scores ranging from 2 to 21. The final variable set included Bio2 (mean diurnal range), Bio4 (temperature seasonality), Bio12 (annual precipitation), Bio15 (precipitation seasonality), and elevation. While it is understood that high multicollinearity exists at VIF values over 10, it is not necessarily good practice to exclude a variable just because it has a high VIF score, particularly if it is known to have important biological relevance. It does, however, become important that any patterns of multicollinearity remain constant over time and space where models are projected (Sillero et al., 2021). If collinearity does not remain constant across scenarios, then error is introduced into the models, creating ineffective projections. PCAs, correlation matrices, and Mantel tests were all utilized to check for constancy in collinearity. All of our variables exhibited constant collinearity across all time and SSP scenarios. There is no variable selection process for the approach used in crop modeling (EcoCrop, a mechanistic model), as the variables are based on the necessary ecological parameters needed to model crop cycles. However, as models were going to be projected, patterns of multicollinearity were still checked.

Correlative Ecological & Mechanistic Niche Modeling

Correlative Niche Models

Ecological niche modeling identifies the environmental correlates of a species' current distribution to explore the environmental or climatic niche of the species (Korstjens, 2019). This type of model is correlative in nature, examining relationships between environmental variables and the presence of a species. Correlative niche models are generally accepted to be a way of exploring the realized niche of a species, which is the space a species occupies, informed by suitable biotic and abiotic factors (Sillero et al., 2021). These methods have been utilized previously in studying island endemics, and some general guidelines have been suggested for leveraging the approaches in island systems, which we follow where possible (Benavides Rios et al., 2024). This study utilizes a Generalized Linear Model (GLM), or a presence-absence approach. Given our aim to investigate range changes and long-term population viability for the Zanzibar red colobus under climate change, a generalized linear modeling approach was selected as it provides the probability of species occurrence in any given pixel.

For these models, parts of Zanzibar's west coast were left out due to the degree of urbanization or density of buildings (Center for International Earth Science Information Network, 2021). Before models could be built, all the data had to be cleaned and processed to the same extent and projected coordinate system. This was done utilizing either ArcMap v10.8.1 or R v4.1.2, depending on the size and type of data being processed. Once all the occurrence and environmental data were processed, models were built using the Biomod2 package (v4.2.2) in R. The first step was to build a full presence-absence dataset for the GLM, since we only had presence data. This was done using the Biomod2 package by building 10 different absence

datasets, each with 250 absences, using the ‘disk’ method which selects pseudo-absences within circles around presence points at user-defined minimum and maximum distances. Our pseudo-absences were set to be generated no closer than 2.5km from a presence and at a maximum distance of 30km, which allowed us to generate pseudo-absences over the entire extent of our study area. Creating 10 pseudo-absence sets of 250 should generate 2,500 absences in total, but as the extent of our study is rather small, we ended up with around 1,900 unique absences as some locations were repeated between repetitions. For model validation, we split our dataset internally into training and testing partitions based on distance using the package BlockCV v3.0.2 (Valavi et al., 2019).

Biomod2 allows the user to tune the formula and parameters used to run GLMs in several ways. To determine which type of GLM formula would best suit our data, we inspected the environmental variables in locations where Zanzibar red colobus are found. The shape of our data was all relatively symmetrical unimodal curves, so a quadratic linear formula was chosen for the GLM. The rest of the parameters for the GLM were left as the defaults for Biomod2. The GLM was set to run 20 repetitions over the presence-absence datasets, with each run’s performance evaluated using the TSS (true skill statistic) and ROC (receiver operating characteristic). This produced 100 total runs of the model. Model runs were kept if they were not overfit and met performance thresholds which indicated that they had good predictive power ($\text{ROC/TSS} > 0.70$), which 67 of the 100 runs did. Once the model was finalized, we proceeded to project them into the future under varying climate conditions.

Mechanistic Niche Model (EcoCrop)

While correlative models pair distribution data with environmental variables, mechanistic models are built on some combination of morphological, physiological, and behavioral data (Kearney & Porter, 2009). In terms of niche, mechanistic models enable researchers to examine organisms' fundamental and potential niche (Sillero et al., 2021). Mechanistic models operate by translating trait values into performance or fitness values, thus explaining how traits and the environment interact. This allows for both mapping a species potential niche and having clear insight into the processes captured by the model (Buckley et al., 2018; Sillero et al., 2021).

In this study, a simplified mechanistic model, EcoCrop, is employed to assess crop suitability instead of a correlative model as we lack occurrence data (Hijmans et al., 2001; Ramirez-Villegas et al., 2013). EcoCrop evaluates crop suitability across an area based on provided crop ecological parameters and climate data. The output from EcoCrop is a suitability score, ranging between fully unsuitable and optimally suitable (0 = no suitability, 1 = perfect suitability). A score that falls somewhere between 0 and 1 indicates that during the crop growth cycle, there are either permissible yet suboptimal temperatures, or precipitation levels are either too low or too high during the optimal growth period (Manners & Ettan, 2018; Heinz et al., 2024).

We used the *ecocrop* function included in the package *dismo* (v1.3-16; Hijmans, 2024) with the custom ecological parameters detailed in the 'crop data' section. All crops were run as 'rainfed,' using the standard EcoCrop calculations, save growth cycle. Previous studies have noted problems with employing simple maximum and minimum lengths of crop cycle, particularly that the minimum is generally far too short to accurately represent at typical crop cycle. With this in mind, we adjusted our model to use the geometric mean for length of crop cycle following Manners & Ettan (2018).

As mentioned in the ‘crop data’ section, the crop suite utilized for this study was thinned slightly during the modeling process. As this study aims to focus on crops which offer resilience under the combined impacts of climate change and human-wildlife interaction, we elected to remove any crops that failed for any of the given SSPs across the three time periods. These crops were carrot (karoti), cocoyam (nduma), eggplant (biringani), irish potato (viazi ulaya), and wheat (ngano). Additionally, when using the original ecological parameters for paddy rice from the GAEZ database, we had model failure (FAO Global Agro Ecological Zones, 2024). However, climate change concerns over paddy rice irrigation globally have jump-started breeding and genetic engineering efforts towards developing water-saving and drought-resistant varieties. One such variety, WDR-70, developed by the Shanghai Agro-Biological Gene Centre, was rolled out in a pilot program with roughly 300 farmers in Zanzibar in 2024. Based on promising results, the government is expected to approve the use of this rice variety across the island and to distribute it (Zhang et al., 2021; Onyango, 2024). We adjusted our ecological parameters to reflect those of WDR-70 and were able to retain rice as part of our crop suite for modeling. We have intentionally chosen not to exclude areas of the island like we did with our red colobus models, as in many regions agriculture is shifting, not permanent, due to the shallow, less fertile soils of coral rag vegetation (Davenport et al., 2019). For this reason, we wanted to leave our output flexible to land-use changes.

Climate Projection Modeling

For this study, we are projecting forward up to the year 2100 over 30-year increments under three different climate change scenarios (SSP1-2.6, SSP3-7.0, SSP5-8.5) as a way to explore the potential impacts on habitat suitability for red colobus across Zanzibar. Future

climate data were collected from CHELSA again, for the same variables at the same resolution of 30 arcseconds. The data available from CHELSA was downscaled from CMIP6 projections under several GCMs (GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-HR, MRI-ESM2-0, UKESM1-0-LL) which were used to create ensemble projections.

Projections for our GLM were created in RStudio utilizing the package *biomod2*, with AUC and TSS evaluation scores. Once all projections were completed, the threshold calculated by *Biomod2*'s internal evaluation statistics was used to reclassify both the 'current' time-step and the projections of the GLM in order to create binary presence-absence maps. From there, we were able to calculate range changes between specific time-steps of interest for each SSP. Projections for our EcoCrop models were also carried out in RStudio, utilizing the package *dismo* under the same conditions covered in the 'mechanistic niche model' section (Hijmans et al., 2001; Ramirez-Villegas et al., 2013; Hijmans, 2024).

Human-Wildlife Interaction Potential Mapping

In order to create a map of potential human-wildlife interaction mediated by agriculture, we combined the output from both our Zanzibar red colobus and crop modeling utilizing geospatial software (ESRI ArcPro 3.5.0). We reclassified probability of occurrence of Zanzibar red colobus and suitability values for crops into three classes: low, moderate, and high. For Zanzibar red colobus, anything below 50% probability of occurrence was classified as 'restricted', or as absence of red colobus. This threshold was based on the average internal presence-absence cutoffs from all our GLM projections. The rest of the red colobus reclassification was split in the following way: 51-70% low, 71-85% moderate, 86-100% high. Reclassification for crops, similar to previous studies, was split in the following way: 0-50%

low, 51-75% moderate, 76-100% high (Appelt et al., 2023). We then created combined mosaic rasters by overlapping the reclassified maps, using a weighted overlay approach with red colobus set to a weight of 40% and crops set to 60%. Crops were given a slightly higher weight with the simple reasoning that presence of crops is the mediating factor for HWI to occur.

It is important to note that with the crop suitability mapping, high suitability does not necessarily directly equate to presence of the crop. There are a litany of other factors, such as land-tenure and existing infrastructure, which determine actual land-use patterns which are not in our crop suitability maps. Our maps display suitability based purely on ecological and climatic factors. While this exact approach to examining HWI is novel to our knowledge, it roughly follows approaches used by other studies to examine human-wildlife coexistence (Vogel et al., 2023).

Results

Correlative model - Zanzibar red colobus

The GLM model performed well. The first evaluation metrics, TSS and AUC, for the model came internally from Biomod2. TSS ranges from -1 to 1, where values closer to 1 indicate an agreement between predicted and observed occurrences, and values near and below zero indicate the models are no better than a random prediction (Alouche et al., 2006). Similarly, a higher AUC value indicates a better performing model, where 1 is a model performing perfectly in theory (though in practice can mean the model is overfit) and any value <0.5 indicates that the model cannot perform reliably (Philips et al., 2006). For the GLM, the average TSS score was 0.76 and the average AUC was 0.90.

Ecological Niche Model: *P. kirkii*

Generalized Linear Model

Current

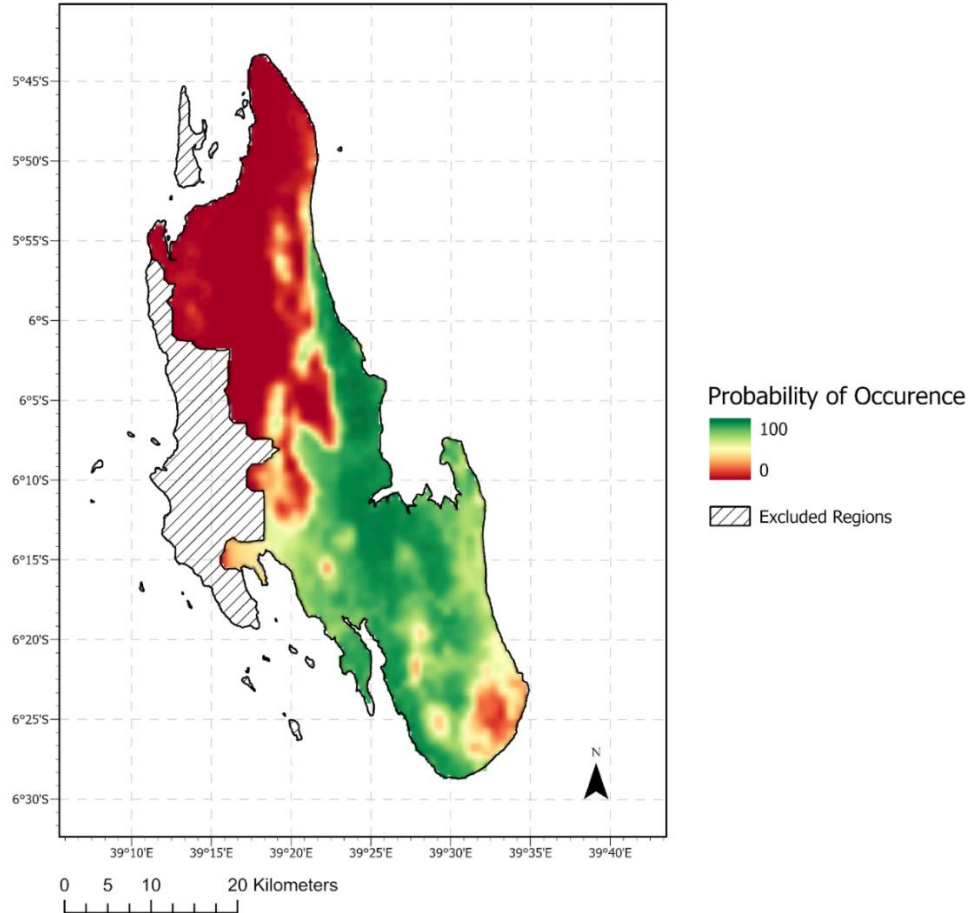


Figure 2: Generalized linear model output displaying the current probability of occurrence for Zanzibar red colobus across Zanzibar.

These internal evaluation statistics alone are often not enough to truly gauge whether a model is performing reliably and if it can predict accurately. In addition to the internal evaluation statistics, we created a null GLM model where all settings and parameters were the same, except for the occurrence data. A fully randomized ‘presence’ dataset was created to be used in this model, so that the internal validation statistics of our actual model could be compared to a null (randomized presences across the full study area, in this case) model. A two-sample t-test was then run on the model’s average TSS, and returned significant P-values, meaning our model

performs significantly better than randomized predictions (GLM: $t=26.6$, $df = 332$, $p\text{-value} < 2.2e^{-16}$). Based on mean variable importance across model replicates, temperature seasonality (bio4) was the most influential predictor, followed by elevation, mean diurnal range (bio2), precipitation seasonality (bio15), and annual precipitation (bio12).

Climate Projections

Maps were generated across all time points and SSPs but only maps for SSP 3-7.0 are shown here in the main text. SSP 1-2.6 and SSP 5-8.5 showed roughly the same general patterns as SSP 3-7.0, and the maps for these additional SSPs can be found in Appendix B. Climate projections for the GLM exhibit decreases in the overall probability of occurrence for the Zanzibar red colobus across all three climate change scenarios, with minor exceptions.

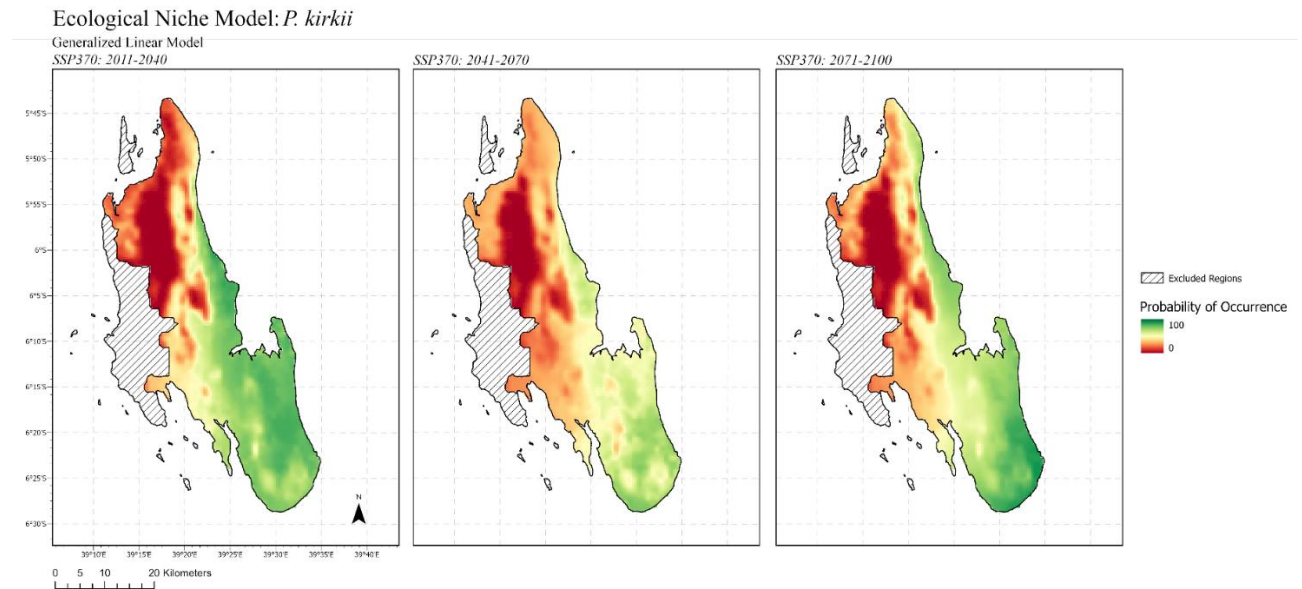


Figure 3: Probability of Zanzibar red colobus occurrence under climate change scenario SSP 3-7.0 throughout the century (See appendix for SSP 1-2.6 and 5-8.5 maps). SSP 3-7.0 reflects general patterns seen across the other SSPs: a loss in overall probability of occurrence for Zanzibar red colobus, range loss along the Northern and Western edges of the current range, with the most suitable areas concentrated in the Southern quadrant of the island.

Compared to the range for our ‘current’ (1981-2010) model, maximum probability of Zanzibar red colobus occurrence drops 8-24% (Table 2). In general, the areas with highest probability of occurrence in the year 2100 are the southern quadrant and along the eastern edge of the island. SSP5-8.5 has the strongest negative impacts on probability of Zanzibar red colobus occurrence at the year 2100.

SSP	2011-2040	2041-2070	2071-2100
1-2.6	0 - 84	0 - 98	0 - 79
3-7.0	0 - 87	0 - 76	0 - 90
5-8.5	0 - 89	0 - 86	0 - 74

Suitability range for 1981–2010: 0-98%

Table 2: Ranges of probability of Zanzibar red colobus occurrence for all climate change scenarios.

Range Shifts

Depending on the climate change scenario, the projections predict anywhere from a 20 – 36% loss of current Zanzibar red colobus range by the end of the century (Table 3). In general, the projections show a restriction along the northern and western edges of the current colobus range, with areas of high probability shifting southwards.

	Percent Lost	Percent Gained	Species Range Change
1-2.6	53	26	-27
3-7.0	42	21	-21
5-8.5	53	17	-36

Table 3: Range changes (in percent lost or gained) for Zanzibar red colobus at the end of the century.

Based on the model for the current time period, probability of occurrence for red colobus within the current red colobus stronghold (Jozani-Chwaka Bay National Park) ranges from 39%

to 96%, with the majority of the park having probabilities well over 75%. By the end of the century, overall probability of occurrence within Jozani-Chwaka Bay National Park drops across all scenarios (Table 4). In addition, the spread in probability of occurrence shrinks for all scenarios, suggesting there may be lower levels of spatial differentiation in Jozani-Chwaka Bay National Park's habitat quality in the future. In all three climate change scenarios, Jambiani-Muyuni Forest Reserve, a proposed protected area to the south of Jozani, displays higher overall probability of occurrence at the end of the century.

SSP	2071-2100
1-2.6	33 - 60
3-7.0	27 - 56
5-8.5	23 - 54

Table 4: Ranges of probability of Zanzibar red colobus occurrence within the boundaries of Jozani-Chwaka Bay National Park at the end of the century.

Mechanistic model - EcoCrop

Results for crops were examined in three ways: all 30 crops were examined individually, similar crops were grouped into classes (e.g., all annual fruits and vegetables), and all crops were examined together. Maps and suitability range tables for each individual crop and crop class can be found in the appendix, however here we mostly highlight unique spatial patterns or high reductions in suitability.

All 30 crops have the potential for cultivation across Unguja through the end of the century under all climate change scenarios (Table 5). Most crops display a moderate to high range of suitability under all scenarios (50-100%), with the lowest suitability range of any crop class being 13-24% (pseudocereals; SSP 5-8.5, 2071-2100).

Crop	2011-2040	2041-2070	2071-2100
<i>All Crops</i>			
SSP1-2.6	91-95	90-95	90-94
SSP3-7.0	91-95	87-93	82-89
SSP5-8.5	90-95	86-93	78-87
<i>Beans & Pulses</i>			
SSP1-2.6	93-100	92-100	94-99
SSP3-7.0	92-99	94-100	96-99
SSP5-8.5	95-100	94-100	94-99
<i>Annual Cash</i>			
SSP1-2.6	71-100	74-100	75-100
SSP3-7.0	76-100	62-100	60-100
SSP5-8.5	70-100	63-100	60-100
<i>Permanent Cash</i>			
SSP1-2.6	99-100	100	99-100
SSP3-7.0	100	96-100	97-100
SSP5-8.5	95-100	97-100	96-100
<i>Cereals</i>			
SSP1-2.6	87-96	87-98	87-97
SSP3-7.0	87-97	86-96	85-93
SSP5-8.5	87-96	85-97	93-93
<i>Annual Fruits & Vegetables</i>			
SSP1-2.6	89-97	88-96	89-96
SSP3-7.0	90-97	84-94	79-89
SSP5-8.5	90-97	84-93	73-86
<i>Permanent Fruit</i>			
SSP1-2.6	93-99	93-100	92-99
SSP3-7.0	93-100	94-99	91-97
SSP5-8.5	93-98	95-99	87-95
<i>Pseudocereals</i>			
SSP1-2.6	40-50	34-45	34-46
SSP3-7.0	39-48	28-40	18-30
SSP5-8.5	39-49	26-38	13-24
<i>Roots & Tubers</i>			
SSP1-2.6	96-99	95-98	95-98
SSP3-7.0	96-99	94-97	85-93
SSP5-8.5	96-99	92-96	80-88
<i>Spices & Herbs</i>			
SSP1-2.6	82-91	76-87	75-87
SSP3-7.0	81-90	63-80	40-60
SSP5-8.5	83-90	58-78	31-49

Table 5: Percent suitability range across Zanzibar for crop classes. Suitability ranges for each individual crop can be found in the appendix.

For the majority of crops, suitability can be described as ‘flat’ across Unguja. By this, we mean that the minimum and maximum in the range of suitability is usually separated by less than 20%. There are spatially structured suitability patterns which may be helpful when deciding between crops for cultivation in a given area. Crop classes beans and pulses, permanent cash, and permanent fruit all maintain very high levels of suitability across the island at the end of the century (beans and pulses: 94-99%; permanent cash: 96-100%; permanent fruit: 87-99%). Roots and tubers, and fruits and vegetables have slightly lower, but still robust, suitability ranges under their worst scenario at 2100 (roots and tubers: 80 – 88%; fruits and vegetables: 73-80%). Pseudocereals and spices and herbs see large decreases in suitability, and under their worst scenarios at 2100 have very low overall suitability ranges (pseudocereals: 13-24%; spices and herbs: 31-49%) (Figures 4-5).

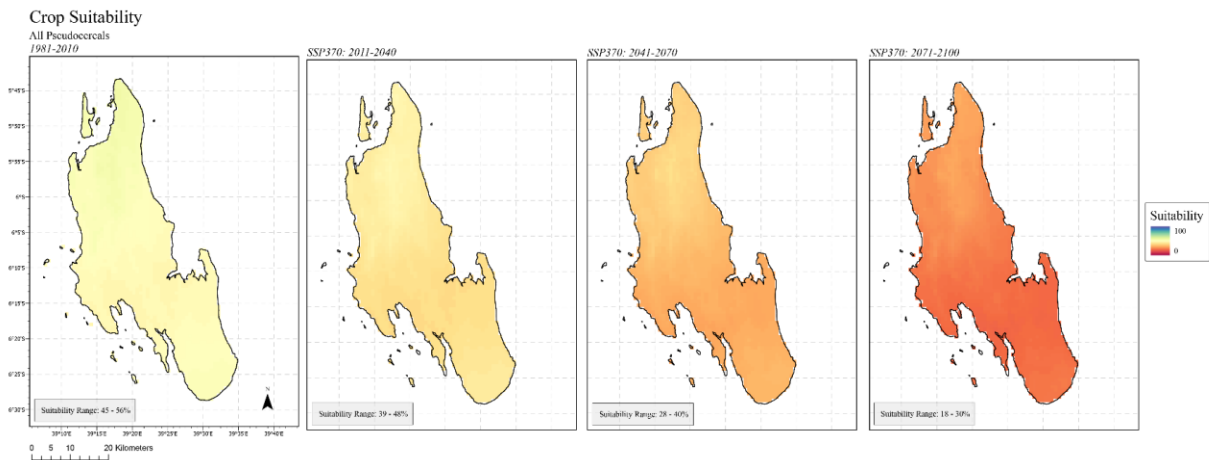


Figure 4: Suitability of all pseudocereals through the end of the century under SSP 3-7.0.

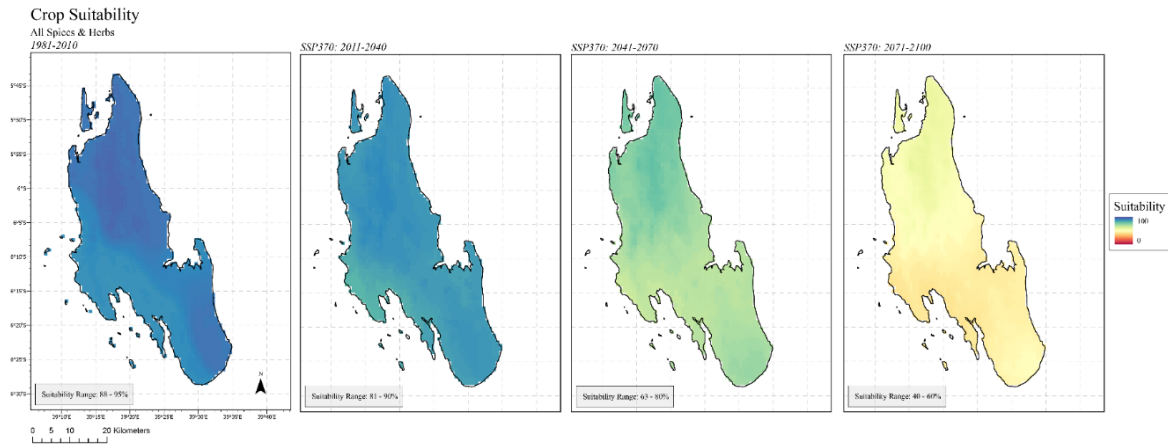


Figure 5: Suitability of all spices and herbs through the end of the century under SSP 3-7.0.

By class, there is not much spatial structuring, but when it is present, the lower end of suitability is overwhelmingly in the southern half of the island. For the majority of crop classes, suitability is similarly flat across the island. The one exception is the ‘all cash’ crops class. This class only has a single crop in it, sugarcane (muwa), which shows restrictions in suitability on the western edge and southern quadrant of the island towards the end of the century and has a range of suitability of 60-100% under both SSPs 3-7.0 and 5-8.5 (Figure 6).

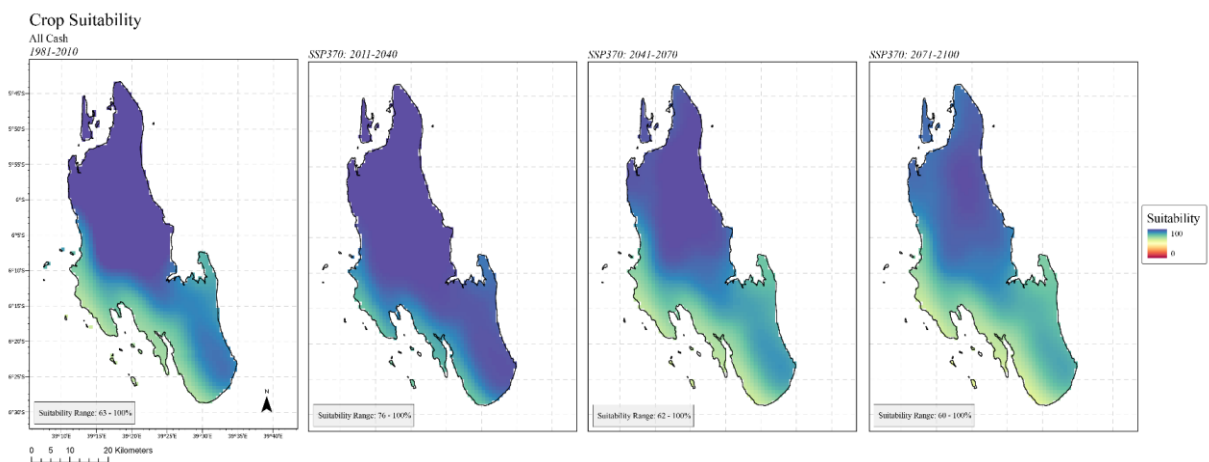


Figure 6: Suitability of all annual cash crops through the end of the century under SSPs 3-7.0.

In terms of individual crops, results pertaining to cocoyam, amaranths, and paddy rice are worth highlighting. Cocoyam (Nduma; *Xanthosoma Sagittifolium*) is the world’s sixth most

important root and tuber crop and is widely grown across West and Central Africa. Previous studies have emphasized cocoyam as an underutilized cultivar for addressing food security in Africa (Boakye et al., 2018; Chemura et al., 2022; Adiele, 2023). However, cocoyam was one of the crops our study discarded, as 26% of our models for this crop failed (i.e., there was 0% suitability for certain areas of the island). Ecological niche and climate projection modeling for cocoyam suitability in Zimbabwe has also shown very restricted suitability for cocoyam under climate change (Chemura et al., 2022). From our modeling, cocoyam does not seem to be an appropriate crop to invest effort in cultivating at scale for Zanzibar, especially with food security as a goal.

Similarly, cultivating members of genus *Amaranthus* has been suggested as a path to improve food security and reduce malnutrition despite climate change, given their nutrient-dense and drought-resistant qualities (Gelaye, 2023; Mukuwapasi et al., 2024; Yadav & Yadav, 2024; Omotayo et al., 2025). Certain amaranth (mchicha wa kisasa) varieties, also known as pseudocereals, are already cultivated in Africa, but productivity of these crops is very low (*A. cruentus*, *A. blitum*, *A. dubius*) (Gelaye, 2023). In our study, we ran models for *A. dubius* and *A. hypochondriacus*, but *A. dubius* was dropped as 8% of the models failed due to precipitation needs. The amaranth we kept in our study ended up being the crop with the lowest ranges of suitability. Amaranths, like cocoyam, do not seem to be a singularly advisable avenue for strengthening food security in the face of climate change for Zanzibar.

Lastly, as previously mentioned, paddy rice is a crucially important crop on Zanzibar, both in terms of the agricultural economy and food security. Paddy rice (mpunga; *Oryza sativa* L.) is a semiaquatic crop, grown on a flooded field of arable land, making it sensitive to changes in rainfall where additional irrigation input is not present. For this reason, there has already been

considerable discussion about the potential for climate change to dramatically impact production of rice in areas with low levels of agricultural technology and infrastructure. One cost-effective approach is to disperse WDR (water-saving, drought-resistant) varieties of rice, as Zanzibar has begun to do with WDR-70 (Luo, 2010; Zhang et al., 2021; Onyango, 2024). We found that even more drought-resistant varieties of rice may have quite low suitability in certain parts of the island under all scenarios. The overall ranges of suitability for paddy rice are wider than most other crops, with up to a 52% difference in suitability in different regions of the island (Table 6). The northeastern quadrant of the island retains the highest levels of suitability for paddy rice, while the western edge of suitable areas pushes east over the century (Figure 7).

	2011-2040	2041-2070	2070-2100
126	45 - 96	50 - 99	47 - 96
370	49 - 99	38 - 90	44 - 90
585	44 - 93	40 - 93	37 - 79

Suitability range for 1981–2010: 40-100%

Table 6: Suitability of WDR paddy rice (mpunga; *Oryza sativa L.*) for Zanzibar.

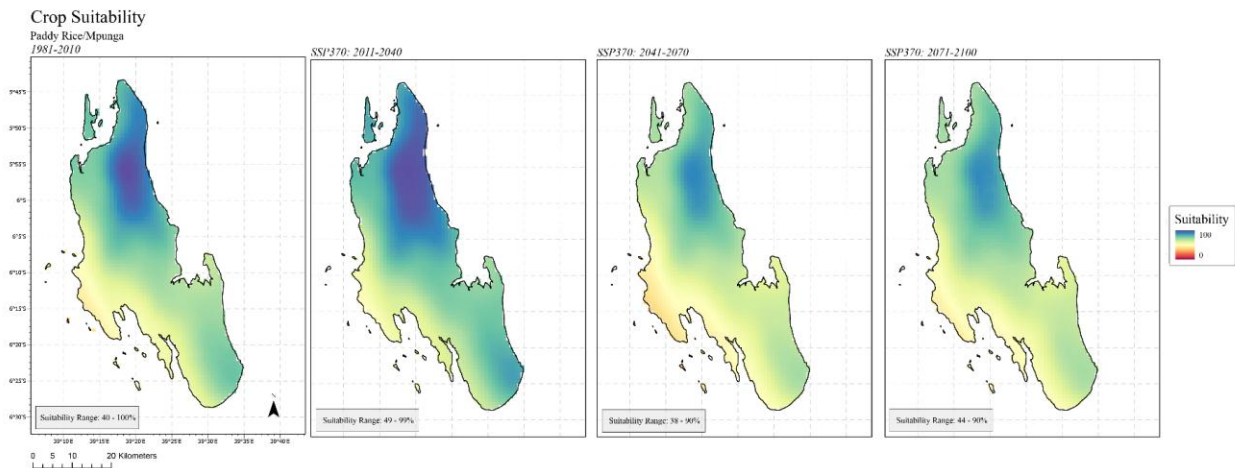


Figure 7: Suitability of paddy rice (mpunga) through the end of the century under SSP 3-7.0.

Below are maps for a few additional individuals crops in which we either saw a reduction of suitability >20%, or signs of spatial structuring across the island. These crops include cabbage (kabichi), cassava (muhogo), kothmir or coriander (giligilani), sweet potato (kiazi kitamu), tomato (mnyanya), and turmeric (manjano) (Figures 8-12).

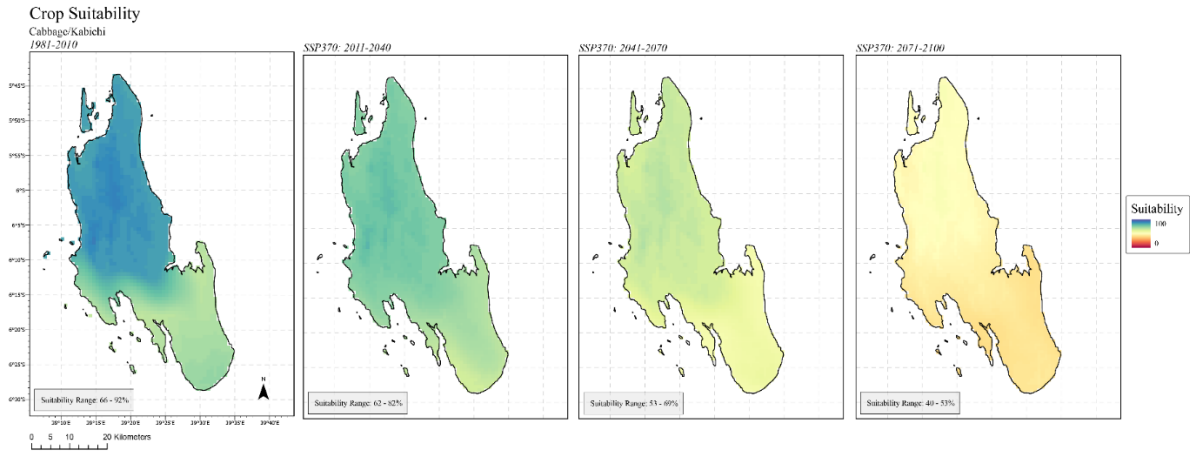


Figure 8: Suitability of cabbage (kabichi) through the end of the century under SSP 3-7.0.

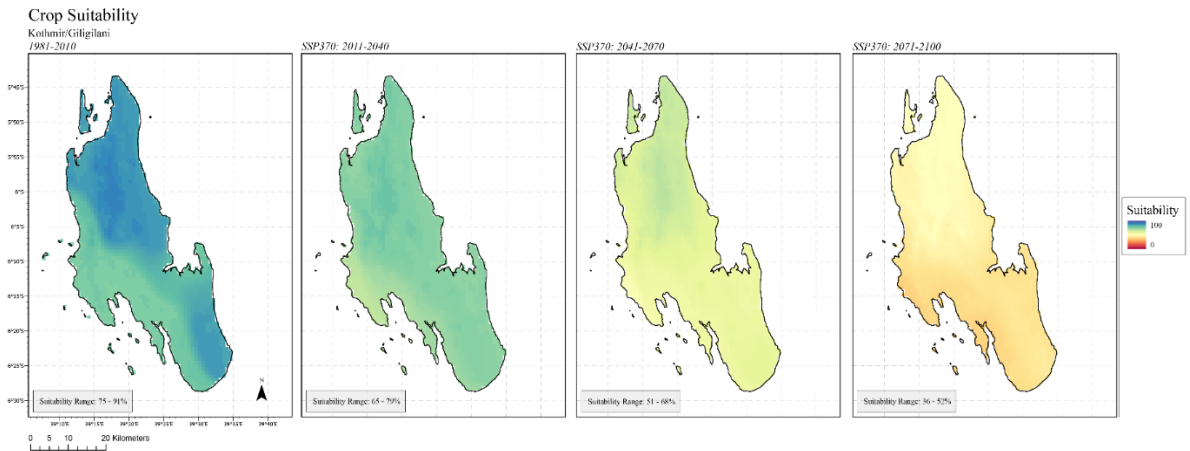


Figure 9: Suitability of kothmir (giligilani) through the end of the century under SSP 3-7.0.

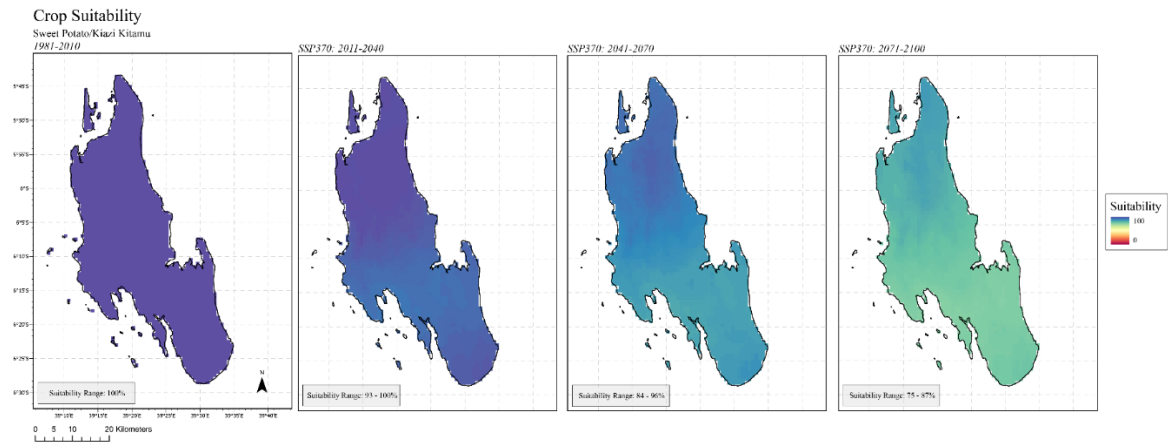


Figure 10: Suitability of sweet potato (kiazi kitamu) through the end of the century under SSP 3-7.0.

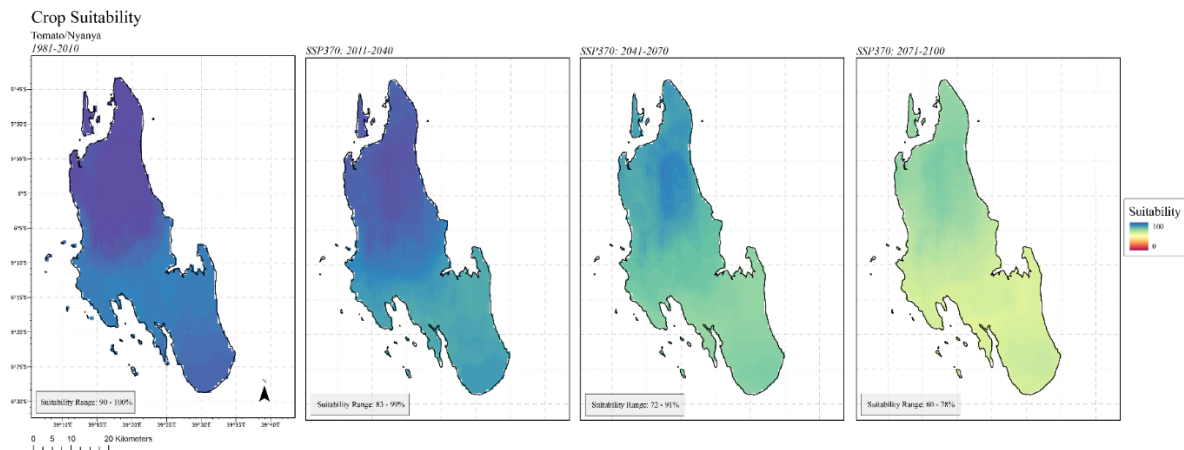


Figure 11: Suitability of tomato (mnyanya) through the end of the century under SSP 3-7.0.

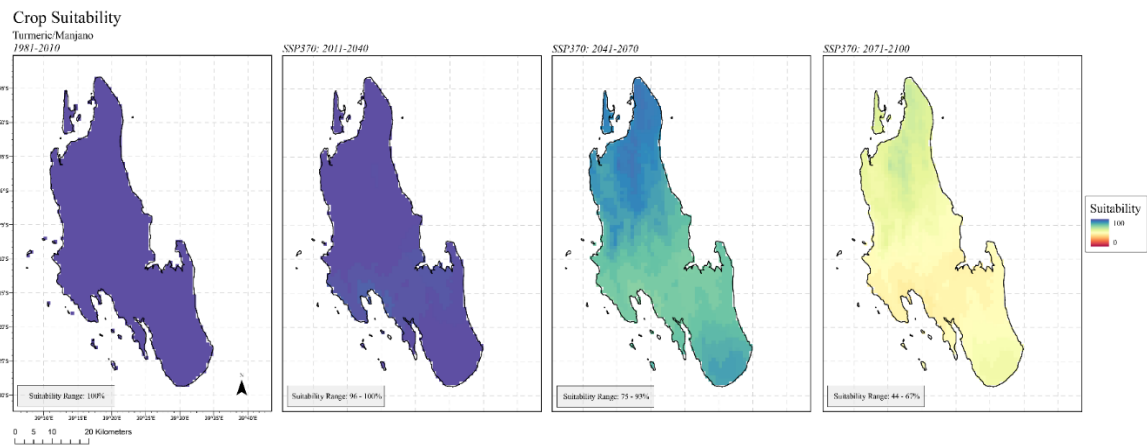


Figure 12: Suitability of turmeric (manjano) through the end of the century under SSP 3-7.0.

Human Wildlife Interaction Potential Mapping

Human-wildlife interactions mediated by subsistence and smallholder agriculture are primarily structured by the range of Zanzibar red colobus. This is because suitability ranges for crop classes do not vary much across the island (often less than 20%). For all climate scenarios and time steps, when all 30 crops are considered together, there are no areas of low human-wildlife interaction, only areas of either moderate or high human-wildlife interaction. HWI is primarily focused on the southern half and eastern edge of the island. As we move towards the end of the century, HWI becomes most concentrated on the southern tip for all SSPs, as well as much of the eastern coastline. Areas where the index reflects high HWI are areas where both probability of red colobus and crop suitability are highest (Zanzibar red colobus >80%; crop suitability >75%). The spatial pattern of HWI for some crop classes differs from the full suite of crops taken together. These differences are caused by lower overall suitability ranges for these crop classes (Figure 13).

Unsurprisingly, the general pattern found in our HWI mapping is that high levels of human-colobus interactions mediated by agriculture decrease towards the end of the century, as probability for red colobus occurrence decreases across the island (Table 7). It is important to note that these findings reflect potential for HWI depending on land-use practices, not necessarily any kind of definitive likelihood. However, potential exists for moderate to high levels of HWI mediated by agriculture to the end of the century under all three SSPs.

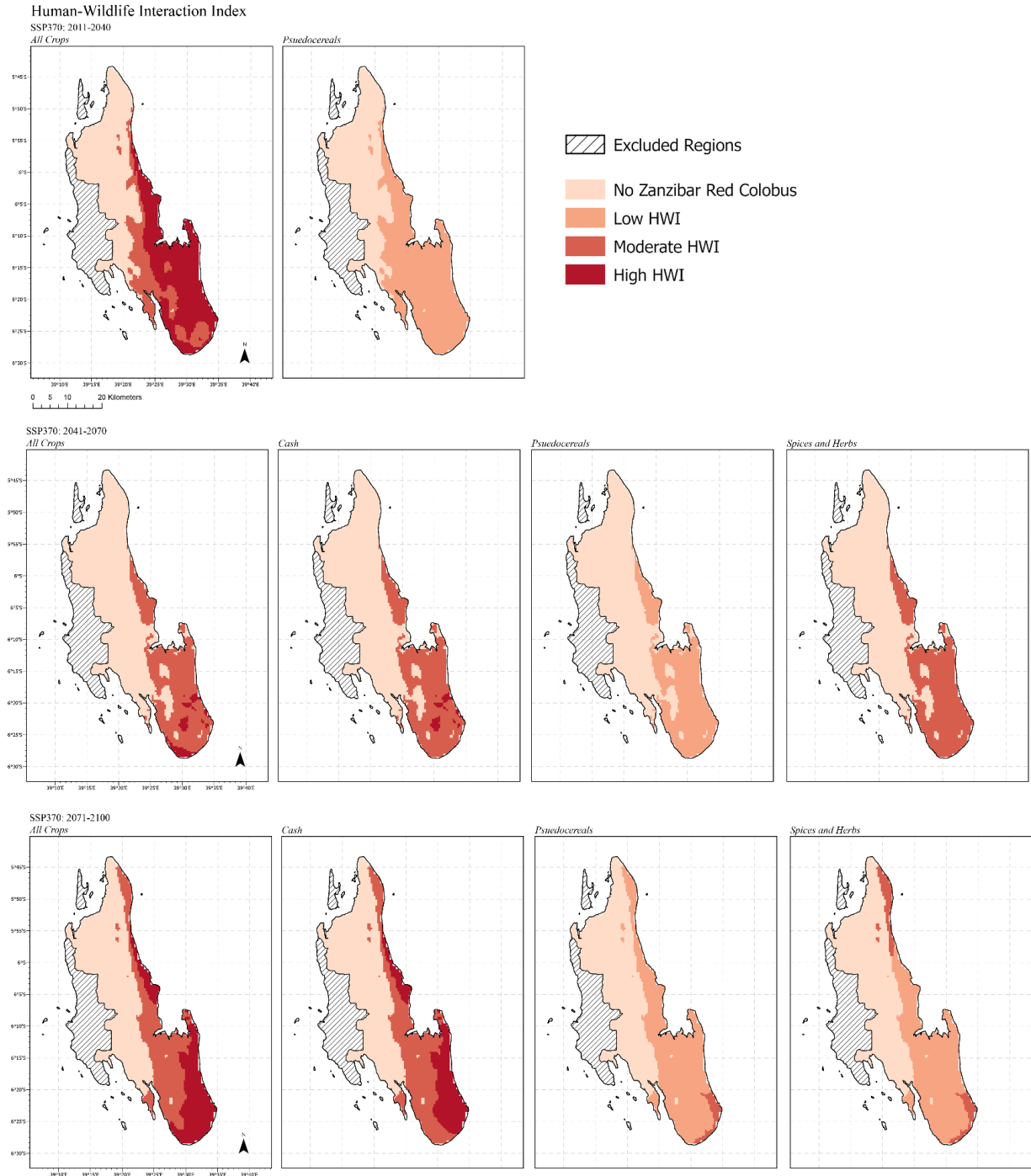


Figure 13: Potential for human-wildlife interaction with red colobus as mediated by agriculture is moderate to high for most crop classes across the southern quadrant and eastern edge of the island. This map is for SSP3.7-0 to the end of the century. The full suite of crops is used for every time period, but we have also pulled out crop sub-classes which have patterns differing from the full suite of crops. HWI indices for SSPs 1-2.6 and 5-8.5 can be found in the supplement.

	Moderate HWI	High HWI
SSP126		
2011-2040	61	39
2041-2070	26	74
2071-2100	84	16
SSP370		
2011-2040	35	65
2041-2070	91	9
2071-2100	59	41
SSP585		
2011-2040	41	59
2041-2070	53	47
2071-2100	97	3

Table 7: Percent of total Zanzibar Red Colobus range which may experience either moderate or high levels of human-wildlife interaction mediated by agriculture. The percent range likely to experience moderate levels of HWI increases towards the end of the century, while high levels decrease, due to the decrease in overall probability of occurrence of Zanzibar red colobus. These calculations utilize the full suite of crops explored in this study. There are subtle differences when crops are examined individually (some crops are less likely to mediate HWI), but these numbers reflect the general patterns seen among the suite of crops.

Discussion

Zanzibar red colobus range and occurrence decrease under climate change

Ecological niche and climate modeling were carried out to explore the potential impacts of climate change on the long-term viability of the endangered Zanzibar red colobus. The overall results of this study reflect a general decline in both probability of occurrence and overall range size for the Zanzibar red colobus.

The GLM results suggest that Zanzibar red colobus may face up to a 36% reduction in their total range. With an estimated EOO (extent of occupancy) of 428 km² in 2019, that could leave the species with only 274 km² of their current range (Davenport et al., 2019). If we assume that Zanzibar red colobus density stays roughly the same as recorded in 2019 (13.7 colobus per km²), this could result in a significant loss of the species by the end of the century. This population decline is only representative of changes brought on by climate and does not account

for the additional anthropogenic pressures, which are likely to create a feedback loop of negative impacts on the Zanzibar red colobus. At present, about 31% of the population lives outside of protected areas and many of the groups making up this proportion of the population are isolated due to a lack of habitat connectivity across the island (Davenport et al., 2019). This is in large part due to the historic clearing of land for agriculture, but also to the continued growth of residential areas and other economic sectors, such as tourism. Zanzibar red colobus groups living in coastal areas, especially in the east, are in a particularly tough spot as they are confined by agriculture to the west and losing more of the eastern edges of what forest is left to hotel development along the coastal beaches (Davenport et al., 2019). It stands to reason that the loss of habitat is much more likely to lead to the loss of these groups before climate change, but in the event small pockets of forest remain, these groups will likely be extirpated via the inability to disperse into other groups for reproduction and the intensified effects of climate change in a fragment. Forest fragments are not only more prone to stochastic weather and natural disaster events, but also to the impacts of climate change writ large. Fragments may, for example, experience constraints on precipitation due to lost evapotranspiration potential and increased temperatures at higher strata due to the increase in forest edges (Malcom, 1998; Laurance & Williamson, 2001; Laurance, 2004).

It's important to note that when considering range restrictions these models leave out a crucial impact of climate change, sea level rise. As previously noted, the island of Unguja sits at essentially sea level except for a small area inland which reaches an elevation of 110m. There are a number of red colobus groups that reside in low-lying mangrove and coastal areas, who will almost certainly lose habitat and experience range shifts due to sea level rise and reduced productivity of mangroves (Davenport et al., 2019). Current estimates for Zanzibar have sea

level rising anywhere from 0.45 – 0.80m by 2100, and numerous studies have demonstrated that sea level rise is likely to lead to high levels of mangrove die-off on tropical coastlines (Saintilan et al., 2020; Fox-Kemper et al., 2021; Garner et al., 2021; Kopp et al., 2023; Carruthers et al., 2024). High emissions scenarios could lead to die-offs in tropical systems within 30 years (Saintilan et al., 2023). With this in mind, Zanzibar red colobus in mangrove areas could either be forced inland or extirpated within the century.

It's difficult to know the degree of impact the declines our projections display might have on the colobus population. However, we expect that both the quantity and quality of food sources for primates will be impacted by climate change; this will be problematic for species with highly specialized diets, such as folivores, due to their lowered flexibility and potential for dietary adaptation (Visser & Both, 2005; Richardson et al., 2013; Becklin et al., 2016; Inouye, 2022). In addition, time-budget models have indicated that rising temperatures lead to folivorous primates needing to rest more, leading to less time spent on foraging. The full picture is then that rising temperatures associated with climate change could create intense pressure directly related to decreases in energy-intake and nutrition for red colobus (Korstjens et al., 2010; Korstjens, 2019; Korstjens & Dunbar, 2007).

The Zanzibar red colobus population is already thought to be in decline across its extent based on low recruitment and survivorship rates (Davenport et al., 2019). If we consider their already low reproductive rates, and the potential impacts of poor diet, weakening of social bonds, increases in disease and human-wildlife conflict due to climate change, we can quickly imagine a future in which the Zanzibar red colobus population tips into the critically endangered category. Over the remainder of this century, active management of the Zanzibar red colobus, as well as

climate mitigation at the local and global levels, will be crucial to keeping the population viable in the long-term.

Many, but not all, crops retain high levels of suitability under climate change

The results from our crop modeling indicate that, overall, the chosen suite of crops should continue to have moderate to high ranges of suitability across the island to the end of the century under all climate change scenarios. These results leave us hopeful that there is room for agricultural economic growth, especially in the smallholder sector, in Zanzibar's future. There are, however, some caveats.

Results pertaining to cocoyam and amaranth highlight that investment in cultivation of crops thought to be more climate resilient is not always an assured avenue to increase food security in the face of climate change. While these crops may have ecological growth parameters which make them generally more tolerant to climatic shifts, they may still be mismatched with the environment of a given area. Cocoyam and amaranth may be helpful for reinforcing food security in other regions of Africa, but they do not appear to be useful as climate-resilient crops for Zanzibar.

The government's investment in rolling out drought-resistant rice varieties is a worthy endeavor for strengthening food security and livelihoods, but even these varieties may struggle in the southern region of the island. Generating the infrastructure necessary for additional irrigation will likely be too high of a barrier for most subsistence and smallholder farms, so to avoid dietary and nutritional gaps, it may be worthwhile to grow additional grains or starches in quantities which can cover any reduction in rice production or yield.

It's very important to note that our models do not include additional factors which can influence crop suitability and productivity. Climate change can lead to reduced soil moisture, reduction in soil fertility, soil erosion, and alterations to microbial activity in the soil. These changes to soil alone could have massive implications for cultivation and crop yields, particularly in Zanzibar's coral rag vegetation heavy landscape, where less fertile soils are already common (Davenport et al., 2019; Malhi et al., 2021).

Agricultural mitigation and adaptation to climate change can take many forms, but for subsistence and smallholder farmers, employing agroecological management systems are likely to be some of the most accessible and beneficial. This includes diversifying the portfolio of crops cultivated and avoiding monocropping schemes, soil management practices, and water harvesting (Lal et al., 2011). These practices can assist in creating more resilient soil, better ensuring both food security and the nutritional quality of crops. Agronomic adjustments, like the adjustment of sowing dates, will likely also be crucial to creating resilient and productive small-scale cropping under climate change (Malhi et al., 2021).

The southern region of the island will likely face coastal erosion, increasing soil salinity, and likely inundation of mangroves, creating a challenging cultivation environment for both inland and coastal farming practices. Most seaweed cultivation and aquaculture is practiced along the southern coastline, and seaweed farming is one of the few economic sectors dominated by women in Zanzibar (Charisiadou et al., 2022). Seaweed farming has already been dramatically reduced in some areas due to warming ocean temperatures and disease, and this is likely to worsen without adaptation and climate mitigation (Msuya, 2014). Inland, most landholders in Zanzibar have somewhere between 1 to 6 acres, so even small decreases in agricultural productivity could spell trouble for subsistence and smallholder farmers (Singer,

1996; National Bureau of Statistics, 2021a). Farmers in this region will likely be impacted by additional stressors, as they are most likely to be dealing with increased red colobus interactions.

HWI is primarily spatially structured by Zanzibar red colobus occurrence

This research is a first step towards building strategies to contend with the wicked problem of overlapping biodiversity and food insecurity. As mentioned previously, decreases in agricultural productivity due to climate change are likely to result in agricultural intensification and expansion, putting biodiversity at risk, and generating additional conflict between biodiversity conservation and food security efforts. There has been increased discussion over the last two decades about two specific ways to respond to these tensions: with either ‘land-sparing’ (strictly separated areas of intensive agriculture and protected natural habitat in a landscape) or ‘land-sharing’ (mosaic landscapes, with low-intensity and wildlife-friendly agriculture) approaches (Kremen and Merenlender 2018; Sidemo-Holm et al 2021). However, empirical evidence for both approaches is still thin, and it is not clear that one paradigm provides a better solution than the other, writ large (Augustiny et al 2025). Instead, the evidence points to the need for context-specific solutions. By generating localized data, as we do in this study, we can develop system and context-specific responses, which are more likely to be effective.

Our results indicate that human-colobus interactions, specifically crop-raiding, will be primarily structured by the presence of colobus, as opposed to being driven by strong spatial structuring of crop suitability in the landscape. If we had found there to be areas where HWI was predicted to be low, with moderate-high red colobus occurrence and low crop suitability, we may have targeted those areas as important places to invest in red colobus conservation with a decreased risk of impacting local agricultural livelihoods. However, since HWI levels are

predicted to be moderate-high across the red colobus range, and suitability for many crops remains moderate-high across the landscape, it seems our best path forward is to generate ‘land sharing’ conservation plans for red colobus that prioritize areas of high red colobus occurrence, while outlining response strategies to HWI and building capacity for increasing food security where possible. One potential avenue for increasing food security in systems where biodiversity and agricultural production overlap follows our research, generating data on crops in areas experiencing HWI which will remain productive under climate change. This enables agricultural planning which increases resilience in livelihoods to climate change and potentially reduces the amount of risk introduced by crop-raiding owing to higher levels of productivity than might otherwise be achieved with less climate resilient crops.

In order to properly outline response strategies to HWI, specifically crop-raiding, we need a thorough understanding of the current breadth of Zanzibar red colobus diet, with a specific focus on agricultural species, and any preferred versus non-preferred crops. In an ideal world, we would integrate climate-resilient cropping systems (FAO 2019; Reckling et al 2023) with those that reduce impacts by wildlife (Matsika et al 2020; Matsika et al 2023) as part of the same conservation action. However, identifying adaptation strategies which both reduce impacts by wildlife and build climate resilience can be difficult. For example, while a common crop-raiding mitigation strategy is to switch to less susceptible or even deterrent crops, this approach often leads to reduced agricultural diversity, which is generally not good for soils, can lead to dietary deficits, and tends to leave livelihoods more exposed to climate risk (McGuinness & Taylor 2014). In Zanzibar, it may be useful to test direct intervention methods, like nets for fruit trees (Campbell-Smith et al 2012) or surrounding preferred crops with non-preferred crops (Matsika et al 2020; Matsika et al 2023). Most of these methods have yet to be tested thoroughly

as interventions for primate crop-raiding (Wszelaki 2024), and the benefits may be minor in a landscape as heterogeneous as the one on Zanzibar, but it is worth exploring these additional mitigation avenues as compensation schemes for crop-raiding losses generally do not cover all associated costs or leave people dissatisfied (Umuziranenge 2019; Baral et al 2021). In addition, the impacts of crop-raiding on people's lives have other less obvious knock-on effects, which introduce risk to livelihoods and cannot be properly addressed by compensation schemes. This includes lowered mental and physical health, with heightened levels of stress and anxiety and adoption of risky behaviors such as guarding crops at night (Galley & Anthony 2024).

In Zanzibar, if food insecurity increases due to climate change, this could be dangerous for the long-term viability of the red colobus population. Negative perceptions of primates are known to drive retaliatory killings and lethal control methods (Hill 2018; (Korstjens et al 2022). When we consider the interplay between climate change and increased negative human-wildlife interactions, Davenport et al's (2019) assertion that the 31% of red colobus living outside protected areas "will not survive in the long term" due to habitat loss seems even more likely. Securing the long-term viability of the Zanzibar red colobus population under the conditions our results have produced is more likely to be successful if additional resilience can be built into human agricultural livelihoods.

Conservation recommendations

- 1) Managing the Zanzibar red colobus population for long-term viability may require an expansion of, or at least bolstering, of the protected areas in the southern region. Jozani-Chwaka Bay National Park, which is where just over half of the current population resides, is projected to experience a decline in probability of occurrence under all

scenarios by the end of the century (Davenport et al., 2019; Korstjens et al., 2022).

Jozani-Chwaka Bay National Park is currently where most resources for Zanzibar red colobus conservation are allocated, and our models suggest it may be prudent to invest some of these resources in protected areas further south, or in studying and ensuring dispersal corridors for colobus between Jozani-Chwaka Bay National Park and other groups in the southern region of the island. There have been recent proposed investments in Jambiani-Muyuni Forest Reserve for conservation and sustainable development purposes, and our work suggests this would be a prudent investment for red colobus conservation, in particular.

- 2) Generating longitudinal datasets concerning red colobus crop-raiding could also prove to be highly beneficial to conservation planning. With accurate knowledge of what crops colobus preferentially choose, specific cultivation schemes which grow choice and non-choice crops side-by-side could be developed to reduce the impacts of red colobus offtake. It would also be advantageous for decision-makers to have concrete data on the rates at which red colobus are engaging in crop raiding versus sympatric Sykes' monkeys (*Cercopithecus mitis albogularis*). It may also be advantageous to invest time in trialing primate crop-raiding intervention methods. In the case of Zanzibar red colobus, tree nets for fruit trees may be a good starting point, as previous studies have noted farmers perceive Zanzibar red colobus to have negative impacts on this particular crop type (Siex & Struhsaker, 1999).

- 3) While agricultural productivity is lower in the Southern district than in others in Zanzibar, plenty of households still rely on subsistence and smallholder agriculture (Office of the Chief Government Statistician, 2012). Based on our results, we can offer some crop-specific recommendations for better productivity under climate change in the Southern district. With regard to grains, households in the Southern district will likely be better served by investing in maize than paddy rice. Similarly, for roots and tubers, yams are projected to perform better under climate change than casava or sweet potato. Economic reliance purely on spices and herbs is something we would dissuade, as these crop types are projected to decrease substantially in suitability. While permanent fruit crops, like mango trees, are projected to do well in the Southern district, we would caution that these crops may be more likely to be targeted by arboreal primates for crop-raiding.
- 4) The risk-management strategies the government has already begun to deploy to create climate-smart agriculture are a strong step towards generating stability in subsistence and smallholder livelihoods. We believe this could be strengthened even further by better integration of formal and informal agricultural systems. Combining locally bred climate-tolerant seeds with bred strains can increase resilience, as can data-informed cropping schemes. These cropping schemes are ideally comprised of crops which perform well under climate change, provide the cultivation diversity needed to maintain healthy soils, and ensure necessary dietary and nutritional requirements can be met. Our hope is that additional resilience from climate-smart agricultural approaches will confer enough stability in human agricultural livelihoods that offtake from colobus crop-raiding will

have minimal impacts on overall productivity and yield. The desired downstream impact is that perceptions of colobus may improve, or at the very least not worsen. In this way, climate-smart agricultural approaches may offer a ‘buffer’ to increased pressure from human-wildlife interactions under climate change.

- 5) In regions where biodiversity conservation and food security constitute a wicked problem for conservation, we require tools to examine local patterns and processes so that we can generate data necessary for long-term, localized conservation planning. This research provides an example of how HWI patterns under climate change can be studied at localized scales, but it is only a first step. In regions where ‘land sharing’ between wildlife and people is necessary, conservation efforts can be strengthened by assessing which crops will remain productive under climate change in small-scale agricultural livelihoods as a way to buffer the impacts of crop-raiding.

Muhtasari wa Matokeo ya Sura ya Tatu

Matokeo - Uwepo wa kima punju na eneo lao wakati wa Mabadiliko ya Tabianchi

Makadirio ya hali ya hewa yanaonyesha, kwa kiasi kikubwa, kupungua kwa uwezekano wa kuwepo kima punju wekundu wa Zanzibar katika matukio yote matatu ya mipangilio ya mabadiliko ya tabianchi (SSP1-2.6, 3-7.0, 5-8.5; SSP = Njia za Pamoja za Maendeleo ya Kijamii na Kiuchumi). Ikilinganishwa nakiasi cha sasa cha modeli (1981-2010), uwezekano mkubwa wa kuwepo kwa kima punju wekundu wa Zanzibar unapungua kwa asilimia 8-24 (Jedwali la 2, katika sura yenyewe). Maeneo yenye uwezekano mkubwa wa kuwepo kima mnamo mwaka

2100 ni wilaya ya Kusini kwenye ukingo wa mashariki wa kisiwa hicho. SSP5-8.5 ina athari mbaya zaidi kwenye uwezekano wa kutokea kwa kima punju Zanzibar.

Makadirio yanatabiri upotevu wa 20 - 36% wa eneo la kuishi la sasa kwa kima punju kufikia mwisho wa karne (Jedwali la 3, katika sura yenyewe). Makadirio hayo yanaonyesha upotevu huo kando ya kingo za kaskazini na magharibi ya eneo la sasa wanakoishi kima punju, huku maeneo yenye uwezekano mkubwawa kuwepo kima punju yakiwa kusini.

Uwezekano wa kuwepo kwa kima punju ndani ya sehemu walimokaa kwa muda mrefu (Hifadhi ya Kitaifa ya Jozani-Chwaka Bay) hupunguka katika hali zote za mabadiliko ya tabianchi (Jedwali 4, katika sura yenyewe). upanuzi wa uwezekano wa kuwepo hupunguka katika hali zote za uwezekano, ikidokeza kwamba kuna uwezo kuwa na viwango vya chini vya utofauti wa ubora wa makazi katika Hifadhi ya Kitaifa ya Jozani-Chwaka Bay katika siku zijazo. Katika matukio yote matatu ya hali za mabadiliko ya tabianchi, Hifadhi ya Msitu ya Jambiani-Muyuni, inaonyesha uwezekano mkubwa wa kuwepo kima punju mwishoni mwa karne.

Matokeo - Mazao ya Kujikimu kwa Wakulima Wadogo nyakati za Mabadiliko ya Tabianchi

Ramani na jedwali za upeo wa kufaa kwa mazao yote na aina zote za mazao ziko kwenye kiambatisho. Mazao mengi yanaonyesha kiwango cha wastani hadi cha juu cha kufaa chini ya hali zote (50-100%), huku kiwango cha chini kabisa cha kufaa cha aina yoyote ya mazao kikiwa 13-24% (nafaka bandia; SSP 5-8.5, 2071-2100).

Kwa mazao mengi, ufaafu unaweza kuelezewa kama 'bapa' kote Unguja. Kwa hili, tunamaanisha kwamba kiwango cha chini na cha juu zaidi katika upeo wa kufaa kinatenganishwa na chini ya asilimia 20. Kwa makundi ya mazao maharagwe na kunde, pesa taslimu ya kudumu, na matunda ya kudumu yote yana viwango vya juu sana vya ufaafu kote

kisiwani mwishoni mwa karne (maharagwe na kunde: 94-99%; pesa taslimu ya kudumu: 96-100%; matunda ya kudumu: 87-99%). Mizizi, viazi, na matunda na mboga mboga yana kiwango cha chini kidogo, lakini bado imara, cha ufaafu chini ya hali mbaya zaidi ifikapo mwaka 2100 (mizizi: 80 - 88%; matunda na mboga mboga: 73-80%). Nafaka bandia, na viungo na mimea, huona kupungua kwa ufaafu mkubwa, na chini ya hali mbaya zaidi mnamo 2100 zina viwango vya chini sana vya ufaafu kwa jumla (nafaka bandia: 13-24%; viungo na mimea: 31-49%) (takwimu 4-5, katika maandishi kuu ya sura).

Matokeo ya nduma, mchicha wa kisasa, na mpunga yanafaa kuangaziwa. Tafiti za awali zimesisitiza nduma kama isiyotumika kikamilifu kushughulikia usalama wa chakula barani Afrika (Boakye et al., 2018; Chemura et al., 2022; Adiele 2023). Hata hivyo, nduma ilikuwa moja ya mazao ambayo utafiti wetu ulitupilia mbali, kwani 26% ya modeli zetu za zao hili hazikufaulu (yaani, kulikuwa na ufaafu wa 0% kwa maeneo fulani ya kisiwa). Kutokana na modeli zetu, nduma haionekani kuwa na thamani ya uwekezaji mkubwa kwa Zanzibar, hasa kwa lengo la usalama wa chakula.

Kupanda mchicha wa kisasa kumependekezwa kwa kuboresha usalama wa chakula na kupunguza utapiamlo licha ya mabadiliko ya hali ya hewa, kutokana na sifa zake za virutubisho vingi na kustahimili ukame (Gelaye, 2023; Mukuwapasi et al., 2024; Yadav & Yadav, 2024; Omotayo et al., 2025). Katika utafiti wetu, tuliandaa modeli kwa *A. dubius* na *A. hypochondiacus*, lakini *A. dubius* iliachwa kwani 8% ya modeli haikufua dafu kutokana na mahitaji ya mvua. Mchicha wa kisasa tuliouweka katika utafiti wetu uliishia kuwa zao lenye viwango vya chini vya kufaa. Kwa hiyo, Mchicha wa kisasa, kama vile nduma, si njia inayoweza kupendekezwa pekee kwa kuimarisha usalama wa chakula chini ya mabadiliko ya hali ya hewa kwa Zanzibar.

Mabadiliko ya tabianchi yanatarajiwa kuathiri pakubwa uzalishaji wa mpunga katika maeneo yenye viwango vya chini vya teknolojia ya kilimo na miundombinu. Mbinu moja ni kusambaza aina za mchele wa WDR (unaohifadhi maji, unaostahimili ukame), kama Zanzibar ilivyoanza kufanya na WDR-70 (Luo, 2010; Zhang et al., 2021; Onyango, 2024). Tuligundua kuwa hata aina za mchele unaostahimili ukame zina ustahimilivu mdogo katika baadhi ya maeneo ya kisiwa chini ya hali zote za modeli za mabadiliko ya tabianchi Ufaafu wa mpunga ni pana zaidi kuliko mazao mengine mengi, huku tofauti ya hadi 52% ikionekana (Jedwali 6, katika sura yenyewe). Kaskazini-mashariki mwa kisiwa hicho inashikilia viwango vya juu zaidi vya ustahimilivu wa mpunga, huku ukingo wa magharibi wa maeneo yanayofaa ukielekea mashariki kwa zaidi kufikia mwisho wa karne (Mchoro 7, sura yenyewe).

Matokeo - Mwingiliano wa Binadamu na Kima Punju wakati wa Mabadiliko ya Tabianchi

Maingiliano ya binadamu na wanyamapori (MBW) kwenye kilimo yameundwa kimsingi na maeneo ya kuishi ya kima punju. Hii ni kwa sababu kufaa kwa makundi ya mazao hautofautiani sana kote kisiwani (mara nyingi chini ya 20%). Kwa hali zote na nyakati tofauti, mazao yote 30 yanapozingatiwa pamoja, hakuna maeneo yenye MBW ya chini, bali ni maeneo yenye MBW ya wastani au ya juu tu. MBW inalenga zaidi nusu ya kusini na ukingo wa mashariki wa kisiwa. Tunapoelekea mwisho wa karne, MBW inajikita zaidi kwenye ncha ya kusini kwa SSP zote, pamoja na sehemu kubwa ya pwani ya mashariki. Maeneo yenye MBW ya juu ni maeneo ambapo uwezekano wa kima punju na kufaa kwa mazao ni kwa juu zaidi (kima punju >80%; kufaa kwa mazao >75%). Kuna tofauti za maeneo ya MBW kwa baadhi ya makundi ya mazao kundi lote la mazao yanapojumuishwa pamoja. Tofauti hizi husababishwa na upeo mdogo wa kufaa kwa makundi hayo ya mazao (Mchoro 13, katika sura yenyewe).

Muundo wa msingi katika uchoraji wetu wa ramani ya MBW unaonyesha kwamba viwango vya juu vya mwingiliano wa MBW kwenye kilimo hupungua kuelekea mwisho wa karne, kadri uwezekano wa kuwepo kwa kima punju unavyopungua kote kisiwani (Jedwali la 7, sura yenyewe). Ni muhimu kutambua kwamba matokeo haya ya utafiti yanaonyesha tu uwezekano wa MBW kufuatana na matumizi ya ardhi, si uwezekano wa hakika. Hata hivyo, kuna uwezekano wa viwango vya wastani hadi vya juu vya MBW katika kilimo hadi mwisho wa karne chini ya hali zote za modeli za mabadiliko ya tabianchi.

Mapendekezo ya Uhifadhi kwa Zanzibar

- 1) Ili kudhibiti idadi ya kima punju kwa muda mrefu kunaweza kuhitaji upanuzi wa, au angalau uimarishaji, wa maeneo yaliyohifadhiwa kusini. Hifadhi ya Kitaifa ya Jozani-Chwaka Bay, ambako zaidi ya nusu ya idadi ya kima punju wanaishi kwa sasa, inakadiriwa kupungukiwa na uwezekano wa kuwepo kima punju katika hali zote za ifikapo mwisho wa karne. Hifadhi ya Kitaifa ya Jozani-Chwaka Bay kwa sasa ndiko rasilimali nyingi za uhifadhi wa kima punju zimetengwa, ila modeli zetu zinaonyesha kuwa itakuwa vizuri kuwekeza baadhi ya rasilimali hizi katika maeneo yaliyohifadhiwa zaidi kusini, au katika kutafiti na kulinda njia za mapito ya kima punju kati ya Hifadhi ya Kitaifa ya Jozani-Chwaka Bay na makundi mengine kusini mwa kisiwa. Kumekuwa na uwekezaji uliopendekezwa hivi karibuni katika Hifadhi ya Msitu ya Jambiani-Muyuni kwa madhumuni ya uhifadhi na maendeleo endelevu, na utafiti wetu unaonyesha kuwa huu ungekuwa uwekezaji mzuri kwa uhifadhi wa kima punju.

- 2) Kutengeneza takwimu na za data za muda mrefu kuhusu uvamizi wa mazao na kima punju pia kunaweza kuwa muhimu katika mipango ya uhifadhi. Uelewa bora wa kile ambacho kima punju hupendelea, mipango maalum inayozalisha mazao yanayopendelewa kandokando na yasiyopendelewainaweza kupunguza athari za uvamizi wa kima punju. Pia itakuwa vizuri kwa wanaofanya maamuzi kuwa na data kuhusu viwango ambavyo kima punju wanashiriki katika uvamizi wa mazao dhidi ya nyani wa Sykes (*Cercopithecus mitis albogularis*).
- 3) Kufuatia matokeo yetu, tunaweza kutoa mapendekezo mahususi ya mazao kwa ajili ya uzalishaji bora wakati wa mabadiliko ya tabianchi Kusini mwa Zanzibar. Kuhusu nafaka, kaya za Kusini huenda zikahudumiwa vyema zaidi kwa kuwekeza katika mahindi kuliko mpunga. Vile vile, kwa viazi, viazi vikuu vinakadiriwa kufanya vizuri zaidi kwa mabadiliko ya tabianchi kuliko muhogo au viazi vitamu. Kutegemea tu kilimo cha viungo na mboga mboga kiuchumi ni jambo ambalo tusingependekeza, kwani mwafaka na kufaa kwa aina hizi za mazao unakadiriwa kupunguka kwa kiasi kikubwa katika siku za usoni.

CHAPTER FOUR:

CONCLUSION

Across Africa, red colobus are under facing a multitude of threats and experiencing population declines, resulting in threat of extinction for all forms (Linder et al., 2024; IUCN, 2025). Like most endangered primates, habitat destruction and hunting are the primary drivers of their threatened status, but there are also a variety of co-acting factors, such as climate change and human-wildlife conflict, which amplify negative impacts. Exploring and addressing these co-acting factors can provide avenues for lessening the intensity of hunting and habitat destruction pressures, but doing so may necessitate novel, context specific approaches. As threats to red colobus continue to increase, there is a need to generate data and conservation recommendations which consider and directly address not only primary drivers of extinction risk, but the synergistic nature of these co-acting factors. In addition, conservation prioritization and planning efforts are greatly strengthened by robust data concerning population metrics, demography, distribution, and evolutionary history. Unfortunately, only a few red colobus populations have been studied in depth, and we lack key data for most species (Linder et al., 2024).

Through this dissertation, I helped address outstanding challenges to red colobus conservation identified for prioritization in the Red Colobus Action Plan (Linder et al., 2021). My work provides both actionable data for an endangered red colobus species (*P. kirkii*), as well as novel and updated methodological approaches for generating data key to effective red colobus conservation. While the bulk of this work was informed by red colobus conservation needs, Chapter Three is comprised of work which has the potential for applicability to conservation issues facing wildlife and human populations in systems all over the world.

In Chapter Two, I optimize and standardize a modernized genetics workflow utilizing STRs to make these methods more accurate and accessible for the needs of Africa colobine conservation. Specifically, this chapter details the first deployment of a reliable high throughput amplicon sequencing approach leveraging next-generation platforms optimized for use on fecal, or other degraded, non-invasively collected samples from wild populations. Part of the impetus for this work was to assist in answering the Red Colobus Action Plan's call to improve knowledge concerning red colobus population ecology and status (Linder et al., 2021), but we were also motivated by the need to shift our approaches as a research community towards a workflow that can leverage newer technologies and prepare our marker panels for future integration with genomics approaches. In part, this also increases accessibility of conservation genetics approaches, as next-generation platforms are much more common now than older capillary electrophoresis instruments and acquiring and running such instruments is costly. Financial accessibility is also increased through this work, as we have done all of the front-end work of testing a multitude of primers, and optimizing PCR and cleanup parameters. A considerable amount of our budget went into that front-end portion of the research, so the optimized workflow we provide in Chapter Two should allow research groups and conservation entities to carry out genetics work on African colobines with less overall financial investment.

As mentioned, we were also driven to standardize efficient marker panels in order to increase cross-taxa and cross-study comparability. One of the shortcomings of STR work via capillary electrophoresis has been that results are often not comparable between laboratories, or even projects within the same lab, because of inconsistent sizing of alleles given differences in electrophoretic conditions (Moran et al., 2006; Forcina et al., 2021). A high throughput amplicon sequencing approach reduces these inconsistencies since it is a sequence-based approach. It also,

more generally, reduces error rates in genotyping, which again helps to reduce barriers to cross-study comparisons (Barbian et al., 2018). This is particularly important for conservation applications where we may want to monitor genetic diversity over time, for example. Increased accuracy in genotyping owing to a by-sequencing method offers higher confidence that any shifts we see in genetic diversity are true signals.

Our STR panel demonstrated the ability to capture measures of diversity comparable with past studies in the same populations as expected. Importantly, when we directly compared markers shared between our study and previous work by Ruiz-Lopez et al (2022), we captured higher levels of allelic diversity. We improved the capture of cryptic alleles, which resulted in changes to previous genotype calls for individuals, increasing the overall proportion of observed heterozygotes. We also demonstrated that this approach more reliably captures allelic dropout, a problem that is particularly common for non-invasive samples (Gagneux et al., 1997; Dai et al., 2015; Forgacs et al., 2019), additionally increasing the accuracy of genotyping.

The workflow resulting from Chapter Two provides an accessible and accurate way to address data deficiencies in red colobus populations which limit our understanding of conservation status and our ability to set conservation priorities. This approach can help us improve knowledge on the distribution, abundance, population size, and demography of all red colobus forms, and allow us to resolve outstanding questions about hybridization and species identity in Eastern Democratic Republic of Congo (Linder et al., 2021). While our main goal was to address the needs of red colobus conservation, our inclusion of black-and-white colobus opens the door for this workflow to be used broadly in African colobine population genetics, looking forward to potential integration with future genomics approaches. Through the work of this chapter, we have lowered barriers for other research groups interested in leveraging next-

generation approaches for studying colobus monkeys, thus facilitating future knowledge production necessary for properly assessing the conservation status of these animals.

In Chapter Three, I generated a novel framework for exploring the interplay between climate change, biodiversity, and food security, and the resulting impacts on human-wildlife interactions. By doing this, I demonstrate an approach for moving from generalized understandings of the ‘wicked problem’ of overlapping biodiversity and food security crises to directly considering these issues in tandem as part of long-term, localized conservation planning. This work represents the first integration of both biodiversity and agricultural niche and projection modeling to explore the spatial nature of human-wildlife interactions under climate change. Zanzibar is used as a model system for applying this framework given its high level of endemic biodiversity, high levels of poverty and food insecurity, and inherent high levels of risk associated with climate change due to it being a small, low-lying island. It was also chosen due to the presence of the endangered Zanzibar red colobus population, the flagship species for Zanzibar, central to ecotourism on the island and an important component of sustainable development plans aimed at poverty relief. Using correlative and mechanistic approaches, I generated niche models for the Zanzibar red colobus monkey, as well as subsistence and smallholder crops. These models were projected to the end of the century under three climate scenarios and then combined in order to examine potential for agriculturally mediated human-colobus interactions. This chapter also directly answers the Red Colobus Action Plan’s calls for a better understanding of species’ ecological needs and identification of protected areas (Linder et al., 2021).

I demonstrate that Zanzibar red colobus are likely to face climate-related population declines under all climate scenarios, with a projected loss of 20-36% of their current range. Their

range is likely to constrict along the northern and western edges, pushing them further southwards. Of particular interest is the fact that their current stronghold in Jozani-Chwaka Bay National Park, where roughly 51% of the population resides (Davenport et al., 2019), is projected to have sharp declines in probability of occurrence. With all of this in mind, our general recommendation regarding planning for long-term viability of the Zanzibar red colobus population is to invest in the proposed Jambiani-Muyuni Forest Reserve as a protected area for red colobus. This work also reflects that localized studies concerning climate change impacts on wildlife are advantageous to understanding the potential breadth of outcomes, and broad spatial patterns which may guide long-term conservation planning. In an ideal world, we would replicate this study for other red colobus species, but as previously mentioned, we generally lack necessary population and census data (Linder et al., 2021). This study highlights just how crucial those data are in the context of long-term conservation planning. Without census data, this modeling could not have been carried out, and we would not have been aware that the habitat quality of the Zanzibar red colobus' current stronghold will likely greatly decline.

My crop modeling for Zanzibar provided evidence that there should be many crops which maintain moderate to high levels of suitability across the entire island to the end of the century, at least as far as climatic inputs are concerned. For the majority of crop classes and individual crops, we found suitability to be 'flat' across the island, or to have a range of suitability which was separated by less than 20% from minimum to maximum, under all climate scenarios. We also specifically investigated a handful of crops which have been put forward in the literature as climate resilient crops advantageous for strengthening food security in Africa (e.g., cocoyam, amaranths) (Boakye et al., 2018; Chemura et al., 2022; Adiele, 2023; Gelaye, 2023; Mukuwapasi et al., 2024; Yadav & Yadav, 2024; Omotayo et al., 2025). My results demonstrate that while

global or regional scale studies on crop suitability can be informative about general patterns, and changes to global productivity and yield under climate change, when considering how to improve food security at a more local scale, finer resolution research is necessary. While increasing the prevalence of cocoyam and amaranths in agriculture may have a positive impact on food security for the African continent, these crops do not appear to provide an effective avenue for strengthening food security in Zanzibar specifically. Reducing food insecurity under climate change is a difficult challenge, but the integration of climate tolerant strains has proven to be an effective way to build adaptive capacity, though adoption of climate-resilient strains is often impacted by access and socioeconomic factors (Acevedo et al., 2020). Crop adaptation to climate in Tanzania primarily tends to use strains sourced through informal seed systems; that is, seeds and improved varieties saved from local farms, as opposed to those strains bred and obtained through formal markets (Westengen & Brysting, 2014). For agriculture-based livelihoods, an integration of informal and formal seed systems can provide additional adaptive capacity to climate change, but again, access is a persistent issue. Zanzibar's government has already begun investing in WDR (water-saving, drought-resistant) varieties of rice in order to strengthen climate-resilience, with the intent to roll them out across the island (Luo, 2010; Zhang et al., 2021; Onyango, 2024). If these more formal approaches can be integrated with informal approaches, the overall seed system will be much more resilient and flexible to climatic shifts.

This research also presents an avenue for moving from strictly 'impact-oriented' approaches for supporting food security under climate change, to an approach which bridges 'impact-oriented' and 'adaptive-capacity' approaches. Impact-oriented approaches tend to primarily highlight regions and crops which are likely to be sensitive to climate change, predicting shifts in crop climates, and generally arriving at recommendations related to

dissemination of stress-tolerant crop strains. Adaptive capacity-oriented approaches, in comparison, tend to focus on the potential impacts of crop shifts to livelihoods, focusing on safety nets, and thus emphasizing the adaptive importance of local crops and traditional ecological knowledge (Smit & Wandel, 2006; Vermeulen et al., 2013; Westengen & Brysting, 2014). We purposely set out to test crops which are already present in Zanzibar's agricultural landscape, as well as those which have been suggested as 'climate-resilient' alternatives, keeping only crops which performed well. In doing so, we have tried to shift from what previous work has identified as wholly 'impact-oriented' approaches, to something in-between impact-oriented and adaptive capacity-oriented approaches. This provides an example of how we can start to consider local adaptive capacity in a very simple way: by basing crop selection on already cultivated suites of crops and by intentionally selecting crops which continue to remain productive under climate change. It is a very small change, but it takes us past simply stating which crops may fail, to providing actionable solutions in the form of well-performing crops which are already a part of the local agricultural lexicon and diet.

With regard to human-wildlife interactions mediated by agriculture on Zanzibar, the results indicate they will be primarily structured by the range of Zanzibar red colobus in the future. Spatially, human-colobus interactions are likely to be highest in the Southern quadrant and along the Eastern edge of the island. The potential for human-colobus interactions decreases as we near the end of the century, very simply because the overall probability of occurrence for Zanzibar red colobus drops. As noted previously, suitability for most crops is 'flat' across the island. However, where we do see spatial structuring, crop suitability is almost always lower on the Southern half of the island (e.g., for SSP3-7.0 at time step 2071 – 2100, annual cash crops reach 100% suitability in the North, but average 60% in the South). This has the potential to

introduce increased pressure on both humans and colobus. Offtake of certain crops could have a much more outsized impact on livelihoods in the south, which could in turn also have increased impacts on the degree of retaliation towards red colobus, or worsening of perceptions.

Retaliatory killings and increased negative perceptions are not only an issue for the colobus.

Zanzibar red colobus is the flagship species for Zanzibar and central to ecotourism, as well as an important component of sustainable development plans aimed at poverty relief in Zanzibar. The long-term health of the Zanzibar red colobus population is therefore not simply of importance for conservation of biodiversity and protection of Zanzibar's natural history, but also for the well-being of the human population.

Where human-wildlife conflict is primarily tied to crop-raiding and resulting impacts on peoples' livelihoods, compensation schemes are a very common tactic to try and mitigate conflict (Ravenelle & Nyhus, 2017). There may be other available avenues which can act as 'buffers' to the impacts of wildlife, however. In Zanzibar, the colobus live sympatrically with *Cercopithecus mitis albogularis* (Sykes' monkey), a frugivorous-generalist species which does well in secondary and disturbed forests (Chapman et al., 2000). Previous research indicates that these monkeys are likely more responsible for crop-raiding and damage than red colobus, but the difference in degree of impact between the species has not been studied in depth. Rates of crop-raiding between Sykes' monkeys and red colobus on Zanzibar, as well as any differentially preferred crops, could be useful information for decision-makers, and offer the ability to more clearly communicate where the impacts of crop-raiding largely originate on Zanzibar. In addition, building resilience in agricultural livelihoods using climate-smart agricultural approaches may provide a buffering effect to the pressure from increased human-wildlife interactions under climate change. In Southern Zanzibar, this could look like a combined effort

between the government and local farmers to integrate formal and informal knowledge as a way to generate cropping schemes which utilize locally derived seed strains with good climate tolerance and provide the cultivation diversity needed to maintain healthy soils, while also ensuring necessary dietary and nutritional requirements can be met. We also presented some specific recommendations with regard to individual crop selection for the Southern district of Zanzibar. For grains, maize is projected to have higher suitability than paddy rice. For roots and tubers, yams are projected to perform better than either cassava or sweet potato. We also note that economic reliance on spices and herbs alone is a very risky undertaking under climate change. There are spice farms across the island, and we would encourage people who derive the bulk of their agricultural income from spices to diversify their cropping.

While Chapter Three used Zanzibar and the red colobus there as a study system, the framework is highly applicable to systems globally. The integration of biodiversity and agricultural modeling provides a unique opportunity to generate data for addressing one of conservation's many 'wicked problems.' Threats to biodiversity, by their nature, are multifactorial and interconnected. While we benefit from studying extinction threats in isolation in order to properly elucidate the mechanisms underpinning risk, it is equally important to have a firm understanding of how these threats interact. The work presented in Chapter Three moves beyond understanding the wicked problem of overlapping endangered biodiversity and food insecurity in a general sense, to articulating how these factors may generate conflict in a specific system and providing solutions for securing better futures for both wildlife and people.

We often highlight the unique nature of red colobus when discussing their threatened status, and that is for good reason. Given their specialized diets, slow reproduction and recruitment rates, and conspicuous nature, they are highly vulnerable to the most prevalent

conservation threats. Red colobus are a ‘canary in the coalmine’ for tropical species, so to speak (Linder et al., 2024); as a model system, they demonstrate how quickly synergistic threats like climate change, human-wildlife conflict, and hunting can lead to negative outcomes. In responding to the conservation needs of red colobus, and other tropical taxa, we have to both meet the present and plan for the future. Through this dissertation, I contributed to these efforts by increasing the accessibility of genetic methods for generating data, while also generating a novel, integrative method to help us plan for long-term conservation and mitigation of human-wildlife interactions under climate change.

APPENDIX A:
SUPPLEMENTAL MATERIALS FOR CHAPTER I

EcoCrop Calculations

The EcoCrop model utilizes 10 ecological parameters in tandem with monthly climate data to calculate suitability on a scale from 0 (unsuitable) to 1 (perfectly suitable).

Ecological Parameters: Kill Minimum Temperature (T_{KILL}), Minimum temperature for optimal range (T_{OPMIN}), Maximum temperature for optimal range (T_{OPMAX}), Maximum absolute temperature (T_{MIN}), Minimum absolute temperature (T_{MAX}) Minimum precipitation for optimal range (R_{OPMIN}), Maximum precipitation for optimal range (R_{OPMAX}), Maximum absolute temperature (R_{MAX}), Minimum absolute temperature (R_{MIN}), Length of crop cycle (G_{AVG}).

Monthly Climate Data, for a given site (P) for each month (i): Monthly minimum temperature (T_{MIN-Pi}), Monthly mean temperature ($T_{MEAN-Pi}$), Monthly total precipitation ($R_{TOTAL-P}$)

The model creates a temperature suitability index and precipitation suitability index, which it uses to assess total suitability. It does this by moving through the following steps:

1). Temperature suitability is calculated for each month along the following guidelines:

- If T_{MIN} of a given month is less than $T_{KILL} + 4^{\circ}\text{C}$, temperature suitability = 0.
- If the mean temperature of the month is lower than T_{MIN} or higher than T_{MAX} , temperature suitability = 0.
- Between T_{MIN} and T_{OPMIN} , suitability for each month (i), is calculated using:
 - $T_{SUITi} = (T_{MEAN-Pi} - T_{MIN}) / (T_{OPMIN} - T_{MIN})$
- If $T_{MEAN-Pi}$ is higher than T_{MIN} , but not high enough to reach T_{OPMIN} , suitability for each month (i) is calculated using:
 - $T_{SUITi} = (T_{MAX} - T_{MEAN-Pi}) - (T_{MAX} - T_{OPMAX})$

2). Precipitation suitability is calculated. EcoCrop assesses total accumulated precipitation over the length of a crop cycle. It evaluates every month as a potential start to the crop cycle, summing rainfall over the period that matches the crop cycle length, including one month before and after said period. For each of the 12 possible periods, it concludes whether rainfall meets absolute or optimal parameters.

- If rainfall for G_{AVG} is lower than R_{MIN} or higher than R_{MAX} , suitability = 0.
- Between R_{MIN} and R_{OPMIN} , suitability is calculated using:

$$\circ \quad R_{SUITi} = (R_{TOTAL-P} - R_{MIN}) / (R_{OPMIN} - R_{MIN})$$

- If accumulated precipitation is higher than R_{MIN} , but high enough to reach R_{OPMIN} , suitability for each month (i) is calculated using:

$$\circ \quad R_{SUITi} = (R_{MAX} - R_{TOTAL-P}) / (R_{MAX} - R_{OPMAX})$$

3). Steps one and two result in 12 suitability values for both temperature and precipitation. These values are then combined by selecting the minimum of either the temperature or precipitation suitability values for the necessary consecutive months to carry the crop through the length of its growth cycle. This creates a new set of 12 combined suitability values which reflect potential suitability of a cropping period starting each month of the year. EcoCrop outputs the highest suitability value, assuming that planting will be done at the best moment, with respect to climate.

*For this study, G_{AVG} for each crop cycle length is the geometric mean, calculated from minimum and maximum crop cycle length.

(Ramirez-Villegas et al., 2013; Manners & Ettan 2018; Manners et al., 2020; Manners et al., 2021; Appelt et al., 2023)

APPENDIX B:

SUPPLEMENTAL MATERIALS FOR CHAPTER II

Locus	% ADO
C19a	35
D1S1675	50
D2S146	47
D2S391	21
D4S243	19
D4S2430	0
D6S264	18
D6S287	8
D6S311	18
D8S260	17
D10S587	20
D10S676	24
D12S372	44
D13S1291	13
D14S306	27
D16S403	22
D17S791	40
D18S57	27
D20S189	33
DXS571.2	25

Table 1: Percent of observed heterozygotes at each locus where allelic dropout was observed in at least one sequencing replicate. This represents our total sample, including both red colobus and black-and-white colobus.

APPENDIX C:

SUPPLEMENTAL MATERIALS FOR CHAPTER III

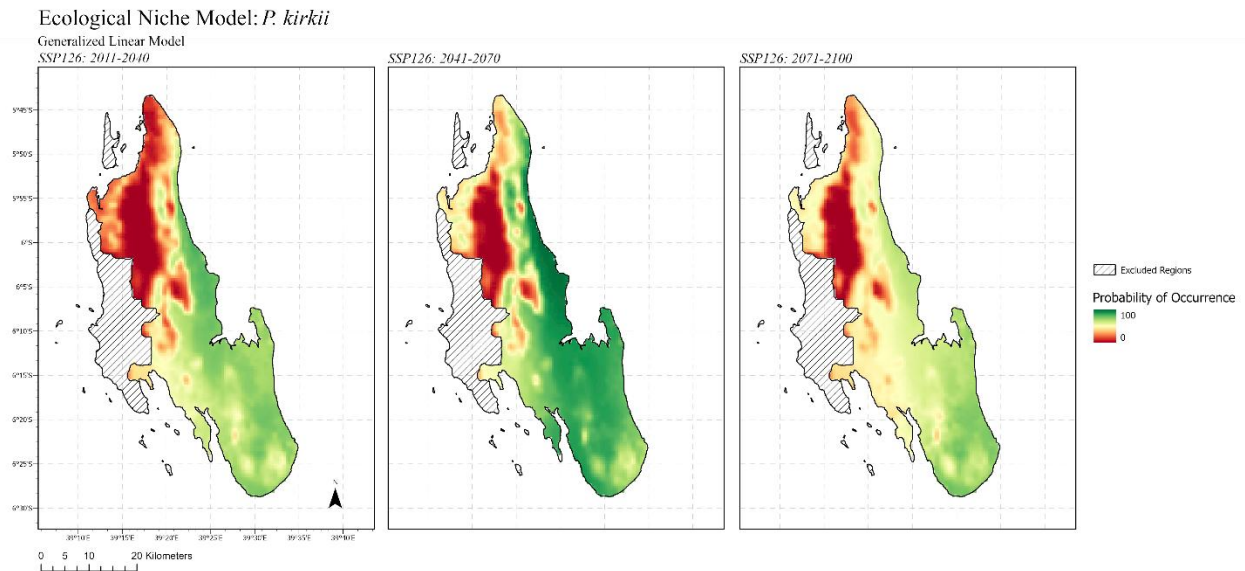


Figure 1: Probability of Zanzibar red colobus occurrence under climate change scenario SSP 1-2.6 throughout the century. SSP 1-2.6 reflects general patterns seen across the other SSPs: a loss in overall probability of occurrence for Zanzibar red colobus, range loss along the Northern and Western edges of the current range, with the most suitable areas concentrated in the Southern quadrant of the island.

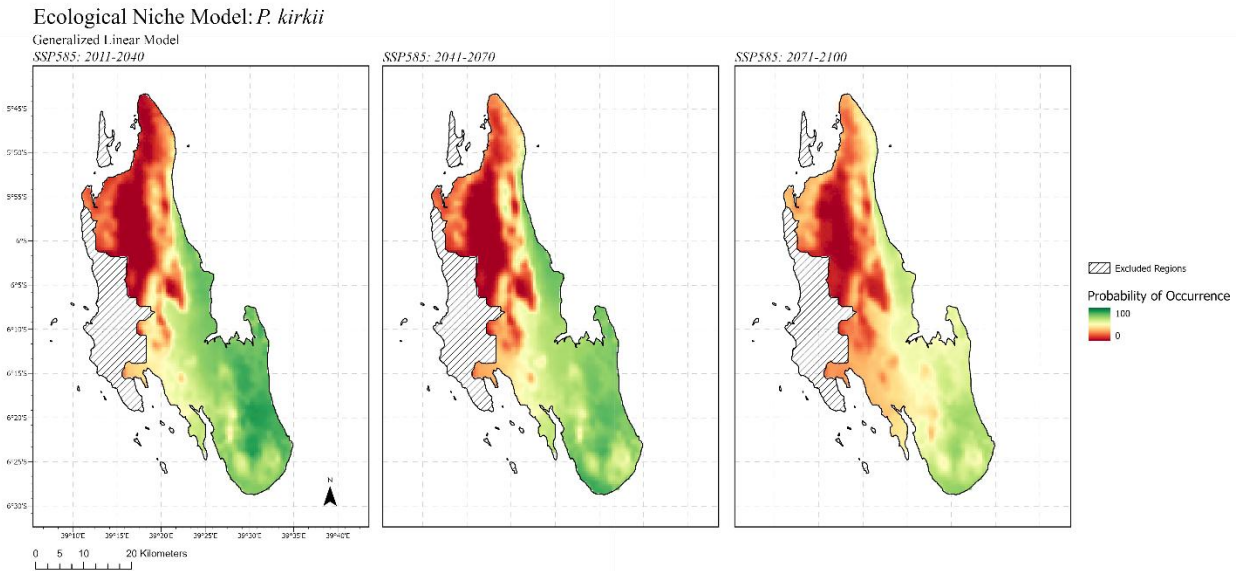


Figure 2: Probability of Zanzibar red colobus occurrence under climate change scenario SSP 5-8.5 throughout the century. SSP 5-8.5 reflects general patterns see across the other SSPs: a loss in overall probability of occurrence for Zanzibar red colobus, range loss along the Northern and Western edges of the current range, with the most suitable areas concentrated in the Southern quadrant of the island.

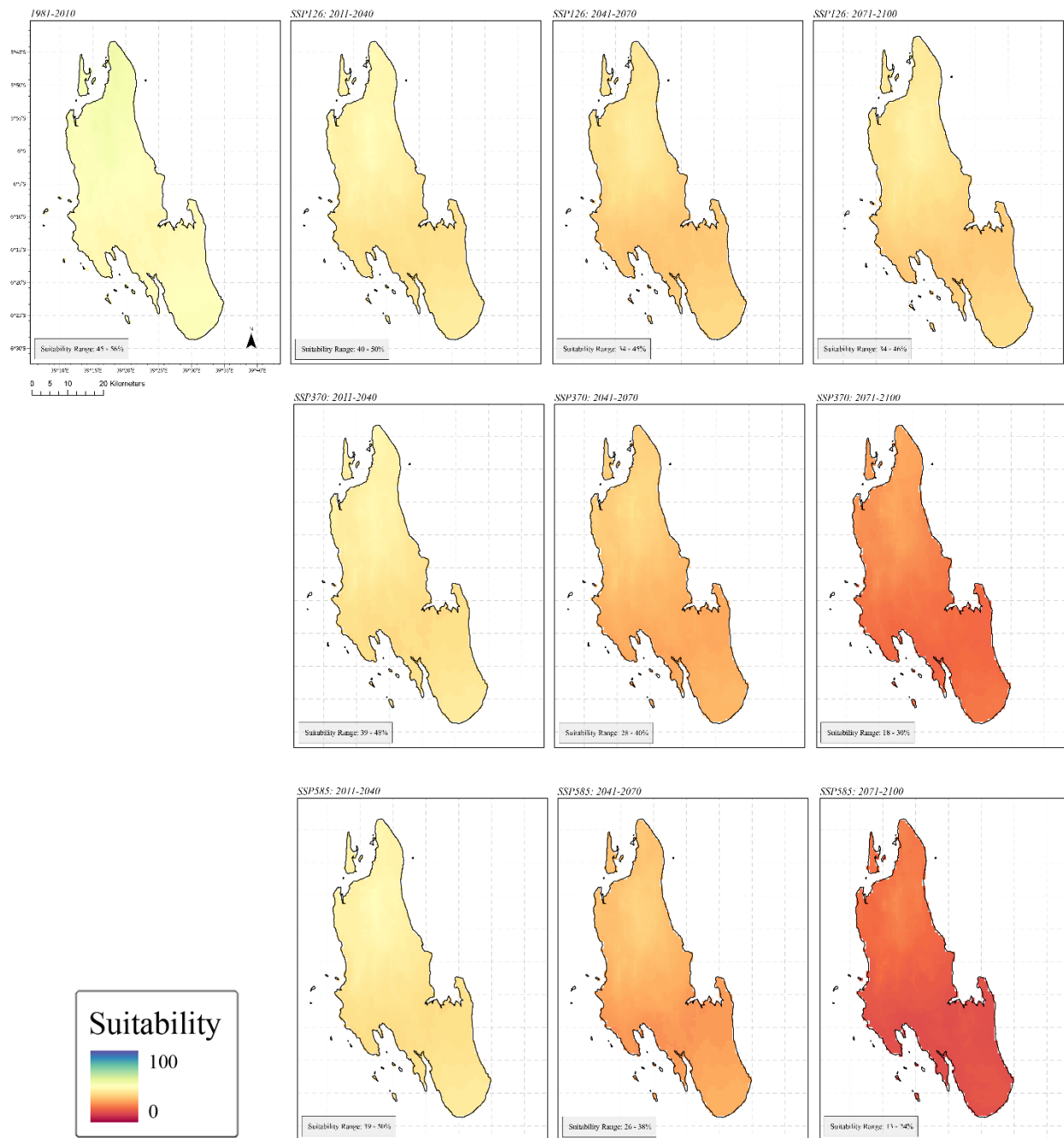


Figure 3: Crop suitability across Unguja for amaranth (mchicha wa kisasa).

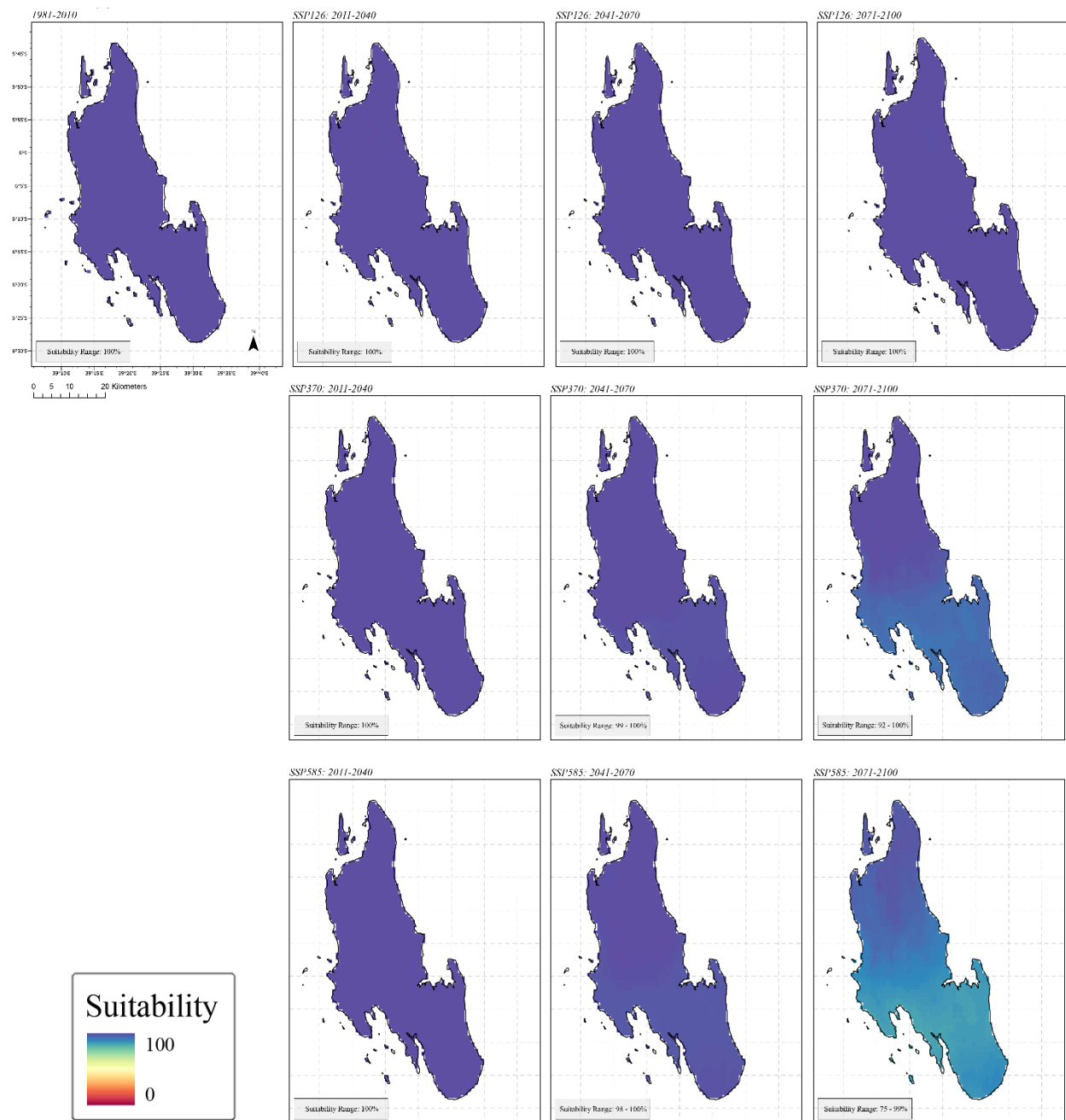


Figure 4: Crop suitability across Unguja for bambara nut (njugu mawe).

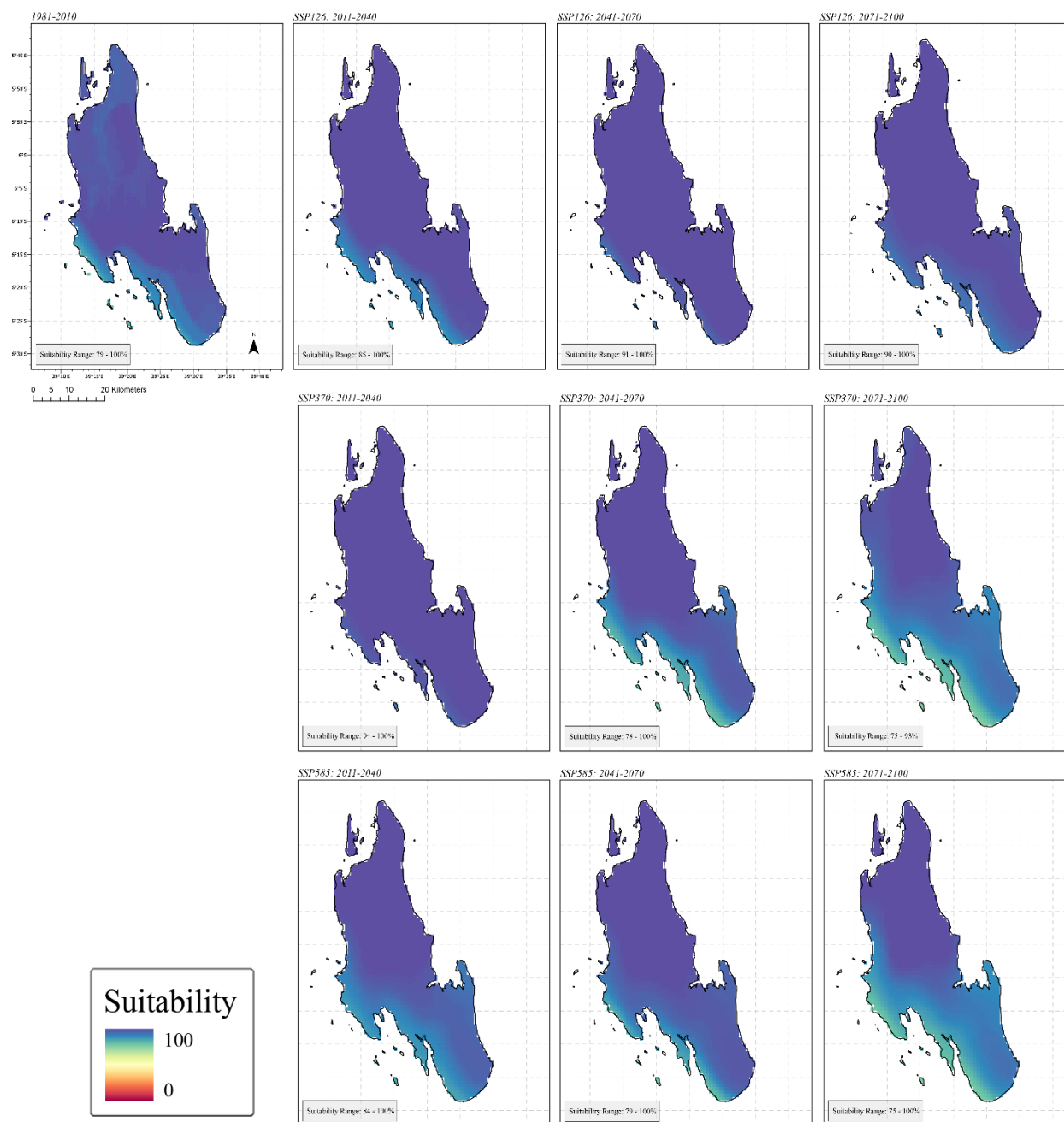


Figure 5: Crop suitability across Unguja for banana (mgomba).

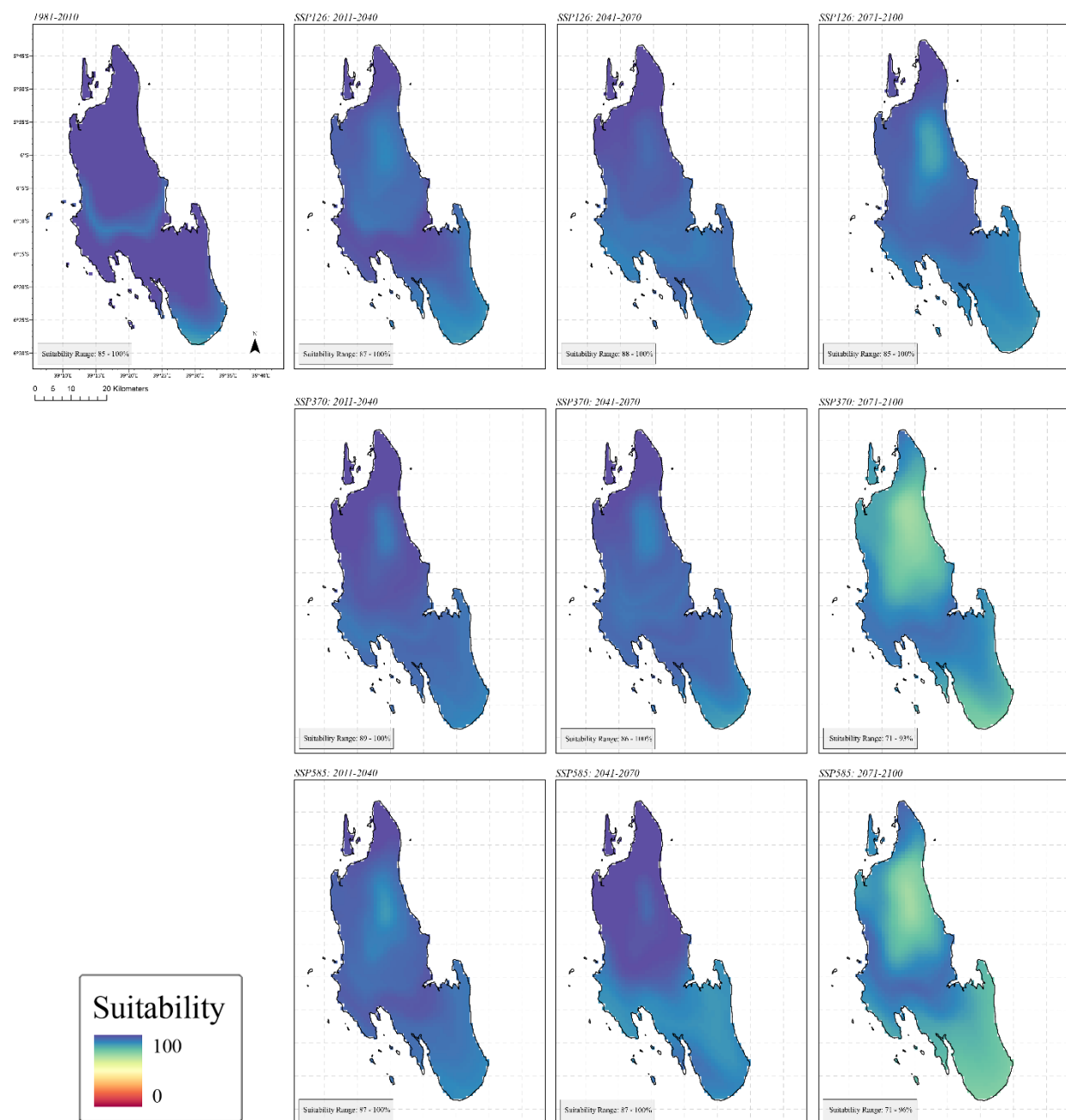


Figure 6: Crop suitability across Unguja for bulrush millet (mawe).

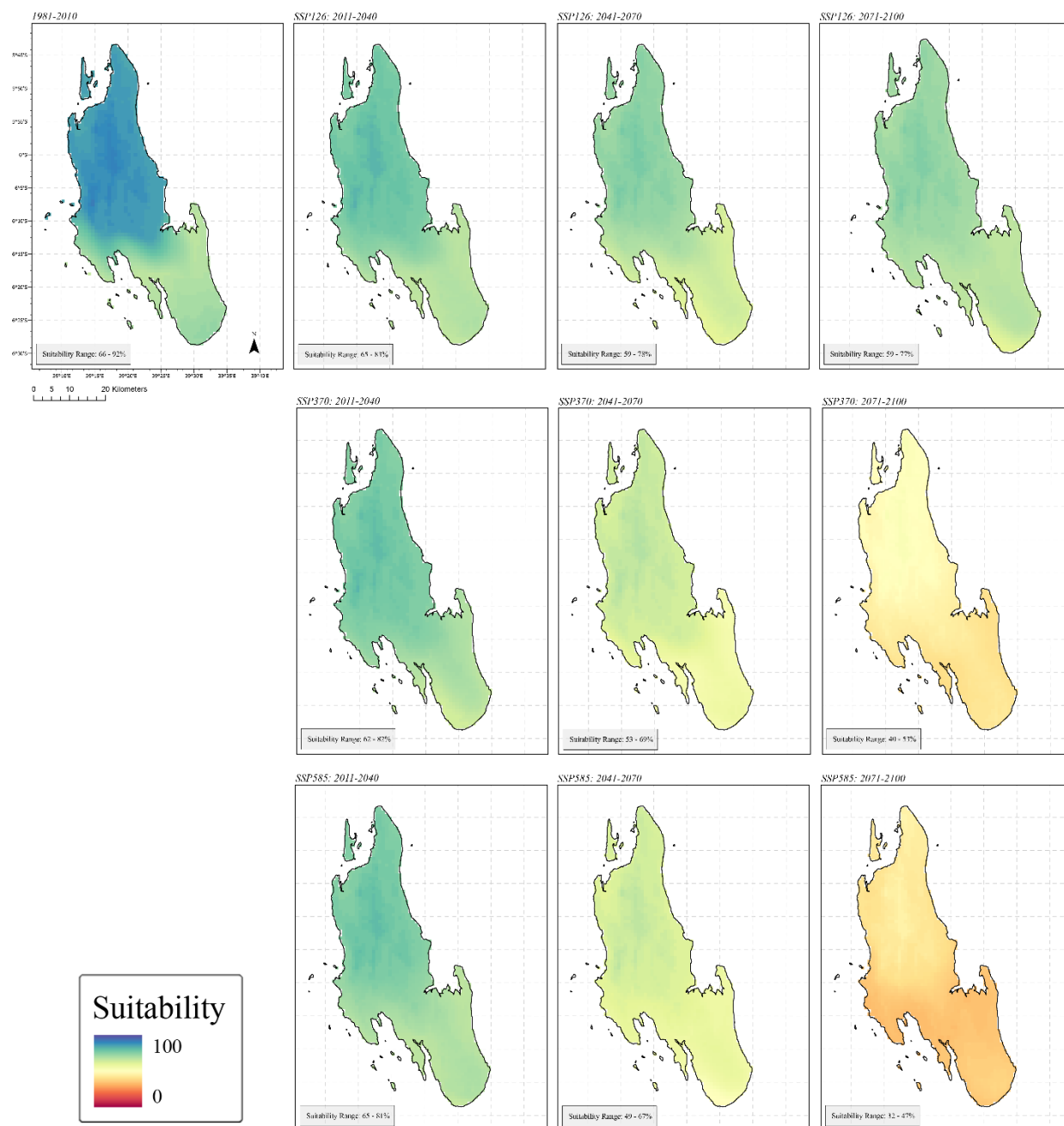


Figure 7: Crop suitability across Unguja for cabbage (kabichi).

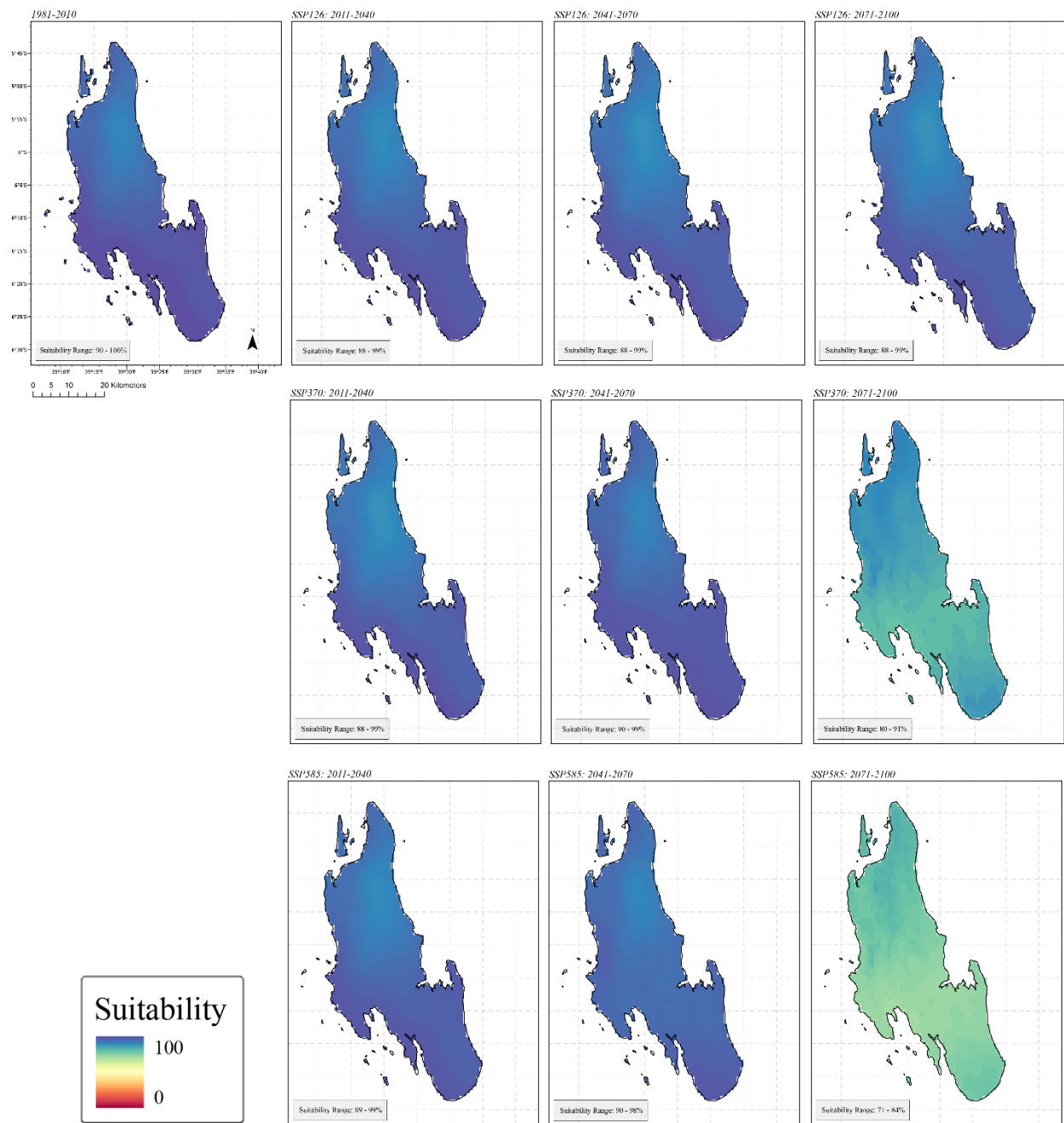


Figure 8: Crop suitability across Unguja for cassava (muhogo).

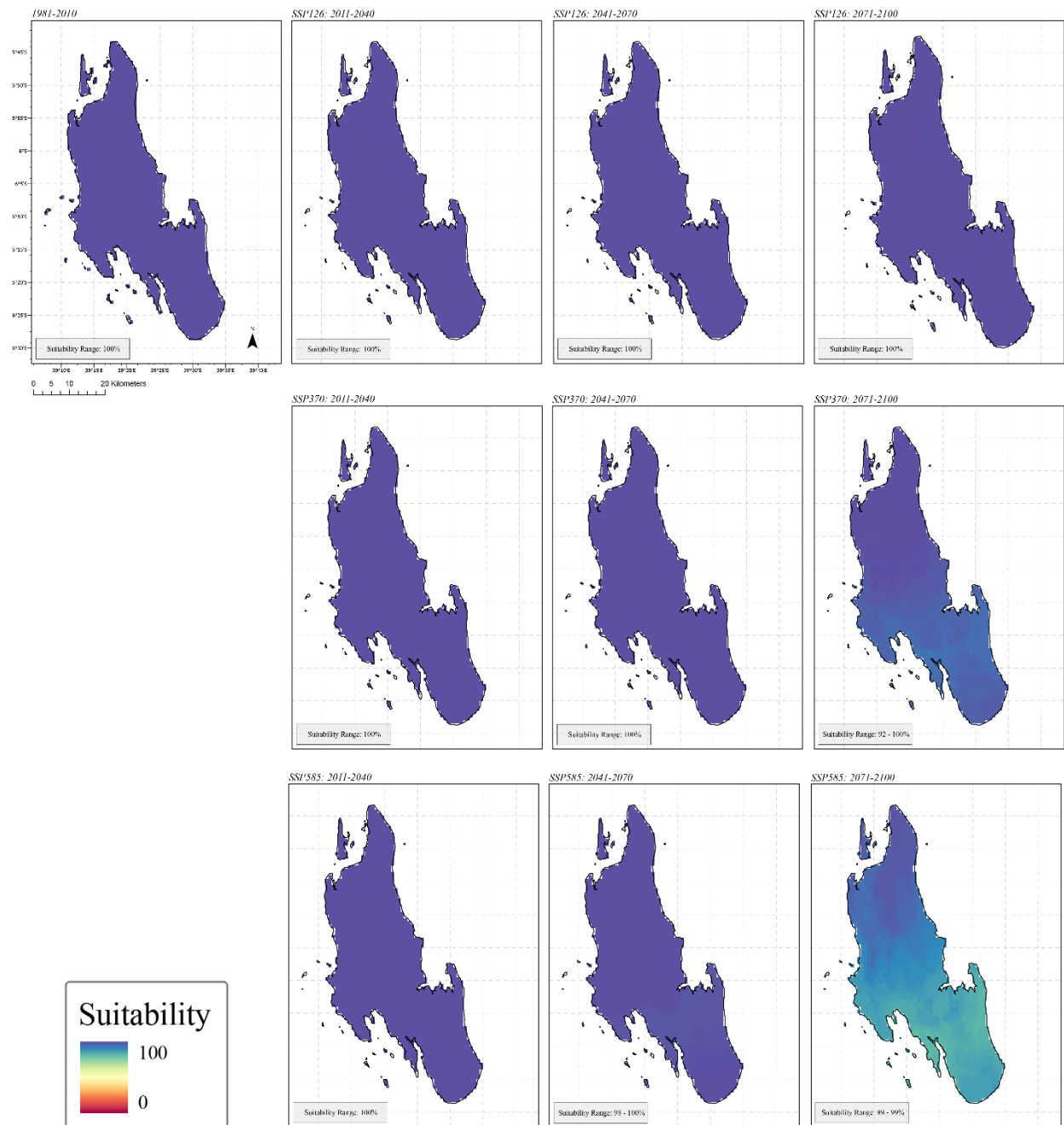


Figure 9: Crop suitability across Unga for chilies (pilipili hoho).

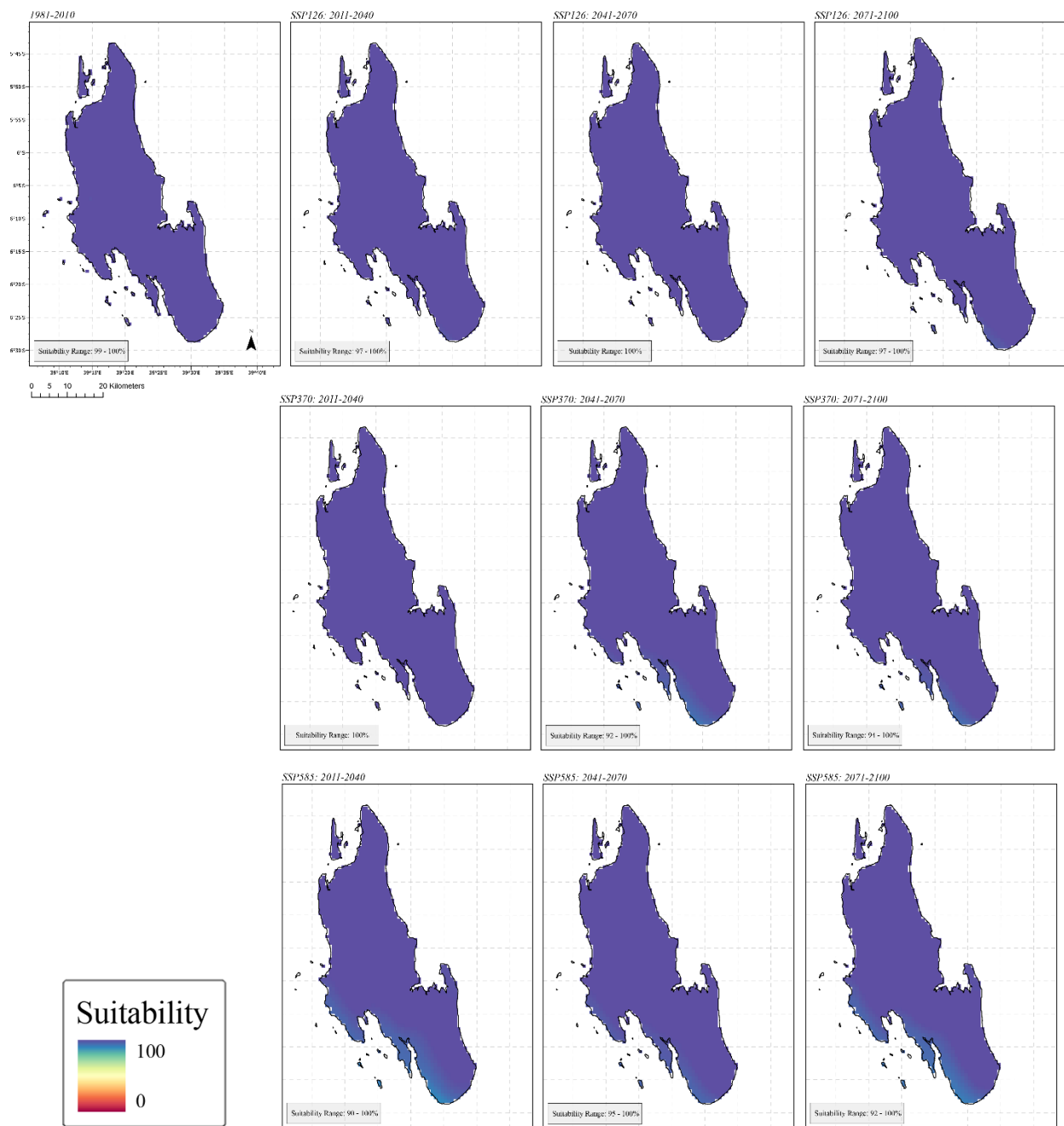


Figure 10: Crop suitability across Unguja for clove (miti ya karafuu).

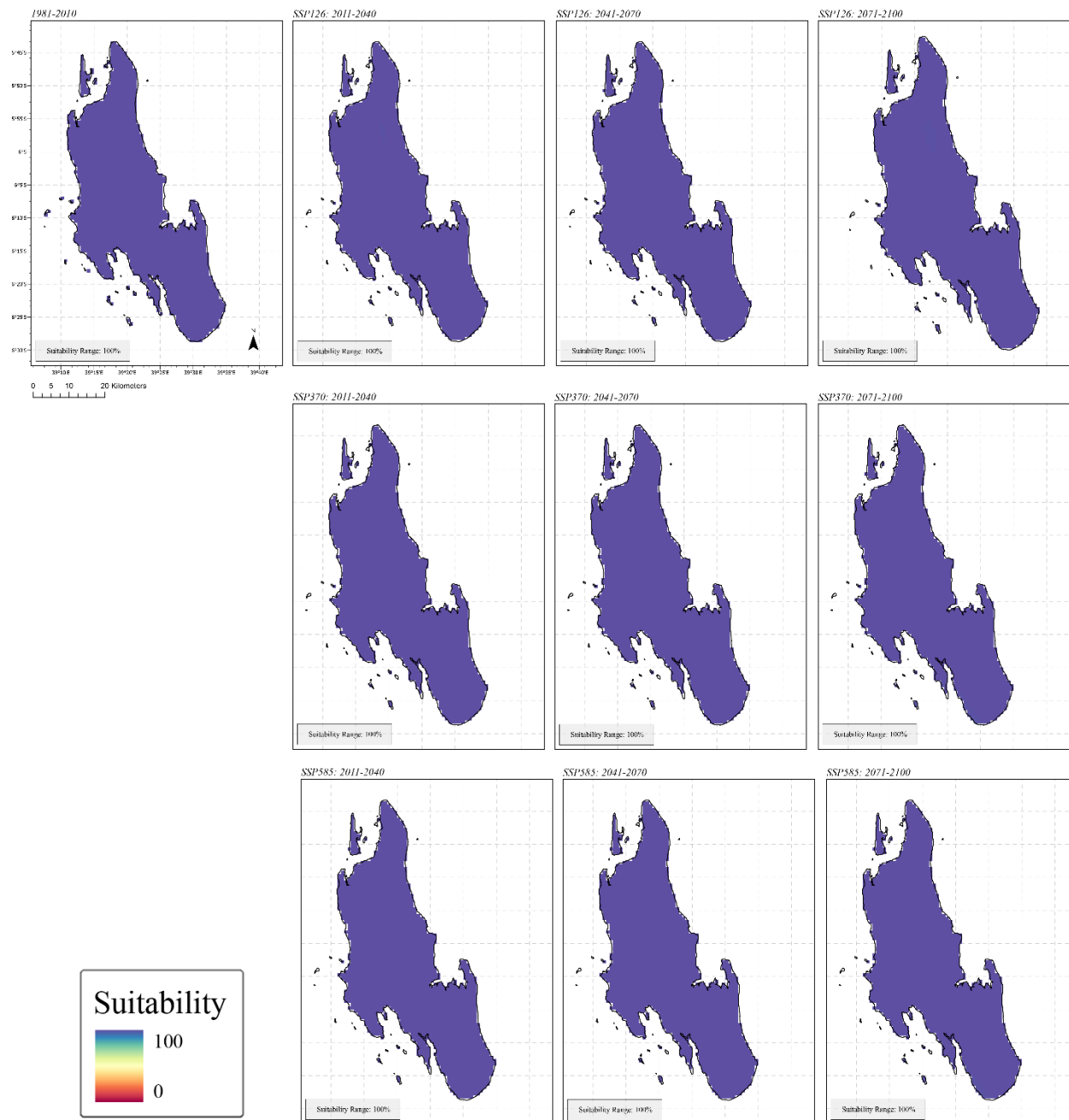


Figure 11: Crop suitability across Unguja for coconut (miti ya nazi).



Figure 12: Crop suitability across Unguja for cowpea (kunde).

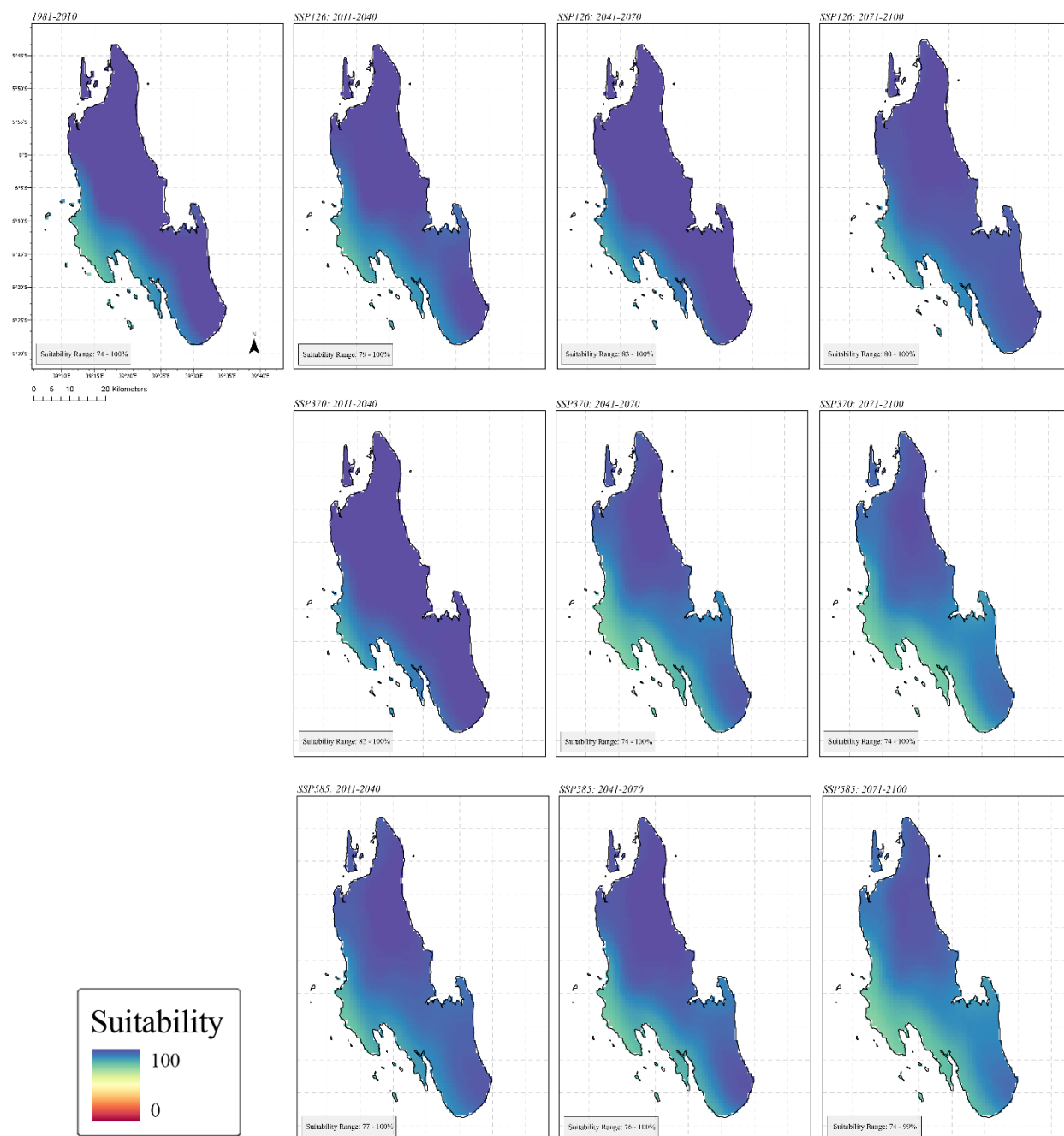


Figure 13: Crop suitability across Uguja for cucumber (tango).



Figure 14: Crop suitability across Unguja for finger millet (ulezi).

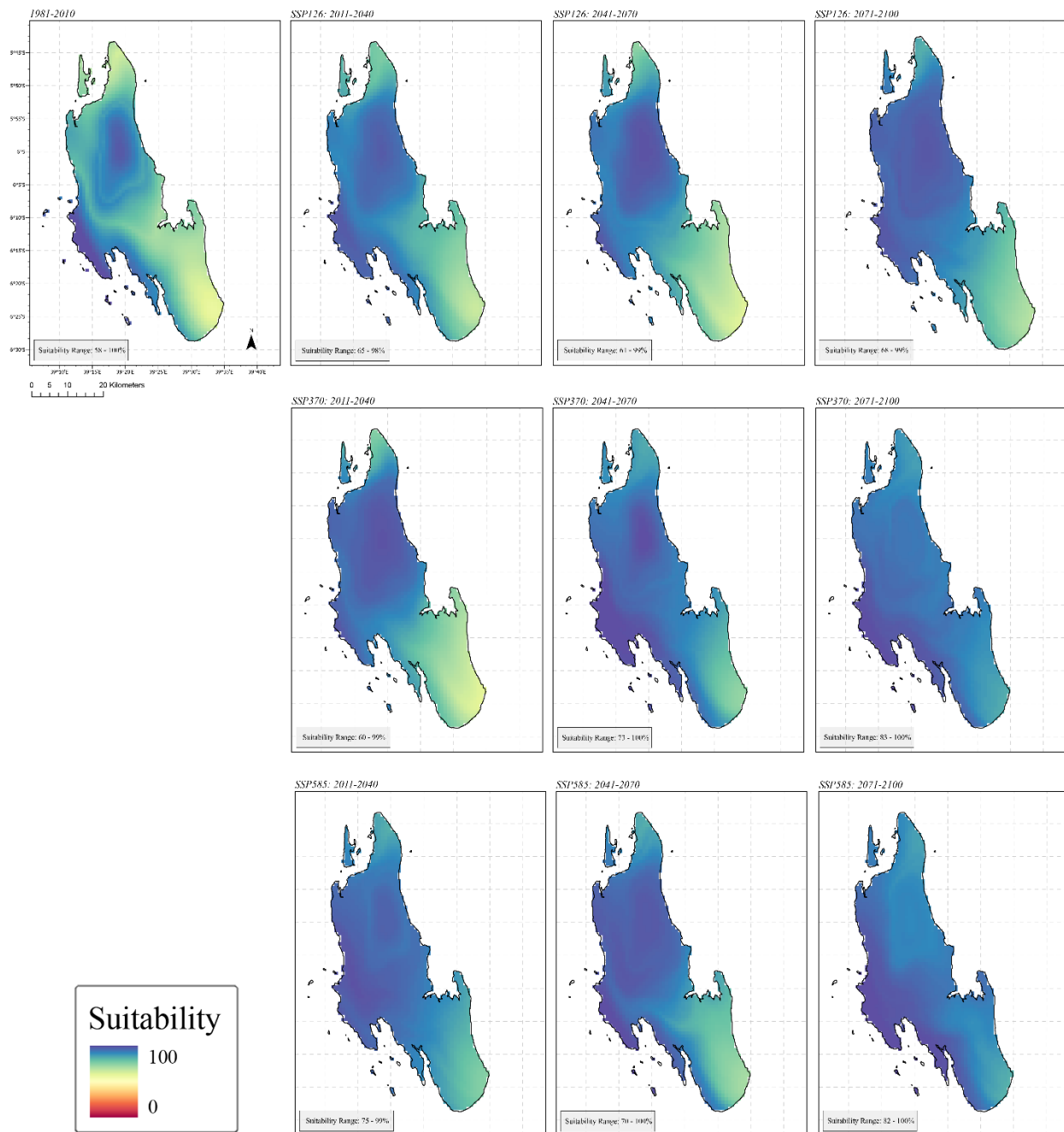


Figure 15: Crop suitability across Uguja for green gram (choroko).



Figure 16: Crop suitability across Unguja for groundnut (karanga).

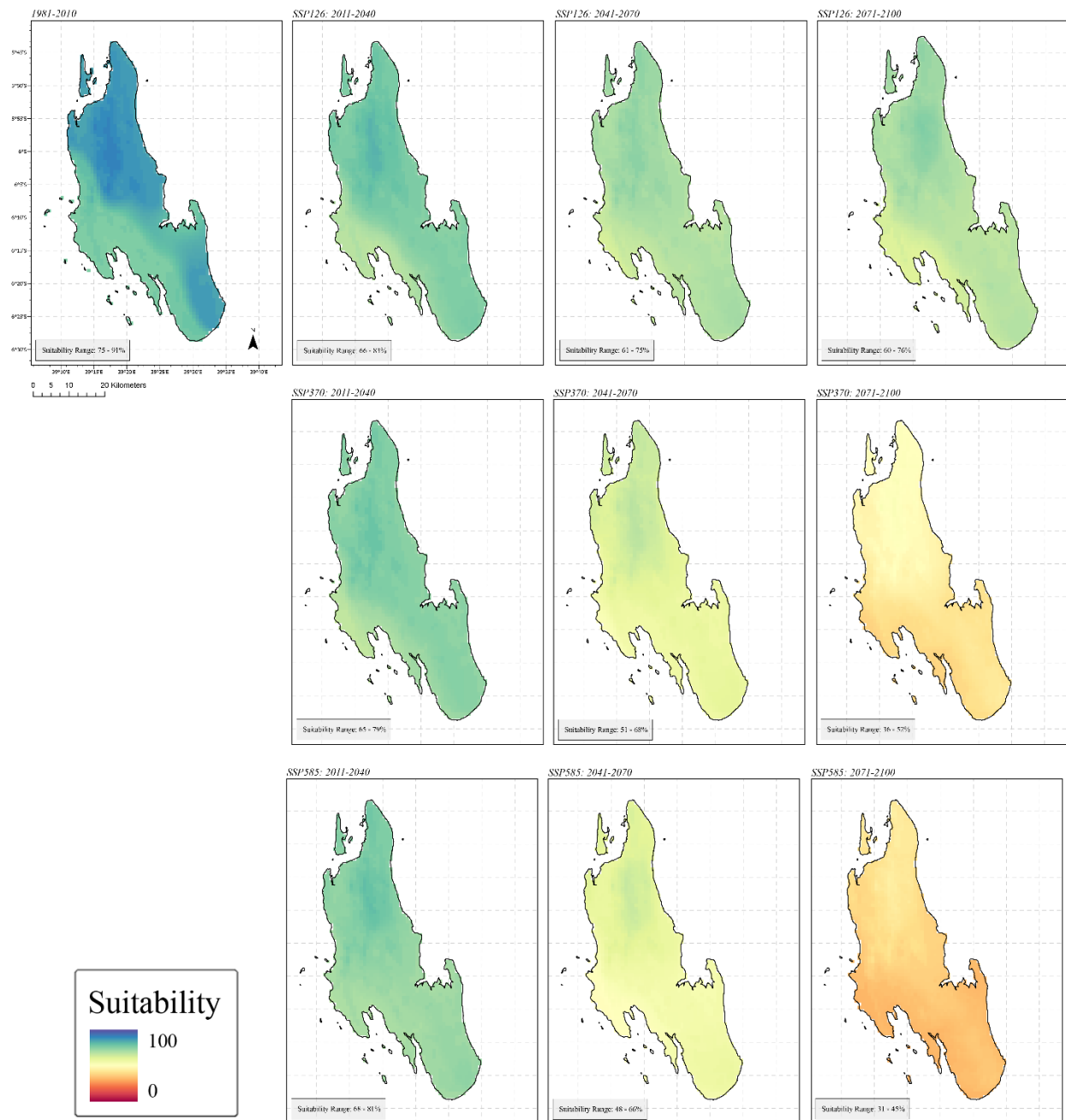


Figure 17: Crop suitability across Unguja for kothmir (gilgilani).



Figure 18: Crop suitability across Unguja for maize (muhindi).

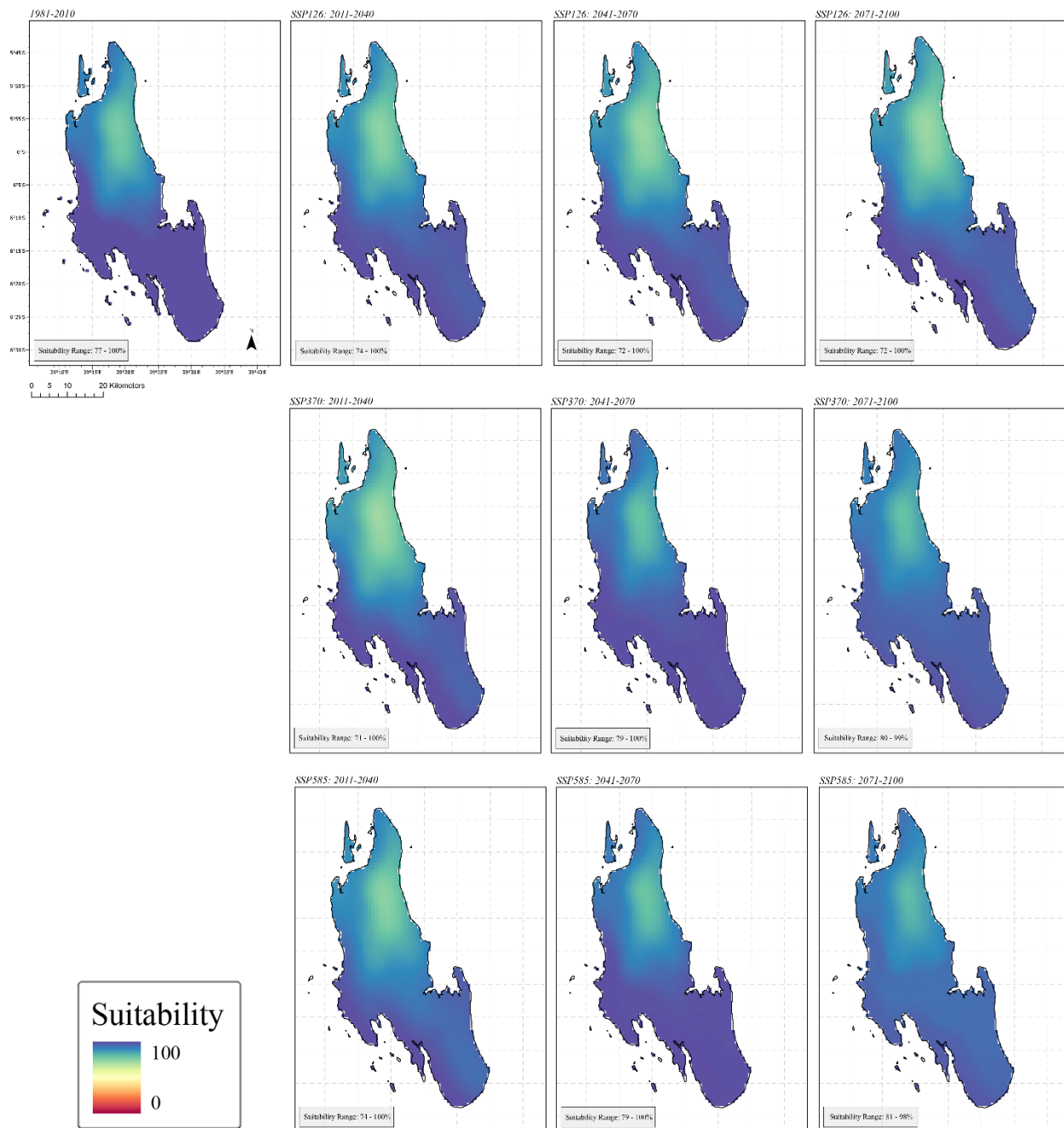


Figure 19: Crop suitability across Unguja for mango (miti ya maembe).

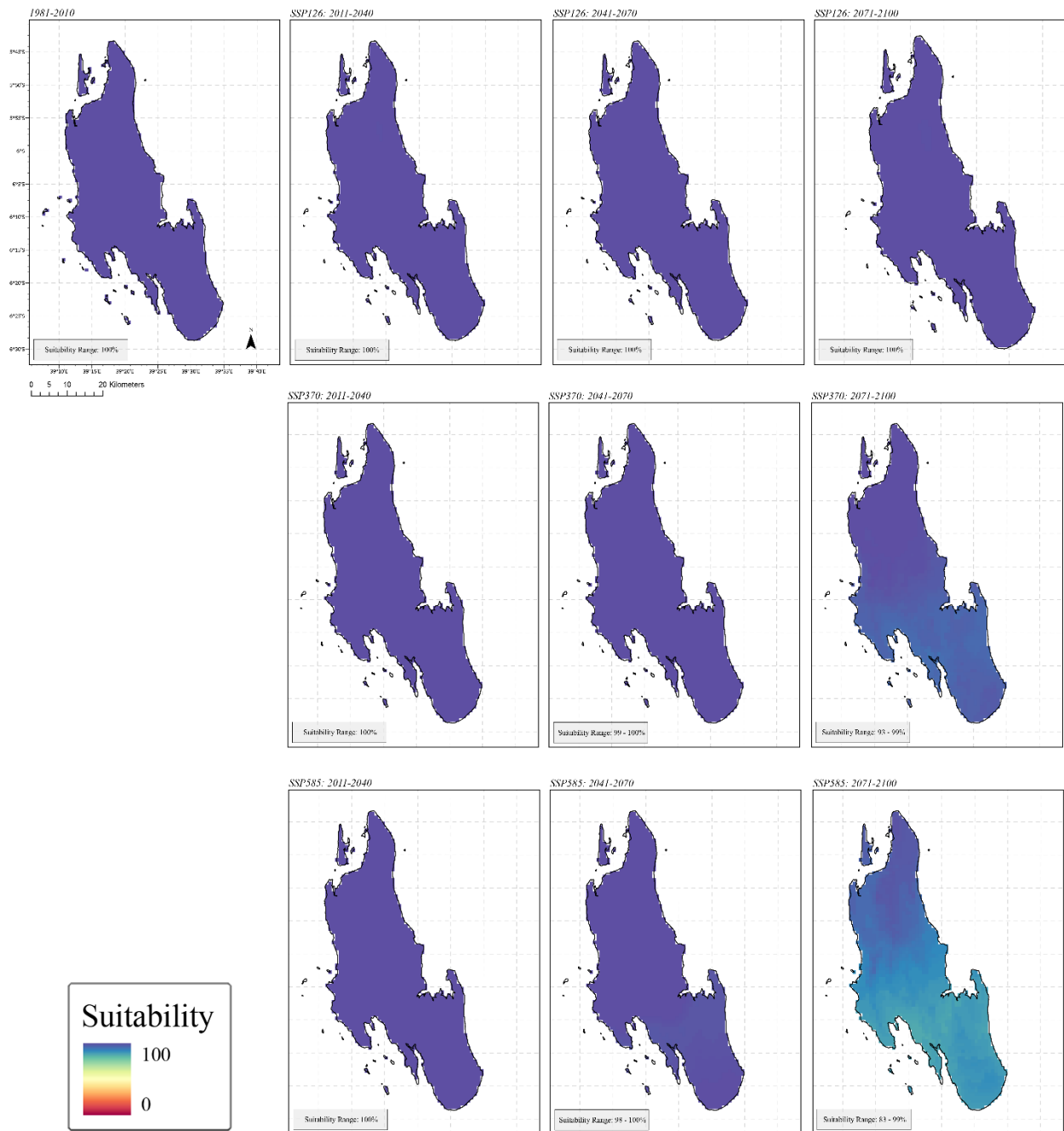


Figure 20: Crop suitability across Unguja for okra (mbamia).

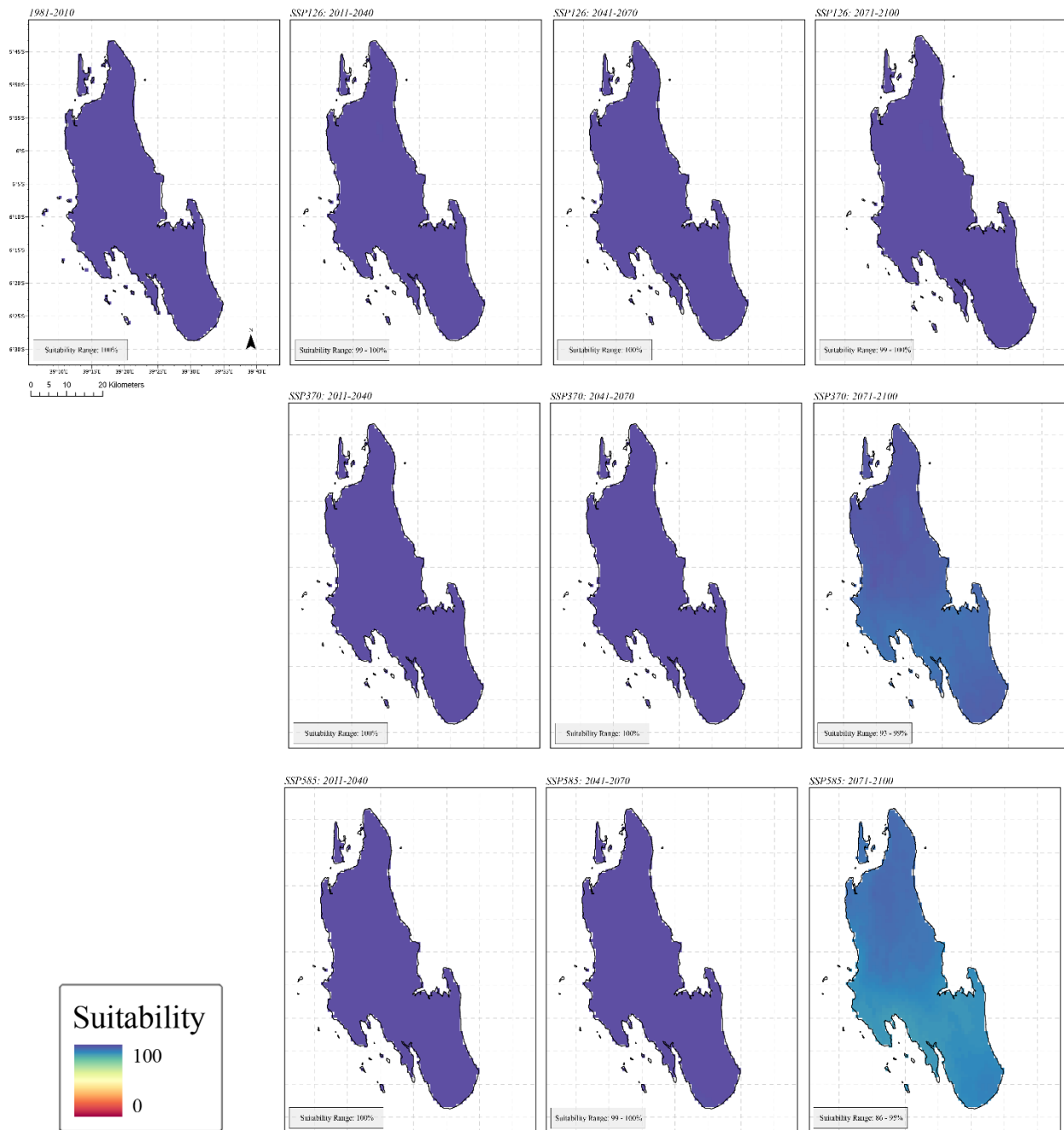


Figure 21: Crop suitability across Unguja for orange (miti ya machungwa).

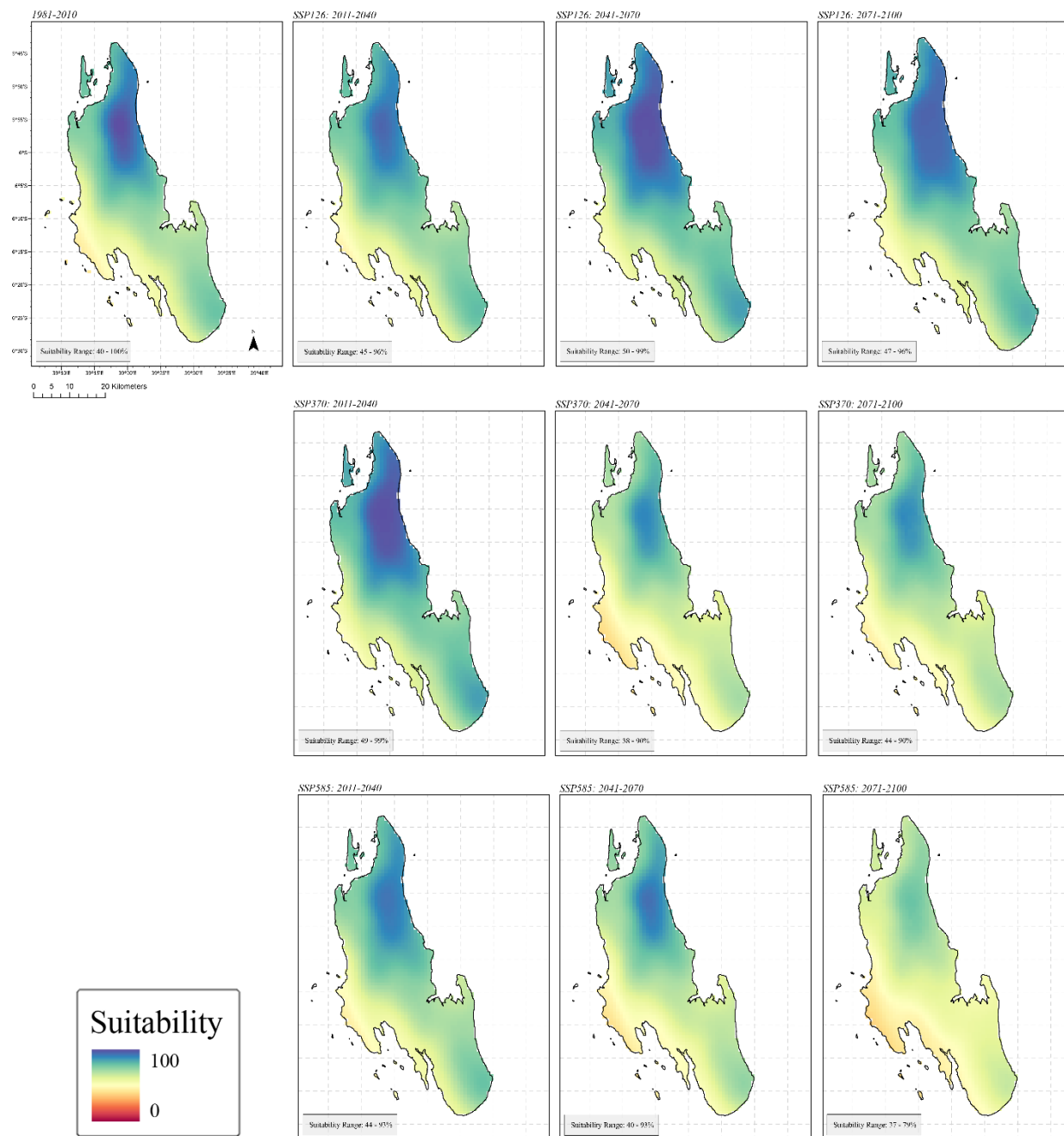


Figure 22: Crop suitability across Unguja for WDR paddy rice (mpunga).



Figure 23: Crop suitability across Unguja for pigeon pea (mbaazi).

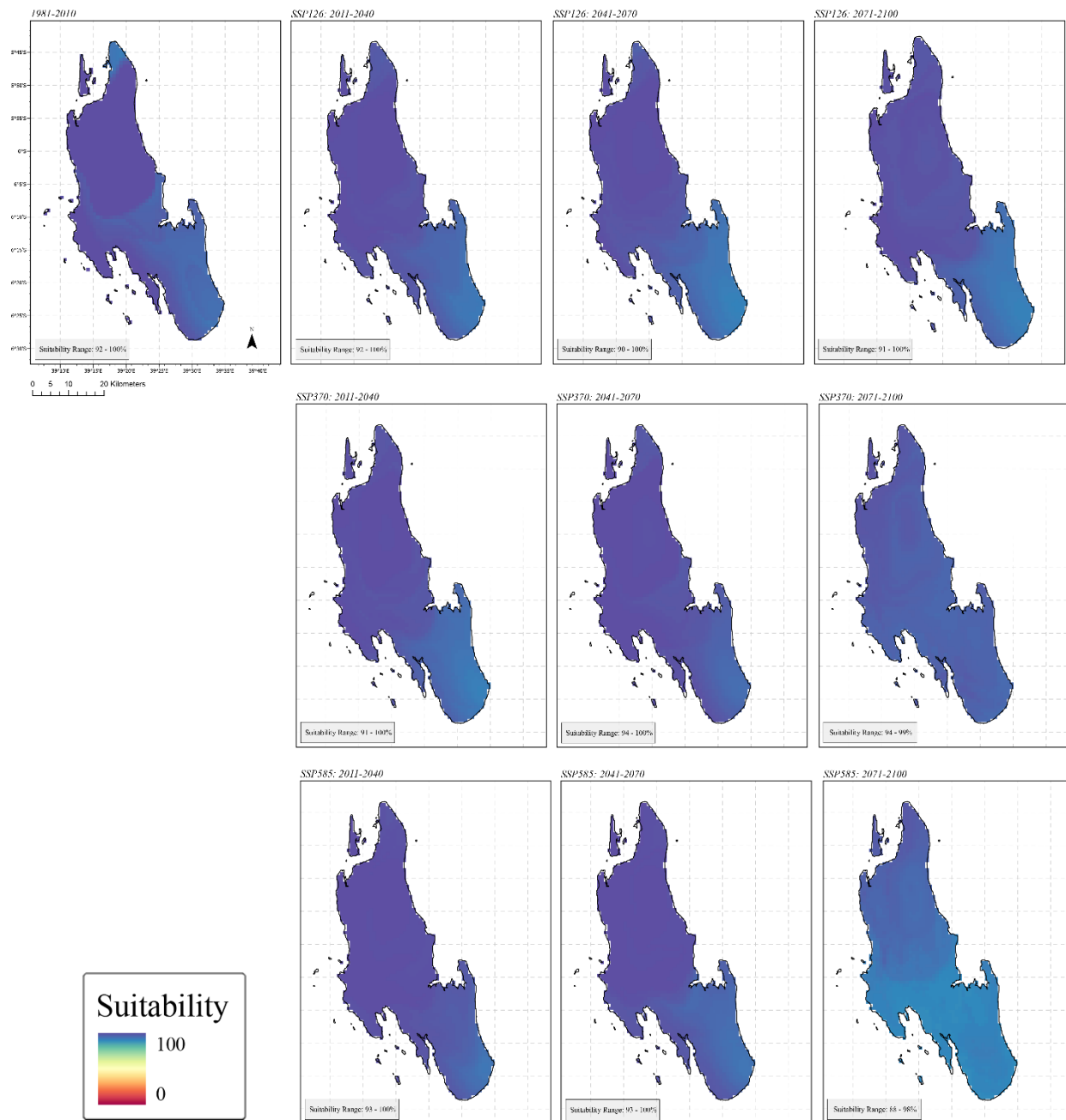


Figure 24: Crop suitability across Unguja for pumpkin (boga).

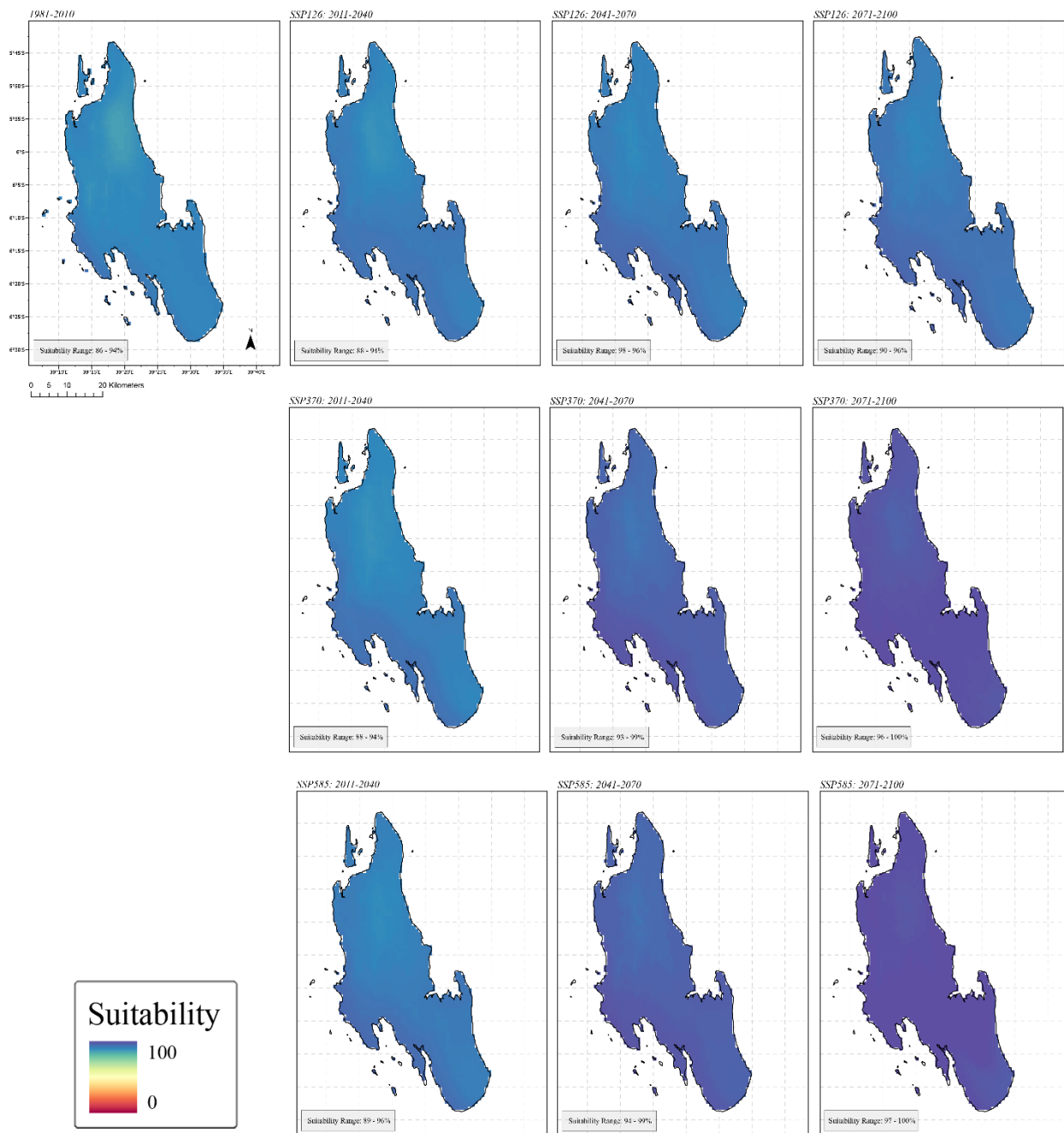


Figure 25: Crop suitability across Unguja for sorghum (mtama).



Figure 26: Crop suitability across Unguja for starfruit (mcarambola).

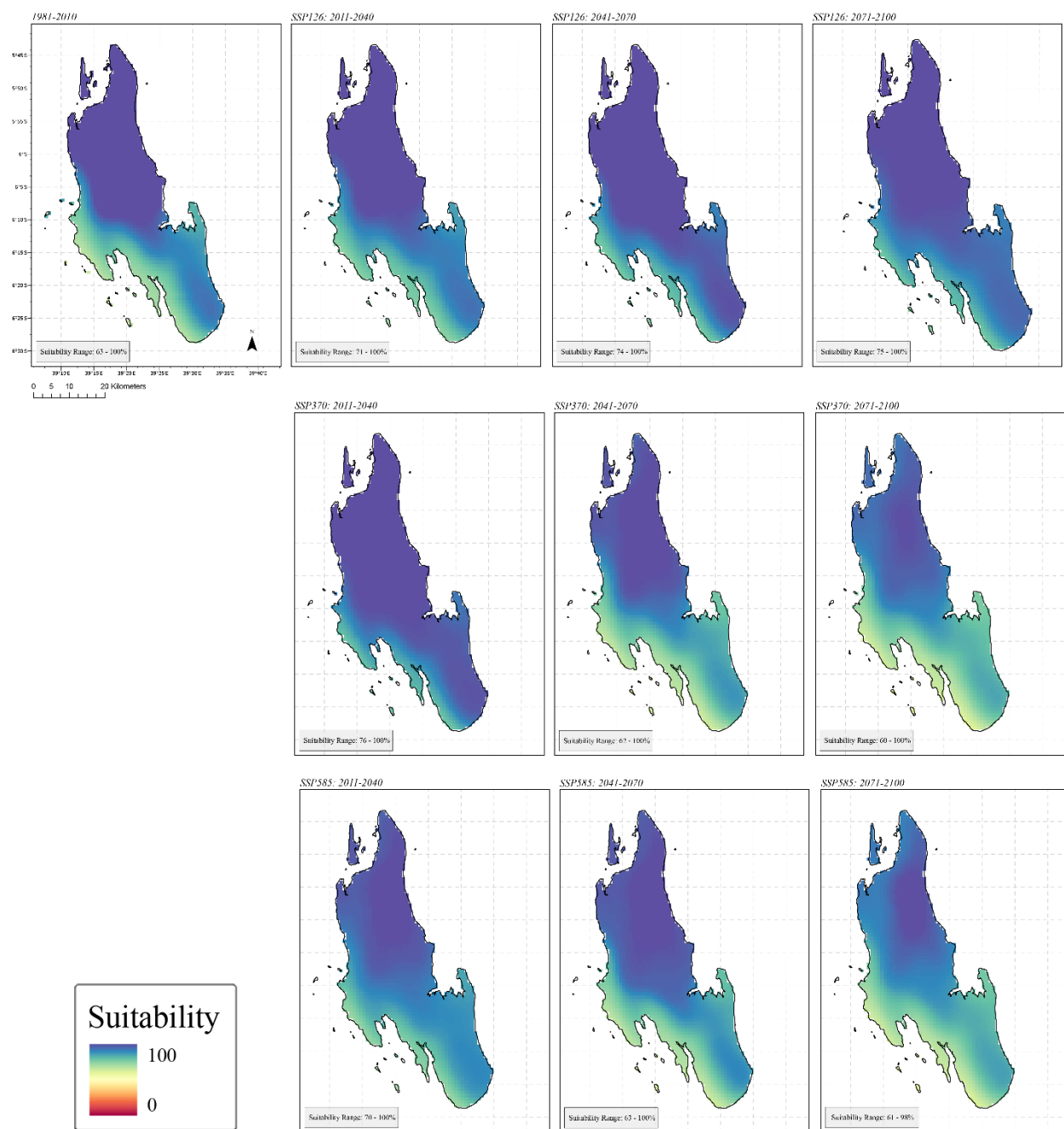


Figure 27: Crop suitability across Unguja for sugarcane (muwa).

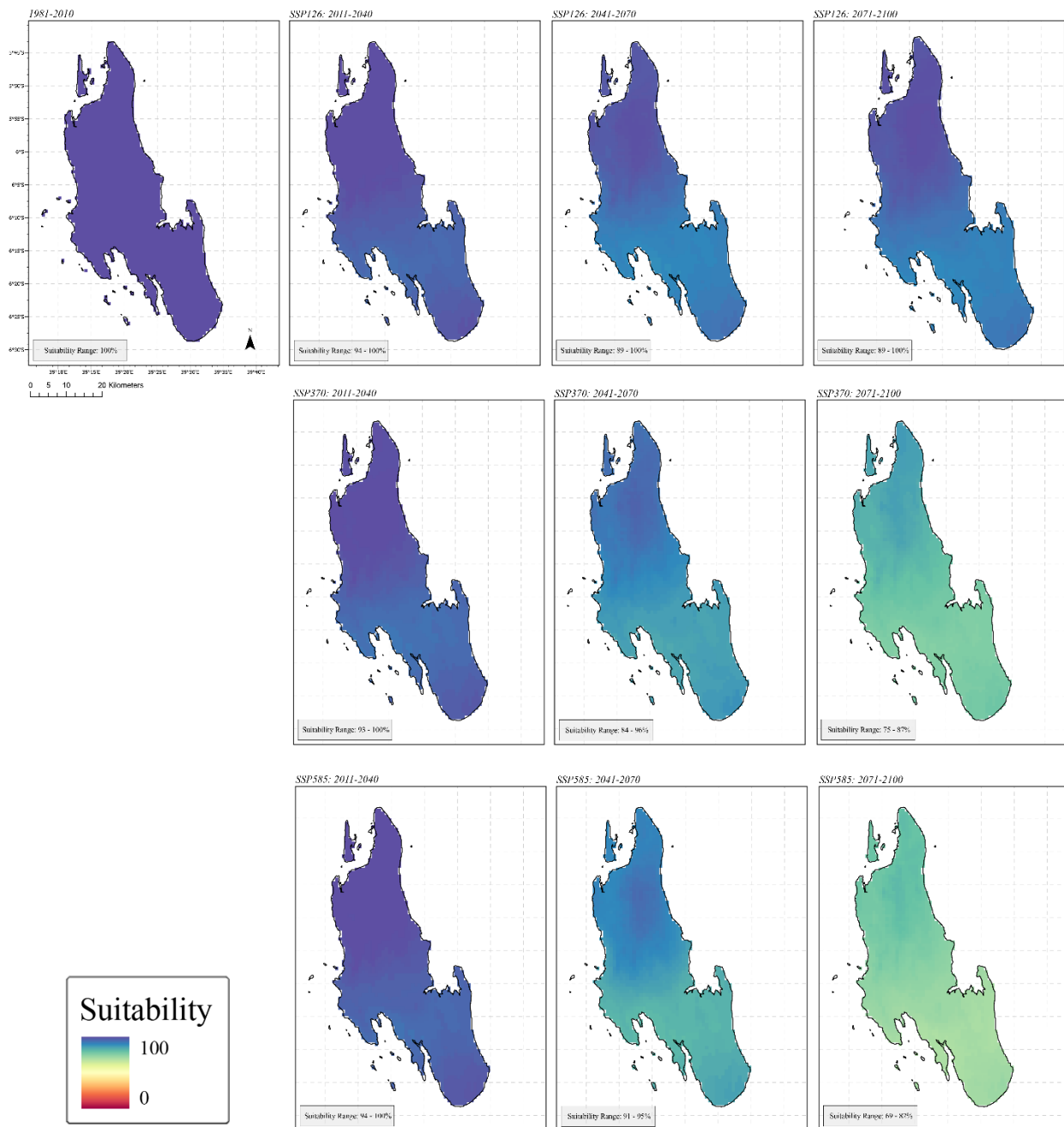


Figure 28: Crop suitability across Unguja for sweet potato (kiazhi kitamu).

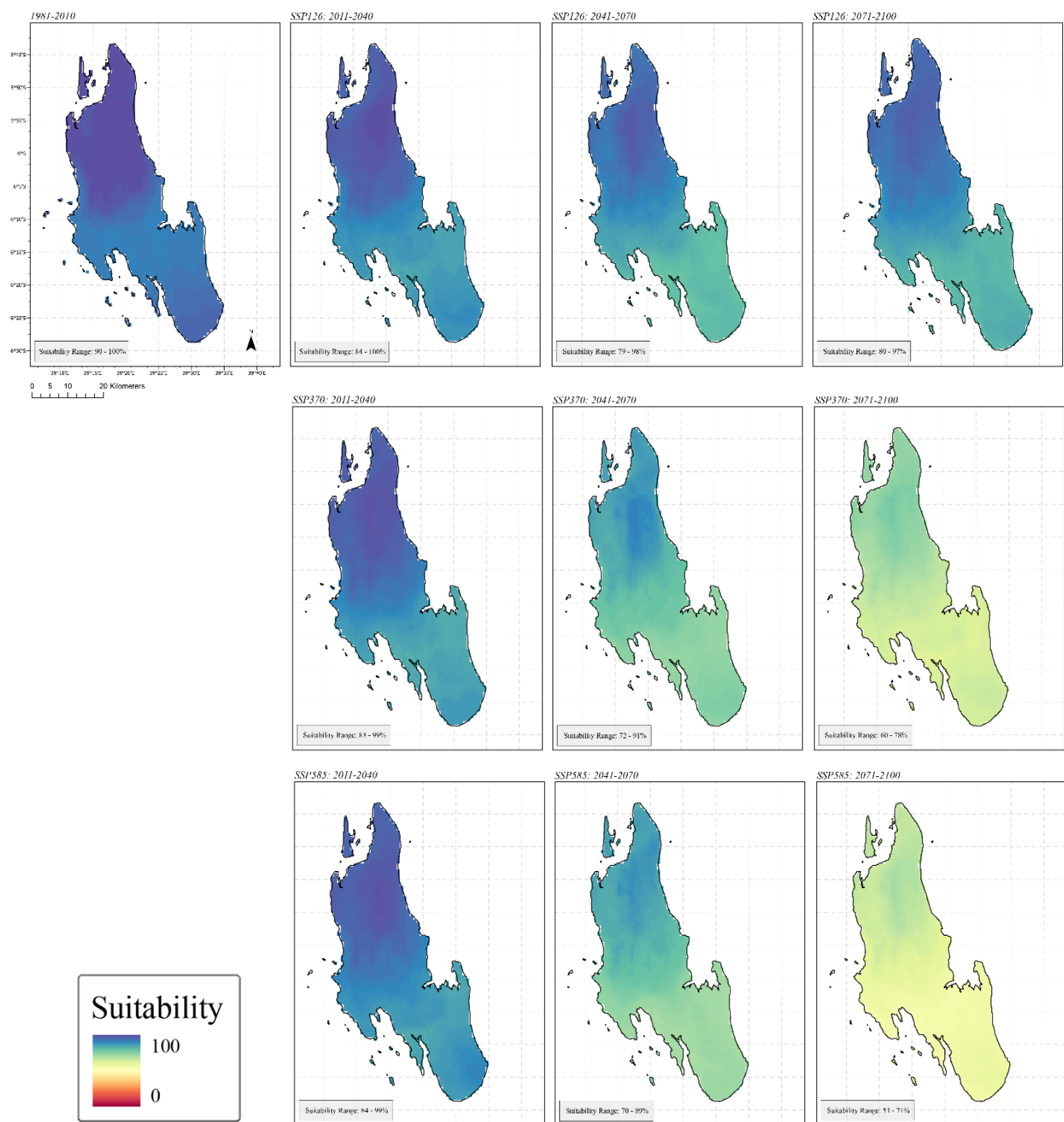


Figure 29: Crop suitability across Unguja for tomato (mnyanya).

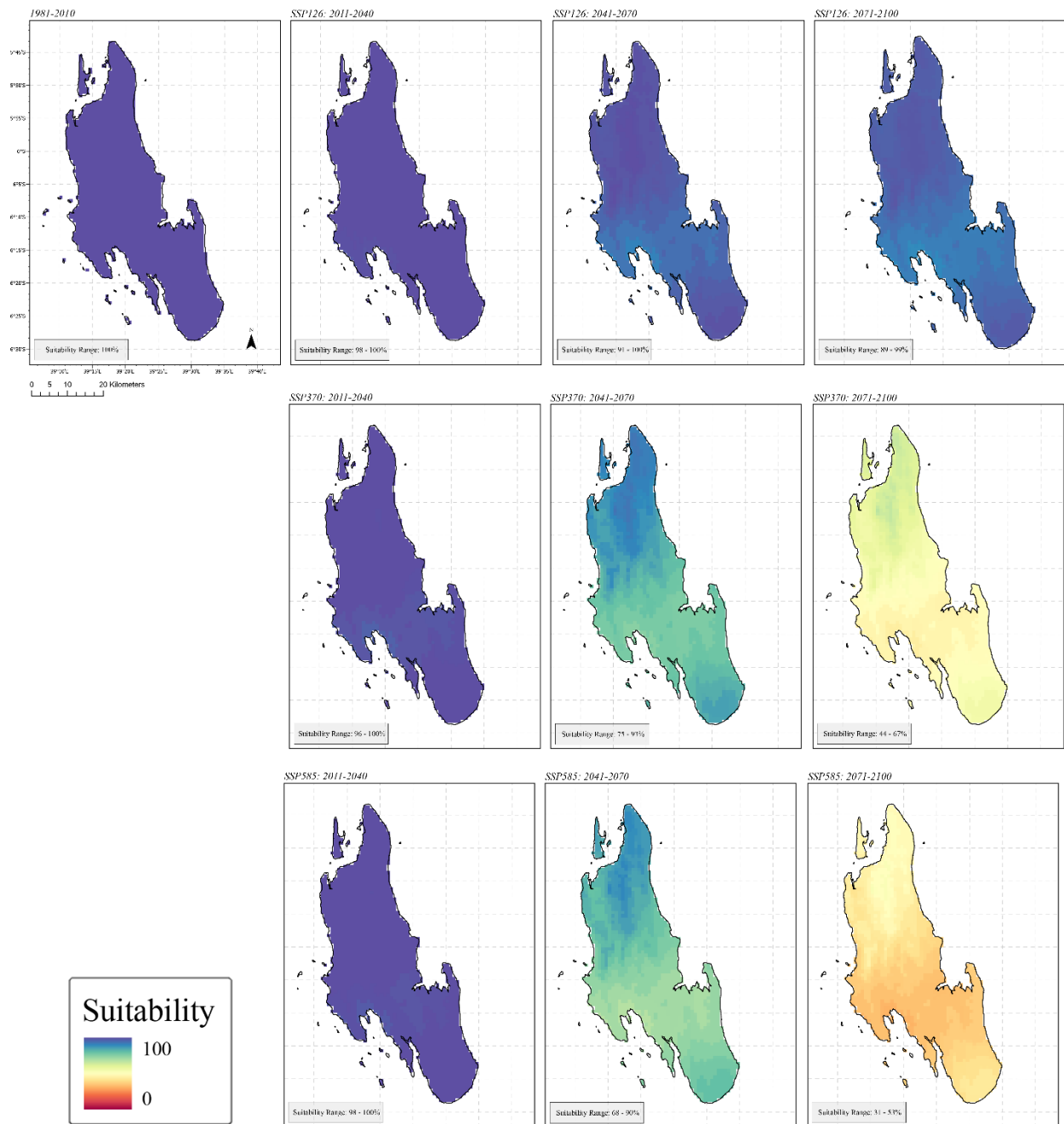


Figure 30: Crop suitability across Unguja for turmeric (manjano).

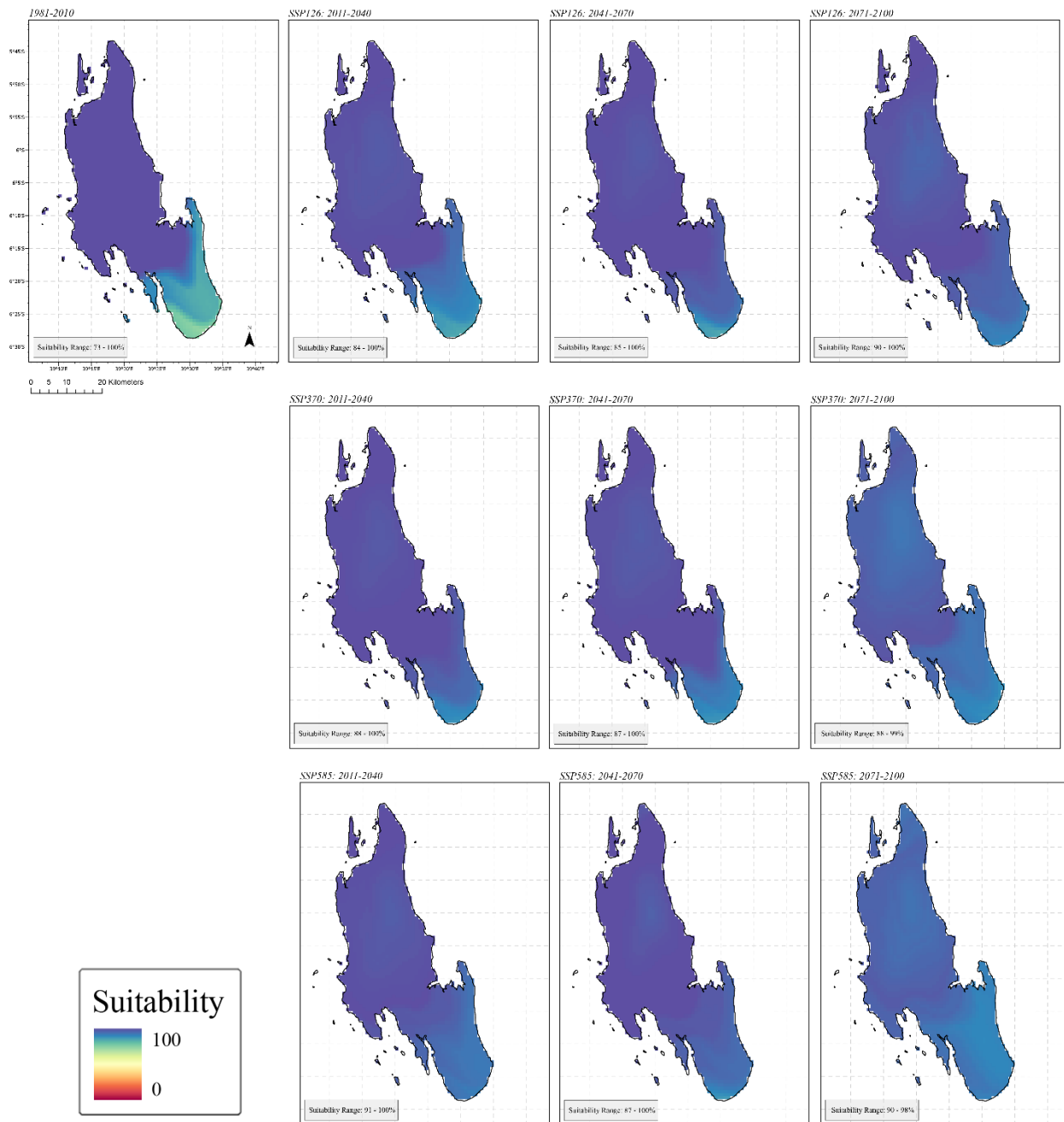


Figure 31: Crop suitability across Unguja for watermelon (tikitimaji).



Figure 32: Crop suitability across Unguja for yam (kiaziki).

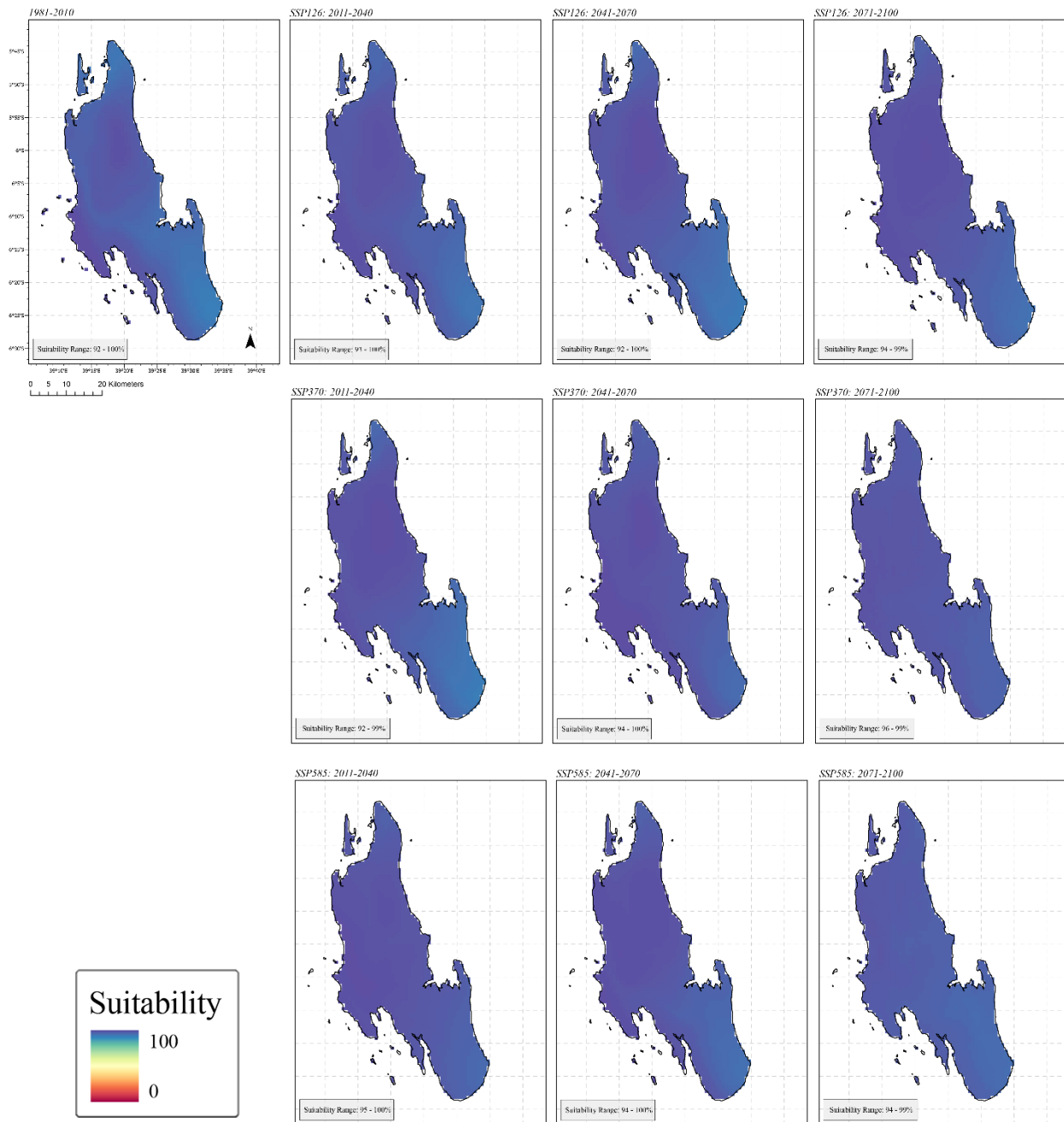


Figure 33: Crop suitability across Unguja for crop class: beans and pulses.

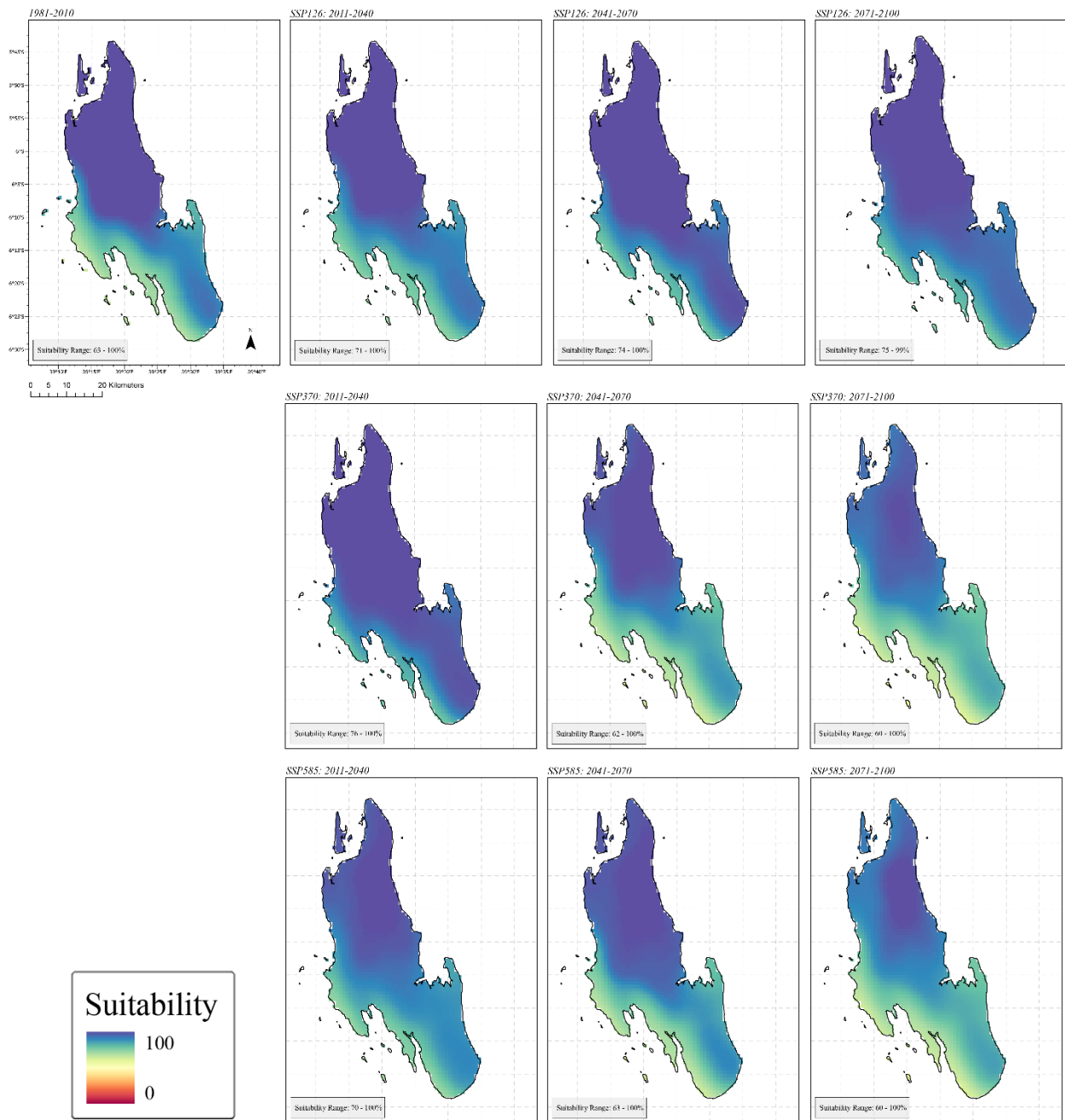


Figure 34: Crop suitability across Unguja for crop class: annual cash crops.

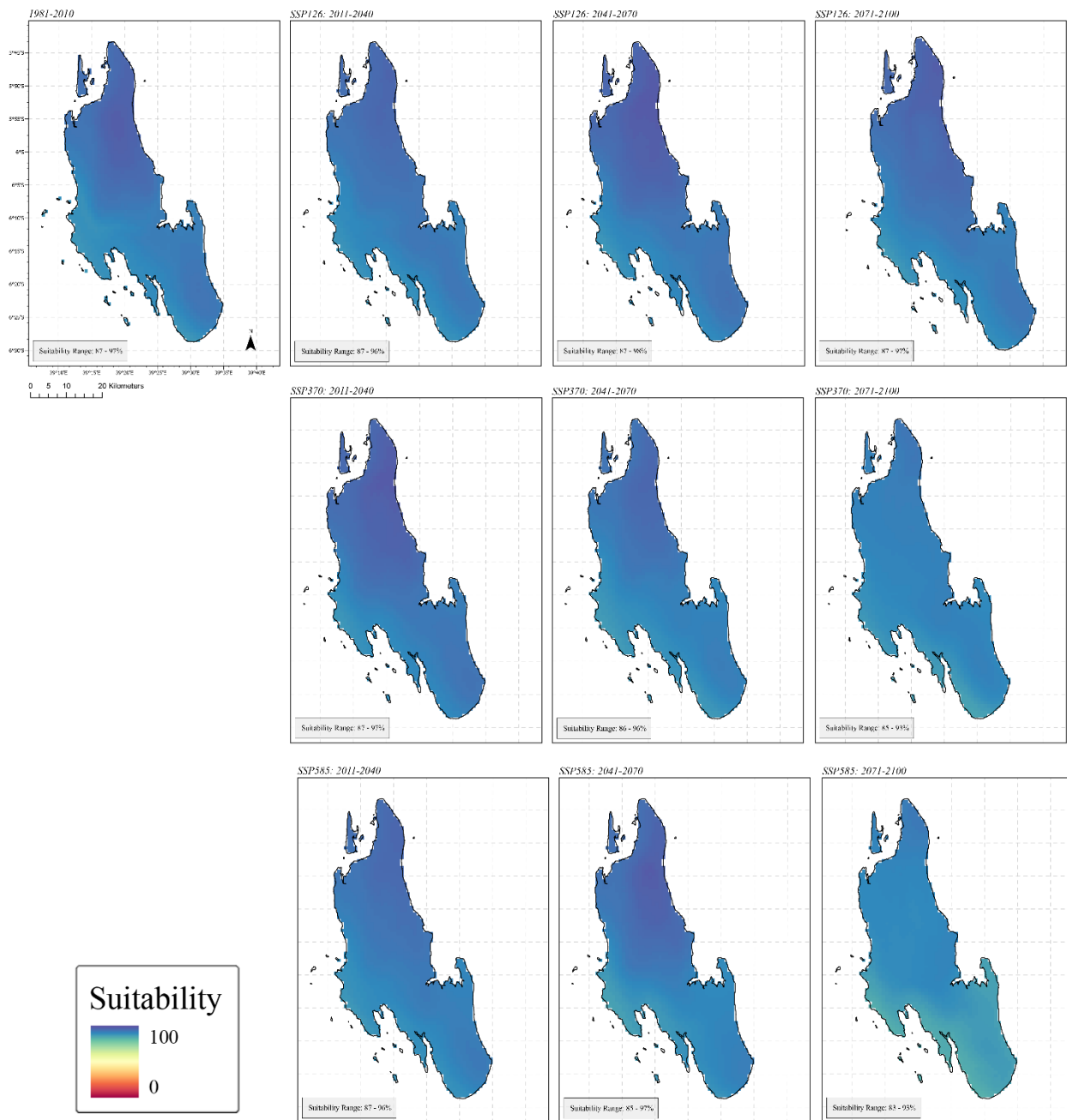


Figure 35: Crop suitability across Unguja for crop class: cereals.

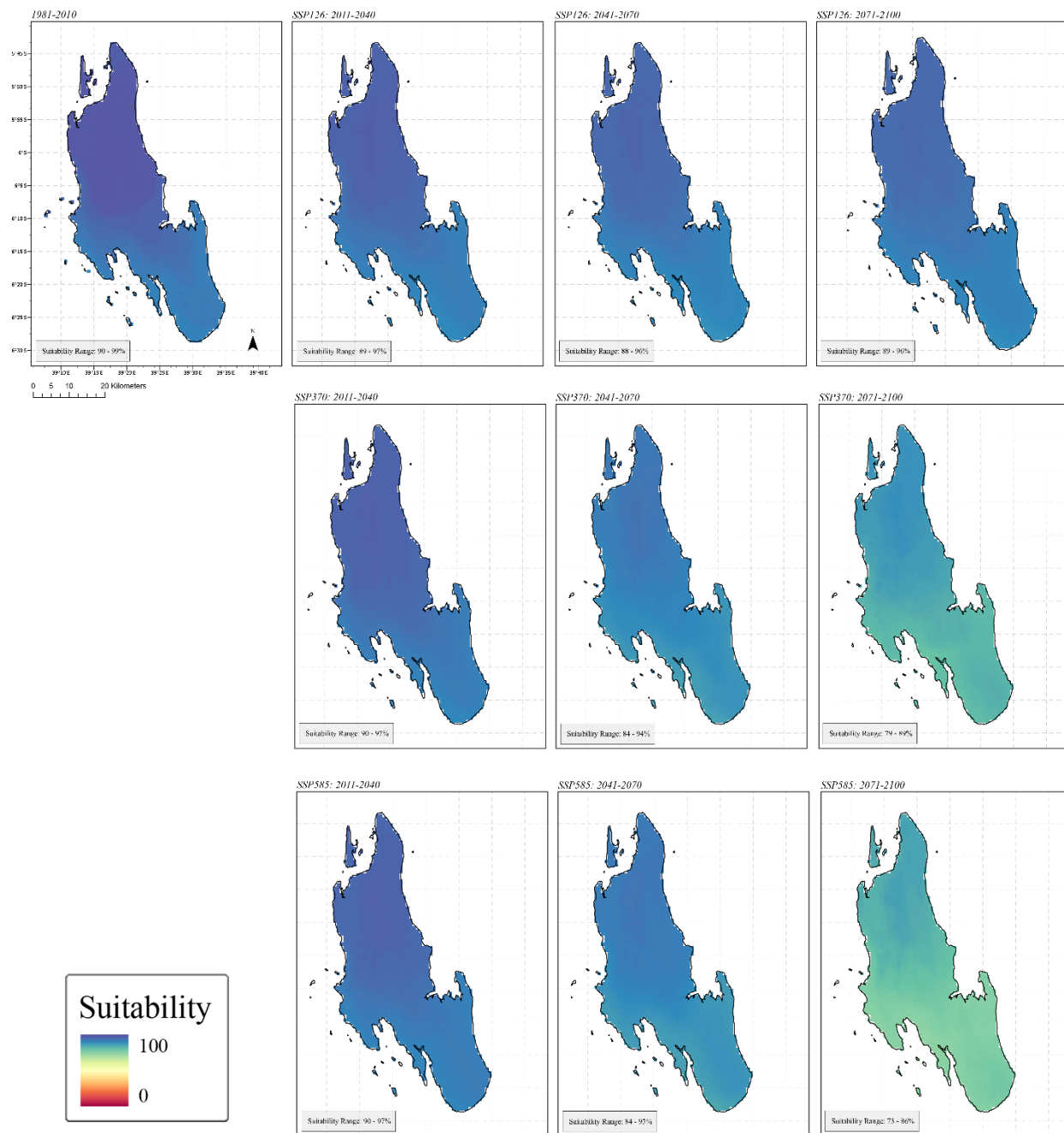


Figure 36: Crop suitability across Unguja for crop class: annual fruits and vegetables.



Figure 37: Crop suitability across Unguja for crop class: permanent cash crops.

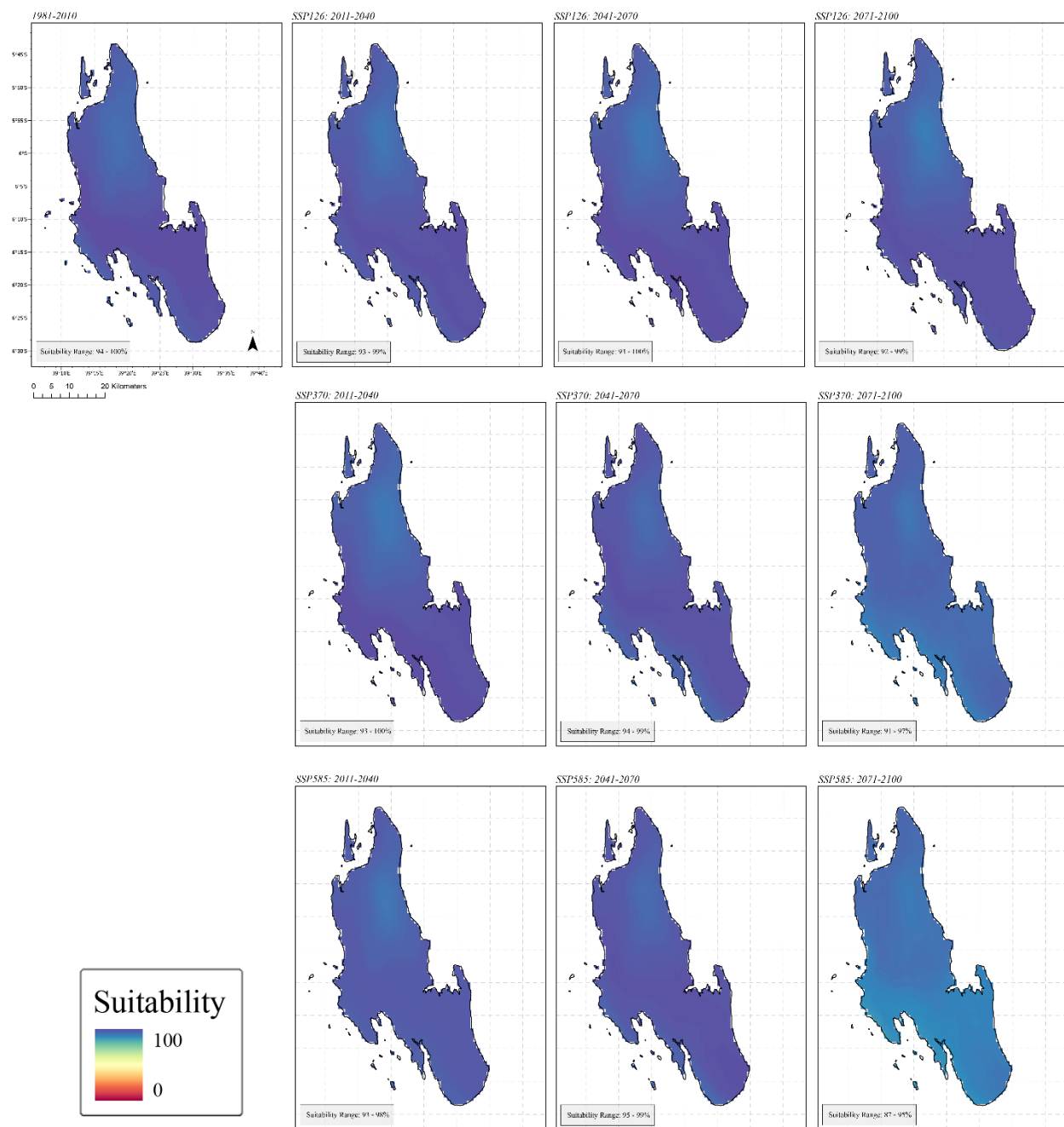


Figure 38: Crop suitability across Unguja for crop class: permanent fruit crops.

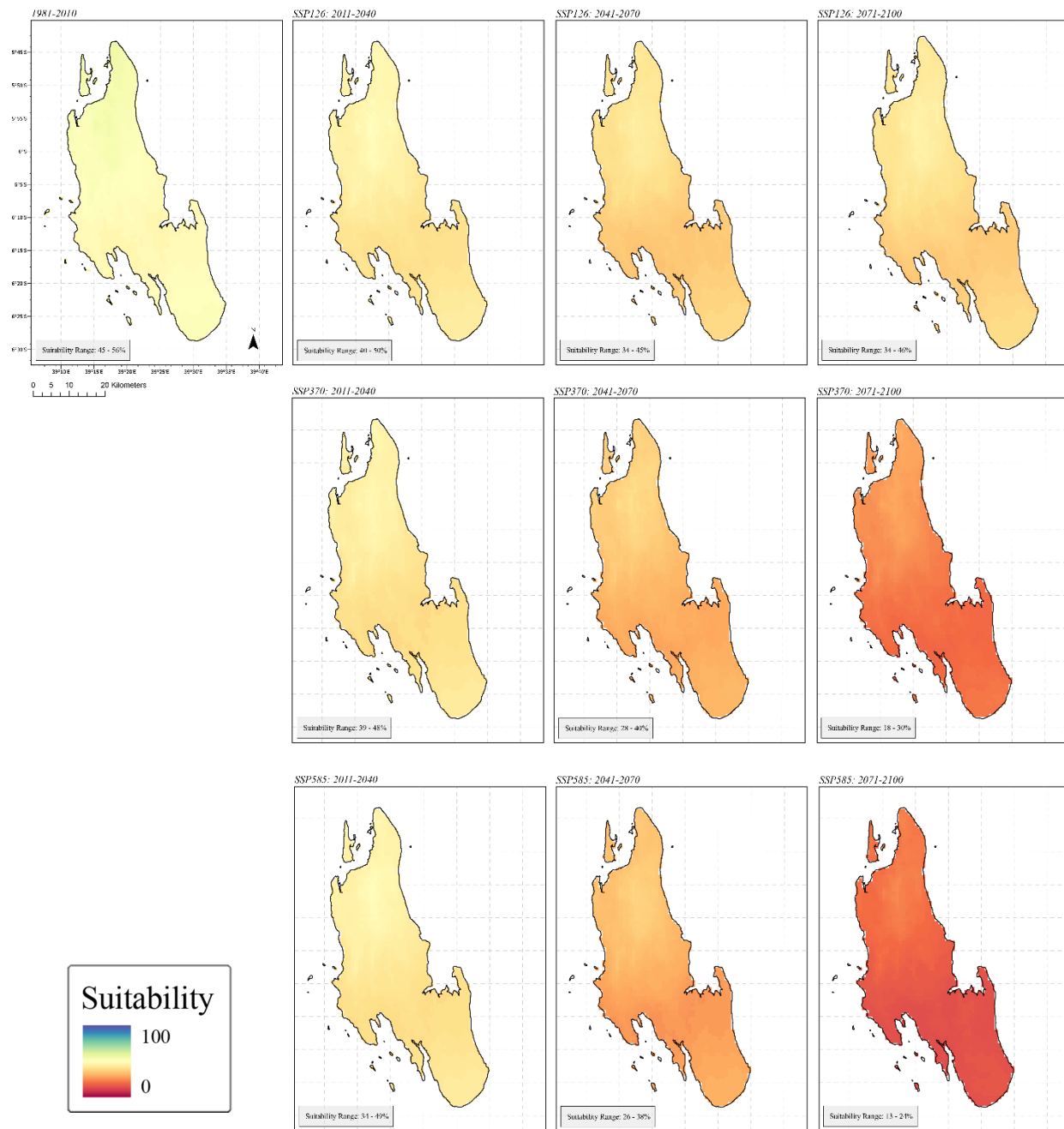


Figure 39: Crop suitability across Unguja for crop class: pseudocereals.

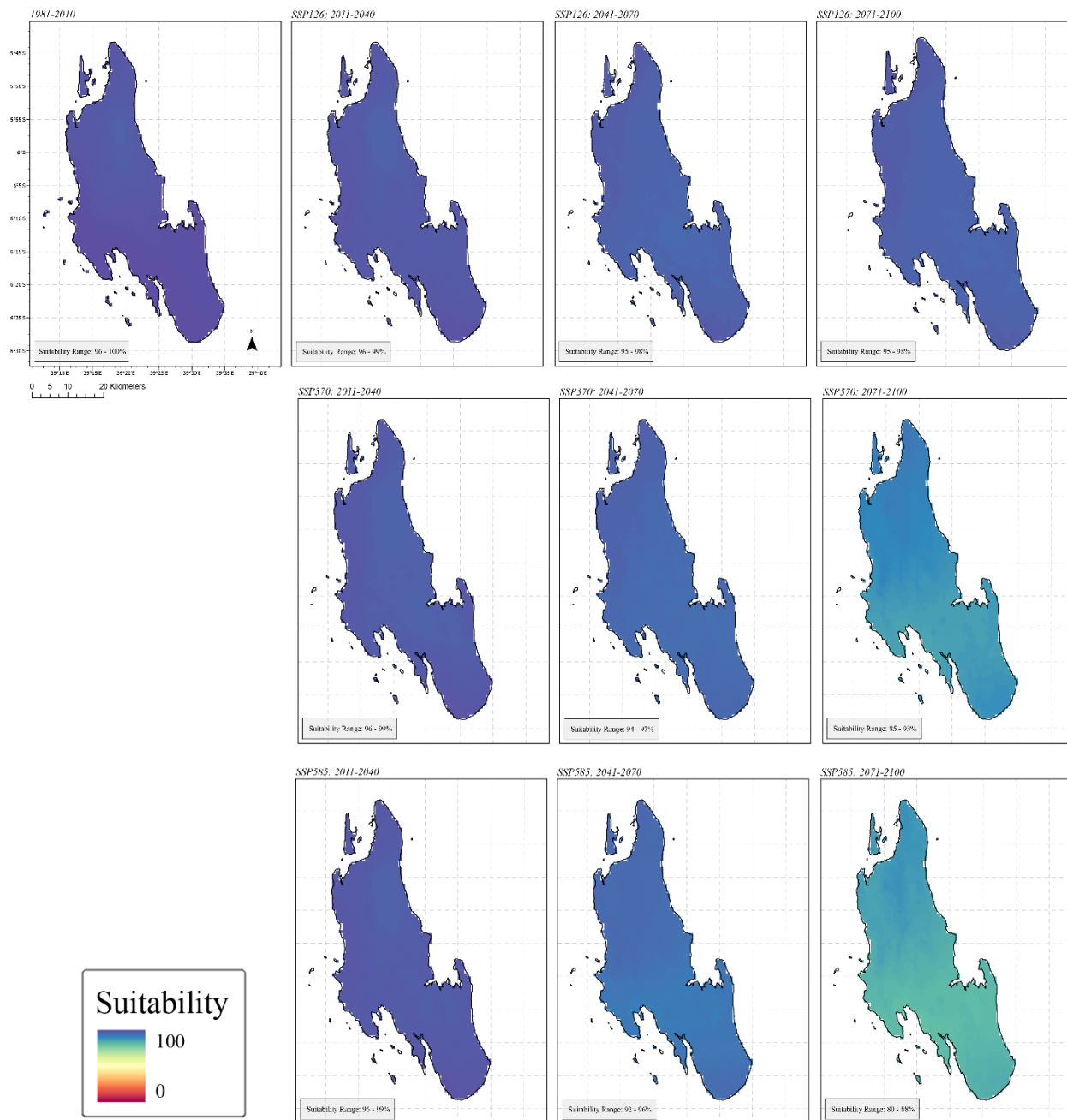


Figure 40: Crop suitability across Unguja for crop class: roots and tubers.

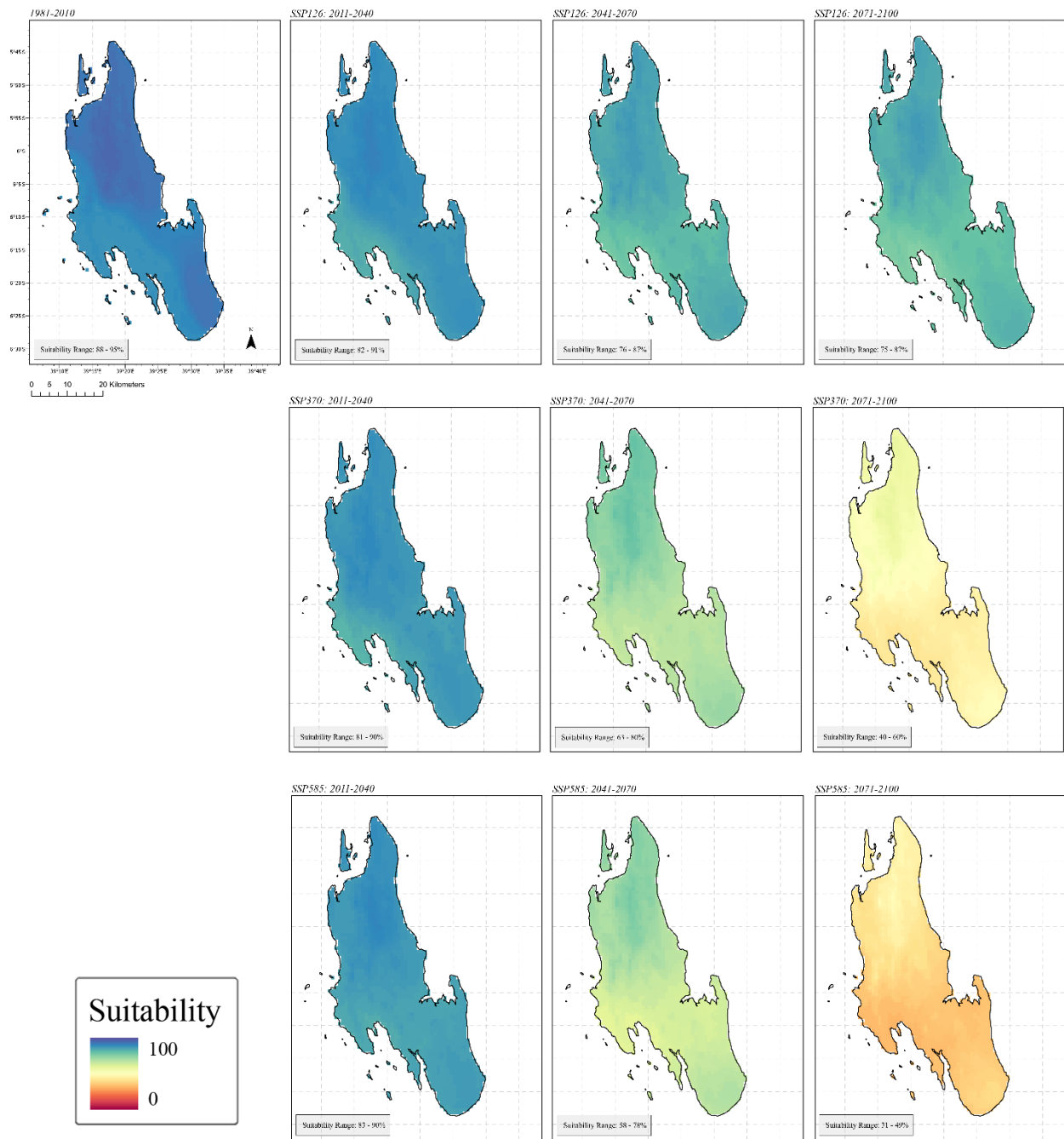


Figure 41: Crop suitability across Unguja for crop class: spices and herbs.

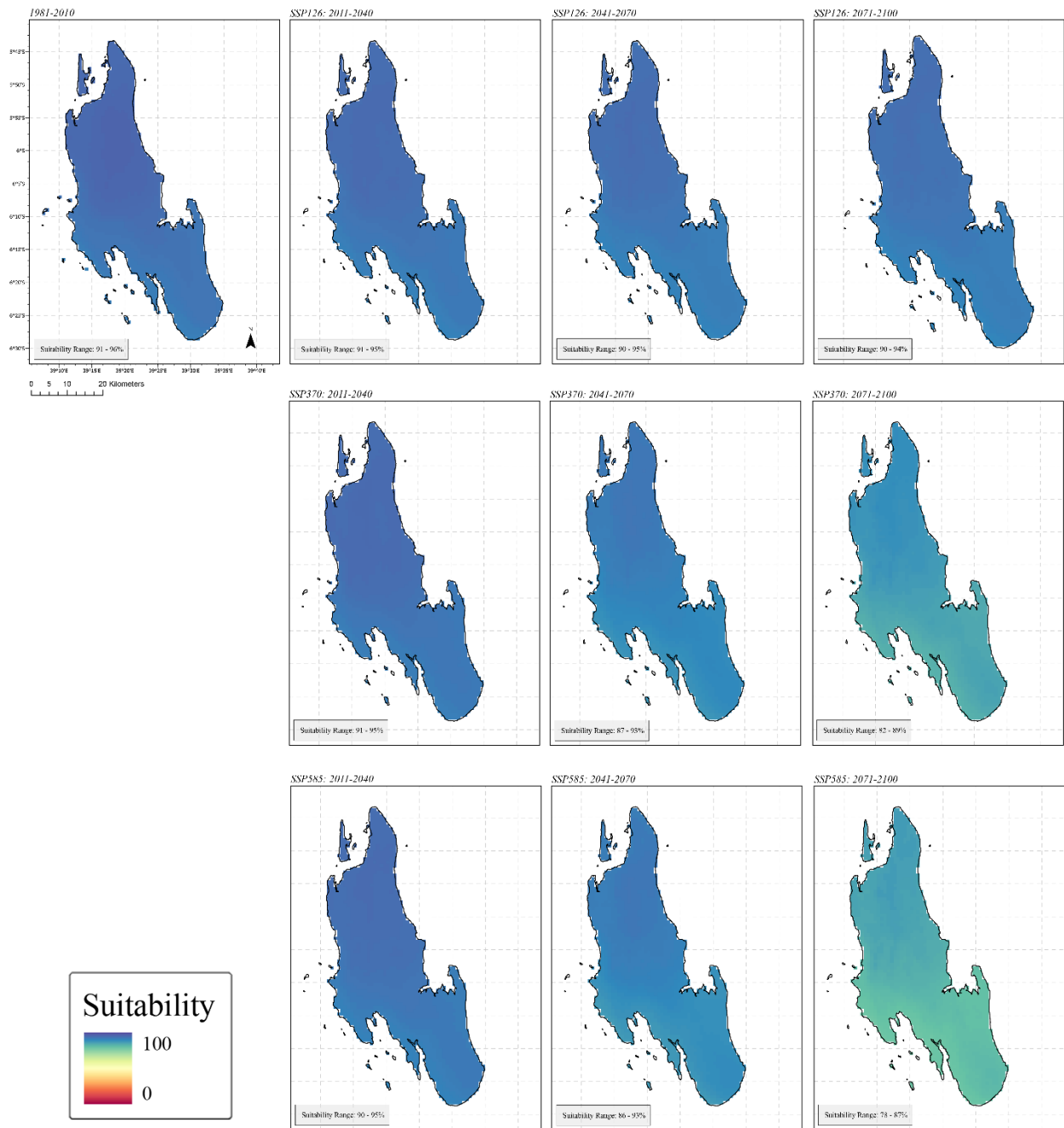


Figure 42: Crop suitability across Unguja for crop class: all crops.

SSP	2011-2040	2041-2070	2070-2100
126	40 - 50	34 - 45	34 - 46
370	39 - 48	28 - 40	18 - 30
585	39 - 50	26 - 38	13 - 24

Table 1: Forecasted suitability ranges for amaranth (mchicha wa kisasa). Forecasted suitability range for 1981-2010: 45-56%.

SSP	2011-2040	2041-2070	2070-2100
126	100	100	100
370	100	99 - 100	92 - 100
585	100	98 - 100	85 - 99

Table 2: Forecasted suitability ranges for bambara nut (njugu mawe). Forecasted suitability range for 1981-2010: 100%.

SSP	2011-2040	2041-2070	2070-2100
126	85 - 100	91 - 100	90 - 100
370	94 - 100	78 - 100	75 - 100
585	84 - 100	79 - 100	75 - 100

Table 3: Forecasted suitability ranges for banana (mgomba). Forecasted suitability range for 1981-2010: 100%.

SSP	2011-2040	2041-2070	2070-2100
126	87 - 100	88 - 100	85 - 100
370	89 - 100	86 - 100	71 - 93
585	87 - 100	87 - 100	71 - 96

Table 4: Forecasted suitability ranges for bulrush millet (mawele). Forecasted suitability range for 1981-2010: 85-100%.

SSP	2011-2040	2041-2070	2070-2100
126	65 - 83	59 - 78	59 - 77
370	62 - 82	53 - 69	40 - 53
585	65 - 81	49 - 67	31 - 47

Table 5: Forecasted suitability ranges for cabbage (kabichi). Forecasted suitability range for 1981-2010: 66-92%.

SSP	2011-2040	2041-2070	2070-2100
126	88 - 99	88 - 99	88 - 99
370	88 - 99	90 - 99	80 - 91
585	89 - 99	90 - 98	71 - 84

Table 6: Forecasted suitability ranges for cassava (muhogo). Forecasted suitability range for 1981-2010: 66-92%.

SSP	2011-2040	2041-2070	2070-2100
126	100	100	100
370	100	92 - 100	100
585	100	98 - 100	89 - 99

Table 7: Forecasted suitability ranges for chilies (pilipili hoho). Forecasted suitability range for 1981-2010: 100%.

SSP	2011-2040	2041-2070	2070-2100
126	97 - 100	100	97 - 100
370	100	92 - 100	94 - 100
585	90 - 100	95 - 100	92 - 100

Table 8: Forecasted suitability ranges for clove (miti ya karafuu). Forecasted suitability range for 1981-2010: 99-100%.

SSP	2011-2040	2041-2070	2071-2100
126	100	100	100
370	100	100	100
585	100	100	100

Table 9: Forecasted suitability ranges for coconut (miti ya nazi). Forecasted suitability range for 1981-2010: 100%.

SSP	2011-2040	2041-2070	2071-2100
126	100	100	100
370	100	100	100
585	100	100	100

Table 10: Forecasted suitability ranges for cowpea (kunde). Forecasted suitability range for 1981-2010: 100%.

SSP	2011-2040	2041-2070	2070-2100
126	79 - 100	83 - 100	80 - 100
370	82 - 100	74 - 100	74 - 100
585	77 - 100	76 - 100	74 - 99

Table 11: Forecasted suitability ranges for cucumber (tango). Forecasted suitability range for 1981-2010: 74-100%.

SSP	2011-2040	2041-2070	2070-2100
126	99 - 100	100	100
370	100	100	98 - 100
585	100	99 - 100	90 - 100

Table 12: Forecasted suitability ranges for finger millet (ulezi). Forecasted suitability range for 1981-2010: 100%.

SSP	2011-2040	2041-2070	2070-2100
126	65 - 98	61 - 99	68 - 99
370	60 - 99	73 - 100	83 - 100
585	75 - 99	70 - 100	82 - 100

Table 13: Forecasted suitability ranges for green gram (choroko). Forecasted suitability range for 1981-2010: 58-100%.

SSP	2011-2040	2041-2070	2071-2100
126	100	100	100
370	100	100	100
585	100	100	100

Table 14: Forecasted suitability ranges for groundnut (karanga). Forecasted suitability range for 1981-2010: 100%.

SSP	2011-2040	2041-2070	2070-2100
126	66 - 83	61 - 75	60 - 76
370	65 - 79	51 - 68	36 - 51
585	68 - 81	48 - 66	31 - 45

Table 15: Forecasted suitability ranges for kothmir (giligilani). Forecasted suitability range for 1981-2010: 75-100%.

SSP	2011-2040	2041-2070	2070-2100
126	99 - 100	96 - 100	99 - 100
370	98 - 100	100	99 - 100
585	99 - 100	100	98 - 100

Table 16: Forecasted suitability ranges for maize (muhindi). Forecasted suitability range for 1981-2010: 100%.

SSP	2011-2040	2041-2070	2070-2100
126	74 - 100	72 - 100	72 - 100
370	71 - 100	79 - 100	80 - 99
585	74 - 100	79 - 100	81 - 98

Table 17: Forecasted suitability ranges for mango (miti ya maembe). Forecasted suitability range for 1981-2010: 77-100%.

SSP	2011-2040	2041-2070	2070-2100
126	100	100	100
370	100	99 - 100	93 - 100
585	100	98 - 100	83 - 99

Table 18: Forecasted suitability ranges for okra (mbamia). Forecasted suitability range for 1981-2010: 100%.

SSP	2011-2040	2041-2070	2070-2100
126	99 - 100	100	99 - 100
370	100	100	39 - 99
585	100	99 - 100	86 - 95

Table 19: Forecasted suitability ranges for orange (miti ya machungwa). Forecasted suitability range for 1981-2010: 100%.

SSP	2011-2040	2041-2070	2070-2100
126	45 - 96	50 - 99	47 - 96
370	49 - 99	38 - 90	44 - 90
585	44 - 93	40 - 93	37 - 79

Table 20: Forecasted suitability ranges for WDR paddy rice (mpunga). Forecasted suitability range for 1981-2010: 40-100%.

SSP	2011-2040	2041-2070	2071-2100
126	100	100	100
370	100	100	100
585	100	100	100

Table 21: Forecasted suitability ranges for pigeon pea (mbaazi). Forecasted suitability range for 1981-2010: 40-100%.

SSP	2011-2040	2041-2070	2070-2100
126	92 - 100	90 - 100	91 - 100
370	91 - 100	94 - 100	94 - 99
585	93 - 100	93 - 100	99 - 98

Table 22: Forecasted suitability ranges for pumpkin (boga). Forecasted suitability range for 1981-2010: 92-100%.

SSP	2011-2040	2041-2070	2070-2100
126	88 - 94	89 - 96	90 - 96
370	88 - 94	93 - 99	96 - 100
585	89 - 96	94 - 99	97 - 100

Table 23: Forecasted suitability ranges for sorghum (mtama). Forecasted suitability range for 1981-2010: 86-94%.

SSP	2011-2040	2041-2070	2070-2100
126	98 - 100	98 - 100	96 - 100
370	98 - 100	99 - 100	94 - 99
585	97 - 100	99 - 100	87 - 95

Table 24: Forecasted suitability ranges for starfruit (mcarambola). Forecasted suitability range for 1981-2010: 100%.

SSP	2011-2040	2041-2070	2070-2100
126	71 - 100	74 - 100	75 - 100
370	76 - 100	62 - 100	60 - 100
585	70 - 100	63 - 100	61 - 100

Table 25: Forecasted suitability ranges for sugarcane (muwa). Forecasted suitability range for 1981-2010: 63-100%.

SSP	2011-2040	2041-2070	2070-2100
126	94 - 100	89 - 100	89 - 100
370	93 - 100	84 - 96	75 - 87
585	94 - 100	81 - 95	69 - 82

Table 26: Forecasted suitability ranges for sweet potato (kiazhi kitamu). Forecasted suitability range for 1981-2010: 100%.

SSP	2011-2040	2041-2070	2070-2100
126	84 - 100	79 - 98	80 - 97
370	83 - 99	72 - 91	60 - 78
585	84 - 99	70 - 89	53 - 71

Table 27: Forecasted suitability ranges for tomato (mnyanya). Forecasted suitability range for 1981-2010: 90-100%.

SSP	2011-2040	2041-2070	2070-2100
126	98 - 100	91 - 100	89 - 99
370	96 - 100	75 - 93	44 - 67
585	98 - 100	68 - 90	31 - 53

Table 28: Forecasted suitability ranges for turmeric (manjano). Forecasted suitability range for 1981-2010: 100%.

SSP	2011-2040	2041-2070	2070-2100
126	84 - 100	85 -100	90 - 100
370	88 - 100	87 - 100	88 - 99
585	91 - 100	87 - 100	90 - 98

Table 29: Forecasted suitability ranges for watermelon (tikitimaji). Forecasted suitability range for 1981-2010: 73-100%.

SSP	2011-2040	2041-2070	2070-2100
126	100	100	10
370	100	100	99 - 100
585	100	100	100

Table 30: Forecasted suitability ranges for yam (kiazi kikuu). Forecasted suitability range for 1981-2010: 100%.

SSP	2011-2040	2041-2070	2070-2100
126	93-100	92-100	94-99
370	92-99	94-100	96-99
585	95-100	94-100	94-99

Table 31: Forecasted suitability ranges for all beans and pulses. Forecasted suitability range for 1981-2010: 92-100%.

SSP	2011-2040	2041-2070	2070-2100
126	71-100	74-100	75-100
370	76-100	62-100	60-100
585	70-100	63-100	60-100

Table 32: Forecasted suitability ranges for all annual cash crops. Forecasted suitability range for 1981-2010: 63-100%.

SSP	2011-2040	2041-2070	2070-2100
126	87-96	87-98	87-97
370	87-97	86-96	85-93
585	87-96	85-97	83-93

Table 33: Forecasted suitability ranges for all cereals. Forecasted suitability range for 1981-2010: 87-97%.

SSP	2011-2040	2041-2070	2070-2100
126	89-97	88-96	89-96
370	90-97	84-94	79-89
585	90-97	84-93	73-86

Table 34: Forecasted suitability ranges for all annual fruits and vegetables. Forecasted suitability range for 1981-2010: 90-99%.

SSP	2011-2040	2041-2070	2070-2100
126	99-100	100	99-100
370	100	96-100	97-100
585	95-100	97-100	96-100

Table 35: Forecasted suitability ranges for all permanent cash crops. Forecasted suitability range for 1981-2010: 99-100%.

SSP	2011-2040	2041-2070	2070-2100
126	93-99	93-100	92-99
370	93-100	94-99	91-97
585	93-98	95-99	87-95

Table 36: Forecasted suitability ranges for all permanent fruit crops. Forecasted suitability range for 1981-2010: 94-100%.

SSP	2011-2040	2041-2070	2070-2100
126	40-50	34-45	34-46
370	39-48	28-40	18-30
585	39-49	26-38	13-24

Table 37: Forecasted suitability ranges for all pseudocereals. Forecasted suitability range for 1981-2010: 45-56%.

SSP	2011-2040	2041-2070	2070-2100
126	96-99	95-98	95-98
370	96-99	94-97	85-93
585	96-99	92-96	80-88

Table 38: Forecasted suitability ranges for all roots and tubers. Forecasted suitability range for 1981-2010: 96-100%.

SSP	2011-2040	2041-2070	2070-2100
126	82-91	76-87	75-87
370	81-90	63-80	40-60
585	83-90	58-78	31-49

Table 39: Forecasted suitability ranges for all spices and herbs. Forecasted suitability range for 1981-2010: 88-95%.

SSP	2011-2040	2041-2070	2070-2100
126	91-95	90-95	90-94
370	91-95	87-93	82-89
585	90-95	86-93	78-87

Table 40: Forecasted suitability ranges for all crops. Forecasted suitability range for 1981-2010: 91-96%.

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